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► To cite this version:

Joseph Tisseyre, David Amarantini, Jessica Tallet. Behavioural and cerebral asymmetries of mirror movements are specific to rhythmic task and related to higher attentional and executive control. Behavioural Brain Research, 2021, 412, pp.113429. <10.1016/j.bbr.2021.113429>. <hal-04364604>

HAL Id: hal-04364604

<https://hal.science/hal-04364604v1>

Submitted on 22 Jul 2024

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1 **Behavioural and cerebral asymmetries of mirror movements are specific to rhythmic task and**
2 **related to higher attentional and executive control**

3

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16

17 **HIGHLIGHTS**

- 18 • Mirror movements (MM) and its EEG correlates were compared between a rhythmic and a
19 non-rhythmic task.
- 20 • Behavioural and cerebral motor asymmetries of MM were specific to the rhythmic task.
- 21 • Greater attentional and executive activations were found in the rhythmic task.

1 **Abstract**

2 Mirror movements (MM) refer to the involuntary movements or contractions occurring in homologous
3 muscles contralateral to the unilateral voluntary movements. This behavioural manifestation increases
4 in elderly. In right-handed adults, some studies report asymmetry in MM production, with greater MM
5 in the right dominant hand during voluntary movements of the left non-dominant hand than the
6 opposite. However, other studies report contradictory results, suggesting that MM asymmetry could
7 depend on the characteristics of the task. The present study investigates the behavioural asymmetry of
8 MM and its associated cerebral correlates during a rhythmic task and a non-rhythmic task **using low-**
9 **force contractions (i.e., 25% MVC)**. We determined the quantity and the intensity of MM using
10 electromyography (EMG) and cerebral correlates through electroencephalography (EEG) in right-
11 handed healthy young and middle-aged adults during unimanual rhythmic vs. non-rhythmic tasks.
12 Overall, results revealed (1) behavioural asymmetry of MM specific to the rhythmic task and
13 irrespective of age, (2) cerebral asymmetry of motor activations specific to the rhythmic task and
14 irrespective of age and (3) greater attentional and executive activations in the rhythmic task compared
15 to the non-rhythmic task. In line with our hypotheses, behavioural and cerebral motor asymmetries of
16 MM seem to be specific to the rhythmic task. Results are discussed in terms of cognitive-motor
17 interactions: greater attentional and executive control required in the rhythmic tasks could contribute
18 to the increased occurrence of involuntary movements in both young and middle-aged adults.

19

20 Key-words: EEG, EMG, spectral power, fronto-mesial theta synchronization, parietal alpha
21 desynchronization.

1. INTRODUCTION

Most activities of daily living require independent hand movements and complex coordinated actions. However, the ability to perform independent hand movements is often made difficult by the default tendency to produce symmetrical mirror movements [1,2]. Mirror movements (MM) refer to the involuntary movements or contractions occurring in homologous muscles contralateral to the unilateral voluntary movements, particularly in the distal upper limb muscles [3–5]. Exacerbated MM have been reported in various clinical populations such as brain-injured patients [6,7], Parkinson's disease [8,9], schizophrenia [10,11], attention deficit/hyperactivity disorder [12,13] and developmental coordination disorder [14–16]. In healthy populations, MM are normally present during childhood but are supposed to decrease gradually during the maturation of the central nervous system [17,18]. However, in healthy adults, discreet MM can still be observed during complex rhythmic or effortful tasks through electromyographic (EMG) activity [19–25]. Then, MM subsequently increase again steadily after the age of 32 years [26] to become higher in the elderly compared to young adults [20,27–30].

In healthy adults, it has been suggested that the underlying mechanism of MM is transcallosal facilitation [31]. This bilateral activation theory proposed that the activation of the motor areas in one hemisphere during voluntary movement facilitates the activation of the same motor areas in the opposite hemisphere through transcallosal fibers [31]. Weak interhemispheric inhibition between the two primary motor cortices (M1) has been associated with greater MM in healthy adults [32–34] while strong interhemispheric facilitation was also associated with higher MM in healthy young and old adults [35]. In addition, a reduction in interhemispheric inhibition targeting ipsilateral M1 has been reported in the elderly [36] and may lead to greater activation of ipsilateral M1 [37–39] and produce exacerbated MM [26].

Furthermore, previous behavioural studies in healthy young and older adults suggested that attentional and inhibitory processes are involved in the production of MM [7,20,27–29,40]. With regard to attentional processes, it has been shown that attentional distraction induced by tactile stimulation [29]

1 or the execution of an additional cognitive task [20] during unilateral finger motor task leads to an
2 increase of MM whatever the age of participants. With regard to inhibitory processes, previous studies
3 have found that MM can be voluntarily reduced after participants have been informed of their presence
4 and invited to actively inhibit them in both young [40] and older adults [28]. At the brain level,
5 previous EEG studies have reported attentional and executive activations over the parietal and frontal
6 regions respectively during the effective production of MM [24,40] or during a rhythmic selective stop
7 task known to facilitate the emergence of MM [41–44]. In addition, it has also been shown that these
8 attentional and executive activations could be increased during complex motor tasks, especially with
9 advancing age (e.g., [45,46]). Thus, we could hypothesize that performing a complex motor task,
10 especially with advancing age, involves additional attentional and executive activations that could
11 limit the available cognitive resources to restrict MM.

12

13 In right-handed adults, several studies indicate larger occurrence of MM on the right dominant hand
14 during voluntary movements of the left non-dominant hand than the opposite [3,24,47–54].
15 Interestingly, we previously found that such behavioural asymmetry of MM was associated with
16 greater ipsilateral activation over left motor area during unimanual left-hand rhythmic movements
17 compared to right-hand rhythmic movements in healthy and young right-handed subjects [24]. This
18 finding was in accordance with previous fMRI studies showing more bilateral motor activations
19 during unimanual rhythmic movement with the left limb compared to the right limb in right-handed
20 healthy subjects [55–57], and transcranial magnetic stimulation (TMS) studies showing greater
21 excitability of the ipsilateral M1 during unimanual contraction with the left non-dominant hand
22 compared to the right dominant hand [58–60] or stronger inhibition of the ipsilateral M1 during
23 unimanual contraction with the right dominant hand compared to the left non-dominant hand
24 [50,61,62]. However, many other studies provided contradictory results about the behavioural
25 asymmetry of MM [10,18,20,27,28,31,34,63–70] and suggest that it could depend on the
26 characteristics of the task.

27

1 On this basis, we propose to use two unimanual motor tasks (rhythmic vs. non rhythmic) to investigate
2 the conditions of the emergence of behavioural asymmetry of MM in the non-active hand in healthy
3 right-handed young adults and middle-aged (over 35 years) adults. Given that a steady increase of MM
4 after the age of 32 years has been previously demonstrated [26] and due to the complexity of the
5 rhythmic task involving fine motor control, we expect to find more MM during the rhythmic task
6 compared to the non-rhythmic task in both groups and more MM in middle-aged adults than young
7 adults during both tasks. Likewise, we postulate that the behavioural asymmetry of MM will only be
8 found during the unimanual rhythmic task compared to the non-rhythmic task in both groups.

9 Cerebral correlates of MM were investigated through EEG task-related power (TR-Pow) changes in
10 beta (β : 13-30 Hz), alpha (α : 8-12 Hz) and theta (θ : 4-8 Hz) frequency band. β task-related power
11 decreases (desynchronization) can be interpreted as an electrophysiological correlate of activated
12 cortical areas involved in production of motor behaviour [71,72] whereas β TR-Pow increases
13 (synchronization) may be involved in the active inhibition of sensorimotor processes and reflect the
14 maintenance of the status quo [73,74]. α TR-Pow decreases (desynchronization) may reflect cortical
15 activations involved in attentional process and the release from inhibition of the underlying brain areas
16 while α TR-Pow increases (synchronization) could reflect cortical deactivation or inhibition [75–78].
17 Finally, θ TR-Pow is increased (synchronization) over fronto-mesial areas during response inhibition
18 paradigms and has been proposed to reflect the cortical activation involved in cognitive control and
19 response inhibition [79,80]. In order to unravel the contributions of motor, attentional and executive
20 processes in the production of MM, we investigated the EEG task-related power changes in the beta,
21 alpha and theta bands frequency over the motor, parietal and fronto-mesial cortical areas respectively.
22 We hypothesize that the behavioural asymmetry of MM in the rhythmic task is associated with more
23 bilateral motor activations during the unimanual left-hand movements compared to right-hand
24 movements and to both unimanual movements of the non-rhythmic task in both groups. Finally, due to
25 the complexity of the rhythmic task, we postulate that attentional and executive activations are more
26 pronounced in the rhythmic task compared to the non-rhythmic, especially in the middle-aged adults.

27

28 2. MATERIALS AND METHODS

2.1 Participants

Twenty-four right-handed healthy volunteers divided into a young adults group (n = 12; 6 women; mean age: 23 ± 2 years) and a middle-aged adults group (n = 12; 8 women; mean age: 53 ± 11 years) participated in the study. The age cutoff to be considered middle-aged was set at 35 years given that a steady increase of MM after the age of 32 years has been previously demonstrated in a large cohort [26]. All participants were right-handed as assessed by the Edinburgh inventory ([81], mean laterality quotient: $83 \pm 26\%$) and none reported any history of serious medical, neurological or psychiatric diseases. All participants received explicit information about the experimental design and gave signed informed consent before the experimental procedures began. As it has previously been shown that MM can be voluntarily reduced after participants have been informed of their presence and invited to actively inhibit them [28,40], participants in the present study were not informed that MM were the subject of the experiment. The study protocol was in accordance with the Declaration of Helsinki and followed institutional ethics board guidelines for research on humans.

2.2 Materials

Two calibrated hand dynamometers (model TSD121C; BIOPAC System, Inc., Goleta, CA, USA) were used to record the power grip force in the right and left hands at 1000 Hz with MP150 system (DA100C amplifiers; BIOPAC System, Inc., Goleta, USA). Following appropriate skin preparation [82], surface EMG was recorded on the right and left forearms at 1000 Hz with MP150 system (EMG-100C amplifiers, EL503 Ag–AgCl 11-mm bipolar electrodes with a maximum 2-cm spacing; BIOPAC System, Inc., Goleta, CA, USA) over flexor carpi radialis (FCR) and extensor digitorum communis (EDC), taken as representative hand and fingers flexors and extensors muscles. The reference electrode was positioned over the right elbow.

EEG was recorded at 1024 Hz using a 64-channel ActiveTwo system (BioSemi instrumentation, Amsterdam, The Netherlands), with scalp electrodes arranged according to the International 10–20 system. The Presentation software (Version 14:2, Neurobehavioral Systems, Inc., Albany, CA, USA) was used to display the instructions and the feedback to the participants on a computer screen located 0.8 m in front of them.

1 Force, EMG and EEG data were time-synchronized offline with TTL pulse.

2

3 **2.3 Tasks and procedures**

4 Participants sat comfortably in a quiet room in front of a table with a computer screen to display the
5 instructions and the feedback and with their hands positioned on the dynamometers. After being
6 familiarized with the environment, participants were required to maintain the same position (60–70
7 degree elbow flexion and neutral position of the forearm) during the whole experiment for
8 standardization and to avoid EEG artifacts. First, participants performed pre-experimental Maximal
9 Voluntary Contractions (MVC) to allow necessary normalization of both force and EMG data and then
10 two consecutive experimental tasks in a randomized order. The whole experiment lasted
11 approximatively two hours.

12

13 *Pre-experimental Maximal Voluntary Contractions (MVC)*

14 Participants were instructed to perform three maximal power grip isometric voluntary contractions
15 with their left and right hands separately and both hands together presented in a random order and by
16 fixing a center cross on the screen. Each contraction lasted 4 s and was indicated by a start-end sound
17 and separated by a minimum of 10 s rest before the next contraction. After low-pass filtering at 10 Hz
18 (fourth-order, zero-lag Butterworth filter), MVC force value was the average force during a 2 s
19 window in which the mean force of the corresponding hand of the three maximum voluntary
20 contractions was the highest. The corresponding **mean** EMG activity of each muscle was considered as
21 the maximum reference EMG value for normalization.

22

23 *Rhythmic task*

24 This task included contraction and control trials. In contraction trials, participants performed 20
25 rhythmic unimanual right or left power grip contractions at 25% of MVC in synchronization with an
26 auditory metronome with a period of one second. A familiarization phase of one contraction trial in
27 right and left unimanual conditions was proposed before the beginning of the experiment. Participants
28 were provided with visual feedback on the computer screen of current produced force and force target

1 only on the active hand dynamometer. This feedback allowed participants to control their voluntary
2 contractions to 25% of their MVC but prevented feedback from the inactive hand to avoid the possible
3 voluntary inhibition of MM. In control trials, participants were asked to listen 20 tones of the auditory
4 metronome exactly as in contraction trials with visual feedback of the right or left hand dynamometer
5 but without performing any contraction. Five blocks each including two randomized contraction trials
6 (20 rhythmic power grip contractions with the right hand and 20 with the left) and two corresponding
7 control trials (20 tones with visual feedback of the right hand dynamometer and 20 tones of the left)
8 were proposed to the participants. Overall, participants performed 100 rhythmic power grip
9 contractions with the right hand and 100 with the left. A rest period according to the participant's
10 request was granted between each block.

11

12 *Non-rhythmic task*

13 As for the rhythmic task, this task included contraction and control trials. During contraction trials,
14 participants were asked to maintain one unimanual right or left power grip contraction at 25% of MVC
15 for 6 s indicated by a start-end sound. A horizontal cursor as force target and visual feedback of
16 current produced force only on the active hand dynamometer were displayed on the computer screen.
17 This feedback allowed participants to control their voluntary contractions to 25% of their MVC but
18 prevented feedback from the inactive hand to avoid the possible voluntary inhibition of MM. In
19 control trials, participants were asked to listen start-end sound exactly as in contraction trials with
20 visual feedback of the right or left hand dynamometer but without performing any contraction. Five
21 blocks each including eight randomized contraction trials (four prolonged power grip contractions
22 with the right hand and four with the left) and four corresponding control trials (two trials with start-
23 end sound and visual feedback of the right hand dynamometer and two of the left) were proposed to
24 the participants. Overall, participants performed 20 prolonged power grip contractions with the right
25 hand and 20 with the left. A rest period according to the participant's request was granted between
26 each block. Although there was less individual contraction in the non-rhythmic task, the total duration
27 of all contractions in the two tasks was approximately similar (100-120 seconds), making them
28 comparable in terms of fatigue.

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2.4 Data analysis

All processing and computations for force, EMG and EEG data were performed using Matlab software (v. R2017a, MathWorks, Natick, MA, USA). All filters were 4th-order Butterworth type filters with zero-time lag.

Experimental data preprocessing

Force and EMG data: Isometric force data obtained with hand dynamometers were low-pass filtered at 10 Hz. Raw EMG data were 10–400 Hz band-pass filtered, notched at 49–51 Hz, full-wave rectified by taking the absolute value and then low-pass filtered at 3 Hz to obtain the linear envelope [83,84].

EEG data: Raw EEG data were 3–100 Hz band-pass filtered, notched at 49–51 Hz and then average-referenced.

Segmentation of continuous data

For each contraction trial of the rhythmic task, the continuous dataset was segmented into epochs, from –0.3 to 0.3 s around each force peak and a baseline correction of the same duration as the epoch was applied only for EEG data. **This baseline correction consists of subtracting the mean of the whole epoch from every time point of each epoch.** The identical segmentation is applied to the corresponding control trials based on the same indexes.

For each contraction and control trials of the non-rhythmic task, the continuous dataset was segmented into epochs, from –1 to 9 s around the sound trigger of the movement start and a baseline correction of the same duration as the epoch was applied only for EEG data.

Finally, each epoch was visually inspected to remove epochs where EEG signals were contaminated by any artifacts (eyes movement, muscle artifacts and drifts). When an EEG epoch was rejected, the corresponding EMG and force epochs were also rejected. **The same visual inspection procedure was also applied to the force data to remove epochs where the participant did not follow the instruction (incorrect contraction side or no contraction). As the trial number affects the EEG results, it is important to note that despite the relatively small number of epochs, very few were rejected. Thus, for**

1 the rhythmic task, 20 epochs were always retained because the first 20 non-rejected epochs among the
2 100 possible were selected. For the non-rhythmic task, only 6.04% of epochs were rejected in
3 unimanual right condition (mean of 0.91 per participant) and 6.66% in unimanual left condition (mean
4 of 1 per participant).

5

6 *Experimental data processing*

7 In order to make the two tasks more comparable, we performed matched analyses by considering only
8 the first 20 epochs in each condition of the rhythmic task (*i.e.*, unimanual right and left and
9 corresponding control trials). This procedure is important because the trial number significantly
10 influences the EEG results, especially during time-frequency analysis. In addition, to make the time-
11 window of interest of the two tasks of equal duration (*i.e.*, 0.6 s), the analysis of the epoched signal of
12 the non-rhythmic task focused on the time-window of interest from 4.2 to 4.8 s after the sound trigger
13 of the movement start. **Given that MM amplitude has been shown to increase over time during
14 repeated and prolonged contractions [22,85], this time-window of interest at the end of the 6 s
15 contraction was considered to be the most favourable for the observation of MM.**

16 *EMG data:* For both tasks, the quantity and the intensity of MM were respectively assessed for each
17 participant with the number and the mean amplitude of EMG peaks on the inactive hand for all
18 contraction trials. If peaks were detected on both extensor and flexor muscles, only the maximum peak
19 was counted, corresponding to the same EMG burst. EMG peak detection was performed using the
20 ‘findpeak’ Matlab function with the ‘MinPeakHeight’ option to return only those peaks higher than the
21 threshold value. For each unimanual contraction condition in both tasks (*i.e.*, unimanual right and left),
22 the threshold value was set at two standard deviations above the mean value of EMG envelope
23 recording during all corresponding control trials. If two or more peaks were detected during a 0.6 s
24 epoch of contraction trial, only the highest was retained. An example of EMG peak detection is given
25 in Figure 1. Finally, to standardize data, the number of EMG peaks was expressed as a ratio of the
26 total number of contractions and the mean amplitude of EMG peaks was expressed as a mean
27 percentage of the maximal EMG activity produced during unimanual MVC for each respective
28 muscle.

Please insert Figure 1 here

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EEG data: In order to reduce the effect of volume conduction, laplacian filter was used on epoched data before time-frequency analysis [86]. For both tasks, EEG spectral power was obtained in the time-frequency domain with continuous Morlet wavelet transform with the MATLAB package developed by Grinsted et al. [87] and adapted in Bigot et al. [88]). The scale resolution of the wavelet (parameter 'nvoice'), the number of scales used in the wavelet analysis (parameter 'J1') and the Morlet mother wavelet parameter (parameter 'wavenumber') were set respectively to 7, 50 and 10 to provide a satisfactory compromise between time and resolution for the identification of oscillatory activity on the [0.32×10^{-2} : 0.23 : 79.97] Hz frequency range. In order to optimize the trade-off between temporal and frequency precisions in lower frequencies, the Morlet mother wavelet parameter (parameter 'wavenumber') was adjusted at 3 for analysis in the theta frequency band (4-8 Hz) as used in previous studies (*e.g.*, [89,90]). Then, EEG spectral power was transformed using a logarithmic function in order to reduce the effects of inter-participant and inter-electrode variability in absolute power values. Finally, in both conditions and tasks, EEG spectral power for the entire epoch of 0.6 s recorded during contraction trials was normalized with the spectral power recorded during control trials. Thus, task-related spectral power (TR-Pow) was derived using the following formula:

$$\text{TR-Pow} = \log_{10} (\text{Pow}_{\text{contraction}}) - \log_{10} (\text{Pow}_{\text{control}})$$

Based on our assumptions, previous studies and the inspection of scalp topographic plot, a region of interest (ROI) approach was adopted in three frequency bands: beta (β : 13–30 Hz), alpha (α : 8–12 Hz) and theta (θ : 4–8 Hz).

In the beta frequency band, right and left sensorimotor ROI (C2–C4–CP4–CP2 and C1–C3–CP3–CP1 electrodes respectively) were considered. Then, an asymmetry index (AI) was calculated between mean β TR-Pow in the contralateral and ipsilateral sensorimotor ROI of the movement using the following formula:

$$\text{AI} = \text{Mean contralateral } \beta \text{ TR-Pow} - \text{Mean ipsilateral } \beta \text{ TR-Pow}$$

1 If asymmetry index (AI) is negative, β TR-Pow in contralateral sensorimotor regions of the movement
2 is stronger than ipsilateral while if it is positive the opposite pattern is found. β task-related power
3 decreases (desynchronization) can be interpreted as an electrophysiological correlate of activated
4 cortical areas involved in production of motor behaviour [71,72]. β task-related power increases
5 (synchronization) may be involved in the active inhibition of sensorimotor processes and reflect the
6 maintenance of the status quo [73,74].

7 In the alpha frequency band, mean α TR-Pow was quantified from a parieto-occipital ROI including
8 the following electrodes: P1–P3–P5–PO3–POz–Pz–P2–P4–P6–PO4. α TR-Pow decreases
9 (desynchronization) may reflect cortical activations involved in attentional process and the release
10 from inhibition [76,77,91].

11 In the theta frequency band, mean θ TR-Pow was quantified from a fronto-mesial ROI including the
12 following electrodes: FC1–FCz–FC2. θ TR-Pow increases (synchronization) may reflect cortical
13 activations involved in executive control and response inhibition [79,80].

14

15 **2.5 Statistical analysis**

16 Each data sample was found to be normally distributed with the Kolmogorov–Smirnov test, ranging
17 from $d = 0.100$ to 0.386 , all $p > 0.05$. In addition, the Levene's test used to check homogeneity of
18 variances between age groups in each condition did not reveal significant results, F-value ranging
19 between 1×10^{-4} and 4.468 , all $p > 0.05$.

20 *EMG data:* Three-factor mixed ANOVAs with the within-subjects factors Task (Rhythmic vs Non-
21 rhythmic) and Side of the active hand (Right vs Left) and the between-subjects factor Age (Young vs
22 Middle-aged) were performed on the number and the mean amplitude of EMG peaks.

23 *EEG data:* Three-factors mixed ANOVAs with the within-subjects factors Task (Rhythmic vs Non-
24 rhythmic) and Side of the active hand (Right vs Left) and the between-subjects factor Age (Young vs
25 Middle-aged) were performed on the asymmetry index of β TR-Pow in sensorimotor ROI, α TR-Pow
26 in parieto-occipital ROI and θ TR-Pow in fronto-mesial ROI.

27 For all analyses, the significance level was set at $p < 0.05$. A p-value between 0.05 and 0.10 was
28 considered as a trend. Tukey post hoc were performed based on significant main effects or

1 interactions. Partial eta squared (η^2) and f effect sizes were reported for significant effects and
2 interactions in ANOVA.

3

4 **3. RESULTS**

5 In order to properly interpret our results, we first wanted to ensure that the behavioural performance of
6 participants (*i.e.*, performing contractions at 25% MVC) was comparable across groups, tasks, and
7 conditions. For this purpose, we performed a three-factor mixed ANOVA with the within-subjects
8 factors Task (Rhythmic vs Non-rhythmic) and Side of the active hand (Right vs Left) and the between-
9 subjects factor Age (Young vs Middle-aged) on the mean amplitude of force peaks (among all
10 conserved epochs; expressed in percentage of MVC) produced by the active hand. These results
11 highlight that the force produced by the active hand does not significantly differ between groups, tasks
12 and conditions (F ranging from 0.335 to 3.762; all $p > 0.05$) and remains very close to the target force
13 (overall mean: 27.529 ± 3.966 % of MVC).

14 **3.1 Behavioural results: quantity and intensity of MM**

15 ANOVA on the number of EMG peaks revealed a significant main effect of Task ($F_{1,22} = 24.102$; $p <$
16 $.001$; partial $\eta^2 = 0.522$, f effect size: 1.046) and Side of the active hand ($F_{1,22} = 4.595$; $p = .043$; partial
17 $\eta^2 = 0.172$, f effect size: 0.457). The number of EMG peaks on the inactive hand was greater in the
18 rhythmic task (0.706 ± 0.394) compared to the non-rhythmic (0.400 ± 0.250) and during the
19 unimanual left movement (0.637 ± 0.339) compared to the right (0.468 ± 0.369). Moreover, the
20 interaction Side of the active hand \times Task was also significant on the number of EMG peaks
21 ($F_{1,22} = 9.004$; $p = .006$; partial $\eta^2 = 0.290$, f effect size: 0.639). During the unimanual left movement
22 in the rhythmic task, a greater number of EMG peaks on the inactive hand was found compared to the
23 unimanual right movement in the same task and to the unimanual right and left movement in the non-
24 rhythmic task (Figure 2., left panel; all $p < .001$). In contrast, irrespective of age group and during the
25 non-rhythmic task, EMG peaks on the inactive hand during the unimanual left and right movement
26 were similar. Finally, it should also be noted that the number of EMG peaks tended to be higher in the
27 middle-aged group (0.619 ± 0.202) than in the young group, irrespective of the task and side of the

1 active hand (0.486 ± 0.104 ; main effect of Group: $F_{1,22} = 4.060$; $p = .056$; partial $\eta^2 = 0.155$, f effect
2 size: 0.429).

3 ANOVA on the mean amplitude of EMG peaks revealed only a significant main effect of Task
4 ($F_{1,22} = 12.515$; $p = .001$; partial $\eta^2 = 0.362$, f effect size: 0.754). Irrespective of age group and side of
5 the active hand, the mean amplitude of EMG peaks on the inactive hand was greater in the rhythmic
6 task ($3.635 \pm 4.045\%$) compared to the non-rhythmic ($1.793 \pm 1.365\%$; Figure 2., right panel).

7 *Please insert Figure 2 here*

8 9 **3.2 EEG results**

10 *Asymmetry index of β TRPow over sensorimotor regions*

11 ANOVA on the asymmetry index of β TR-Pow in sensorimotor ROI revealed only a significant
12 interaction Side of the active hand \times Task ($F_{1,22} = 6.908$; $p = .015$; partial $\eta^2 = 0.238$, f effect size:
13 0.560). Post-hoc analyses indicated that the asymmetry index of β TR-Pow in sensorimotor ROI was
14 greater (more positive) in the unimanual left movement compared to the unimanual right movement
15 only for the rhythmic task and irrespective of age group (Figure 3.a; $p = .034$). During the unimanual
16 left movement in the rhythmic task and irrespective of age group, β TR-Pow in ipsilateral left
17 sensorimotor regions was lower (more negative) than contralateral right sensorimotor regions (Figure
18 3.b.).

19 *Please insert Figure 3 here*

20 21 *α TRPow over parietal regions*

22 ANOVA on the α TR-Pow in parieto-occipital ROI revealed a significant main effect of Task
23 ($F_{1,22} = 4.731$; $p = .040$; partial $\eta^2 = 0.177$, f effect size: 0.463). Irrespective of age group and side of
24 the active hand, α TR-Pow in parieto-occipital ROI was lower (more negative) in the rhythmic task

1 compared to the non-rhythmic. Moreover, the interaction Task \times Group was also significant
2 ($F_{1,22} = 4.630$; $p = .042$; partial $\eta^2 = 0.173$, f effect size: 0.458). Post-hoc analyses indicated that α TR-
3 Pow in parieto-occipital ROI was lower (more negative) in the rhythmic task compared to the non-
4 rhythmic task only in the young group (Figure 4; $p = .027$).

5 *Please insert Figure 4 here*

6
7 ***θ TRPow over fronto-mesial regions***

8 ANOVA on the θ TR-Pow in fronto-mesial ROI revealed only a significant main effect of Task
9 ($F_{1,22} = 7.203$; $p = .013$; partial $\eta^2 = 0.246$, f effect size: 0.572). Irrespective of age and side of the
10 active hand, θ TR-Pow in fronto-mesial ROI was greater (more positive) in the rhythmic task
11 (0.019 ± 0.106) compared to the non-rhythmic (-0.044 ± 0.114 ; Figure 5).

12 *Please insert Figure 5 here*

13
14 **4. DISCUSSION**

15 The aim of the present study was to determine the conditions of emergence of behavioural asymmetry
16 of MM and its associated cerebral correlates in right-handed healthy young and middle-aged adults.
17 EMG and EEG signals were recorded during two unimanual motor tasks requiring to produce either
18 rhythmic (rhythmic task) or **prolonged** (non-rhythmic task) power grip **low-force** contractions. The
19 behavioural results revealed (1) a greater quantity and intensity of MM in the rhythmic task compared
20 to the non-rhythmic irrespective of the side of the active hand and age, (2) a behavioural asymmetry of
21 MM specific to the rhythmic task irrespective of age, with a greater quantity of MM on the dominant
22 (right) hand during the unimanual left-hand movement and (3) a **non-significant** trend to produce a
23 greater quantity of MM in middle-aged adults compared to young adults irrespective of the side of the
24 active hand and the task. The EEG results show (1) a cerebral asymmetry specific to the rhythmic task

1 irrespective of age with greater bilateral activations over the motor regions during a unimanual left-
2 hand movement compared to unimanual right-hand movement, (2) greater attentional activations
3 (alpha desynchronization over the parietal regions) irrespective of the side of the active hand in the
4 rhythmic task compared to the non-rhythmic especially in young adults and (3) greater executive
5 activations (theta synchronization over fronto-mesial regions) in the rhythmic task compared to the
6 non-rhythmic irrespective of the side of the active hand and age. These findings are discussed in terms
7 of motor, attentional and executive processes associated with the asymmetry of MM in the rhythmic
8 task. We postulate that the asymmetry of MM is related to the complexity of the rhythmic task that
9 requires greater fine motor control and higher cognitive effort than the non-rhythmic task.

10

11 *Behavioural asymmetry of mirror movements is specific to the rhythmic task*

12 First, irrespective of the side of the active hand and age, we found a greater quantity and intensity of
13 MM in the rhythmic task compared to the non-rhythmic. Many previous studies have reported MM in
14 healthy adults during unilateral rhythmic contractions of the upper limb in healthy adults [7,18,20,23–
15 25,34,53,65,68,70] and young children [16]. However, to our knowledge, no study has yet compared
16 the degree of MM between a rhythmic and a non-rhythmic task. For the first time, our result confirms
17 that a rhythmic motor paradigm involving low-force contractions facilitates the emergence of MM.
18 The frequency of repeated contractions could also affect the degree of MM. Some studies found more
19 MM at maximum frequency [20,68], while other studies reported more MM at low frequencies around
20 1 Hz as in the current study [26,53]. Therefore, a slow or fast rhythm could make the task more
21 complex by increasing the constraint of accuracy and speed and lead to increased MM. In the present
22 study, increased MM in the rhythmic task at 25% of MVC (*i.e.*, low-force contractions) and 1 Hz
23 could be explained by the fact that the task requires more fine motor control, which provides strong
24 evidence that the task complexity also contributes to the emergence of MM. However, a limitation of
25 the present study is that both tasks involved only low-force contractions (25% MVC). Given that many
26 studies report an increase of the amplitude of MM with increasing force level during isometric
27 contractions [30,52,66,67,69,85,92–95], we could hypothesise that the difference of the quantity and
28 intensity of MM between the rhythmic and non-rhythmic task would disappear at high force levels.

1 **Therefore**, further studies would be necessary to determine the exact evolution of MM according to
2 different contraction frequencies **and force level** and by controlling the level of fatigue of each motor
3 task.

4
5 A second significant result of this study is that the behavioural asymmetry of MM seems to be specific
6 to the rhythmic task irrespective of age, with a greater quantity of MM on the dominant (right) hand
7 during the unimanual left-hand movement. This result confirms the behavioural asymmetry of MM in
8 right-handed healthy adults already found in previous studies [3,24,47–54]. As proposed by Todor &
9 Lazarus [52], asymmetry of MM between right and left hands in right-handed healthy adults could be
10 related to differences between hemispheric control of each hand. Thus, our results suggest that
11 performing a more complex (*i.e.*, rhythmic) task **involving low-force contractions** with the non-
12 dominant and less efficient left hand could produce more MM in the right hand. Interestingly, among
13 the studies that fail to find such asymmetry, some have quantified MM only as an involuntary force
14 production [27,28,63,70] or even as an apparent involuntary movement [64]. In addition, most of **these**
15 studies evaluated MM only as intensity (*i.e.*, amplitude of involuntary force or EMG activity) and not
16 as quantity (*i.e.*, frequency of occurrence). **Finally, other studies using isometric rather than rhythmic**
17 **contractions have also failed to find an asymmetry of MM between the right and left sides [66,67,69].**
18 **Taken together, the previous and current results suggest that the behavioural asymmetry of MM is**
19 **observed during rhythmic low-force contractions and when MM are assessed as quantity. However, as**
20 **mentioned above, the behavioural asymmetry of MMs reported in this study is limited to the specific**
21 **low-force level at 25% MVC and further studies would be required to generalise this result to higher**
22 **force levels.**

23
24 To go further, it remains to be known how the rhythmic task leads to an asymmetry of MM. As
25 initially proposed by Armatas & Summers [64], the task characteristics, and in particular the type of
26 required movements, could influence the pattern of MM occurrence in healthy adults. In our study, the
27 non-rhythmic task involves prolonged discrete isometric **low-force** contractions while the rhythmic
28 task involves rhythmic isometric **low-force** contractions considered as periodic repetitions of particular

1 events [96]. Although this is still debated, the current literature suggests that rhythmic and discrete
2 movements form two different classes of movements and involve (at least partially) distinct
3 mechanisms of action control [97–99]. In particular, a recent study suggests that discrete and rhythmic
4 movements would involve different kinds of motor inhibition processes [100]. Although the two tasks
5 of the current study are not strictly comparable, we could hypothesize that greater and more
6 asymmetric MM in the rhythmic task could be related to lower efficiency of the motor inhibition
7 processes involved in rhythmic movements than those involved in discrete movements. Nevertheless,
8 it should be noted that the non-rhythmic task used in the current study does not involve strictly
9 discrete contractions because they last 6 seconds. Therefore, to make the two tasks strictly comparable
10 and to be able to conclude about the observed differences, brief isometric contractions should have
11 been **used** in the non-rhythmic task.

12

13 Lastly, we found an interesting trend in middle-aged adults to produce a greater quantity of MM
14 compared to young adults irrespective of the side of the active hand and the task. This result is
15 consistent with a previous study reporting a steady increase of MM after the age of 32 years [26] and
16 other studies that showed greater MM in the elderly than in young adults [20,27–30]. Beyond
17 **suggesting** that MM seems to increase early with age, we could also hypothesize that, unlike young
18 and/or middle-aged adults, greater MM could be found in the rhythmic and non-rhythmic tasks in
19 elderly people and would reflect compensatory mechanisms related to the task complexity [28,101].

20

21 ***Cerebral motor asymmetry of mirror movements is specific to the rhythmic task***

22 As expected, we found a cerebral motor asymmetry specific to the rhythmic task and irrespective of
23 age, with greater bilateral motor activations over the motor regions during the unimanual left-hand
24 movement compared to unimanual right-hand movement. In contrast, in the non-rhythmic task and
25 both age groups, similar motor activations (*i.e.*, mainly contralateral to the voluntary movement) are
26 observed during both unimanual left and right-hand movement. In a previous EEG study, we reported
27 an association between greater ipsilateral activation over left motor area during unimanual left-hand
28 movements compared to right-hand movements and the behavioural asymmetry of MM in right-

1 handed healthy subjects [24]. In the present study, we extend this result by finding behavioural and
2 cerebral motor asymmetry of MM only in a unimanual rhythmic task compared to a non-rhythmic task
3 and irrespective of age. This finding suggests that the rhythmicity of the task could contribute to the
4 cerebral motor asymmetry by increasing task complexity, especially during left non-dominant hand
5 movement. Indeed, an increase of ipsilateral M1 excitability has been reported for unilateral rhythmic
6 contractions at 1 Hz and 3 Hz compared to 2 Hz and has been associated with reduced task
7 performance measured by greater temporal variability which may reflect greater complexity [102].
8 This result could explain previous studies that found more MM in rhythmic contractions at low
9 frequency around 1 Hz [26,53] but also at maximum frequency [20,68]. Thus, we can hypothesize that
10 unimanual rhythmic contractions at low rate of 1 Hz as in the current study is more complex when
11 performed with the left non-dominant hand and generate additional activations including ipsilateral
12 motor regions. In accordance with this assumption, previous fMRI studies found more bilateral motor
13 activations during unimanual rhythmic movement with the left limb compared to the right limb in
14 right-handed healthy subjects [55–57]. Similarly, other studies reported strong ipsilateral activations
15 during complex unimanual movements [103] and especially in the left hemisphere during left-hand
16 movements [104,105]. Interestingly, these ipsilateral activations involved the primary motor cortex but
17 also the premotor cortex and it was proposed that they reflect the special role of the left hemisphere in
18 motor control especially during complex motor task [104,106,107]. Furthermore, TMS studies also
19 reported a greater facilitation of the ipsilateral M1 during unimanual contraction with the left non-
20 dominant hand compared to the right dominant hand in various complex task as fine-motor
21 manipulation [58,59] and hand-foot coordination [60]. Similarly, a stronger suppression of ipsilateral
22 activations or reduction of ipsilateral excitability during right dominant hand movement compared to
23 the left non-dominant hand was reported in many studies using TMS [50,61,62,108], fMRI [109–111]
24 and EEG [24,112]. Interestingly, this asymmetry of ipsilateral activations may involve asymmetric
25 interhemispheric interactions. For example, previous TMS studies of interhemispheric inhibition have
26 shown that the left dominant hemisphere exhibits a stronger inhibitory influence on right M1
27 compared to the inhibitory effects of the right hemisphere on left M1 [113,114]. In summary, the
28 additional ipsilateral activations found in the current study during unimanual rhythmic contractions

1 with the left non-dominant hand support the greater occurrence of MM on the right dominant hand and
2 could be related to the complexity of the rhythmic task involving fine motor control.

3

4 *Greater attentional and executive control is associated to the rhythmic task*

5 During the rhythmic task and irrespective of the side of the active hand, we found greater attentional
6 activations over the parietal regions especially in young adults and greater executive activations over
7 fronto-mesial regions compared to the non-rhythmic in both age groups. This result is consistent with
8 previous studies that found a strong desynchronization in the alpha frequency band over the parietal
9 regions during a complex rhythmic selective stop task [24,41,44]. Desynchronization in the alpha
10 frequency band over the parietal regions could reflect general task demands and attentional processes
11 involved the rhythmic task [24,77,91,115]. In the current study, greater attentional activations over the
12 parietal regions in the rhythmic task compared to the non-rhythmic probably reflect the higher
13 cognitive effort required to perform this task. In addition, we found similar strong alpha
14 desynchronization over the parietal regions in both tasks in middle-aged adults, whereas only the
15 rhythmic task requires this strong alpha desynchronization in young adults. In line with previous
16 studies showing that older adults demonstrated increased attentional **and** executive activations
17 including prefrontal and posterior parietal regions during motor task [45,116,117], we could
18 hypothesize that the non-rhythmic task is relatively simple for young subjects but becomes more
19 complex as people get older and require additional compensatory attentional resources for the effective
20 task performance [101]. Therefore, this increased attentional demands especially in the non-rhythmic
21 task in middle-aged adults could lead to an increase of MM as previously found in elderly subjects
22 when attention was diverted [20,27,29].

23

24 About executive activations, we also found greater synchronization in the theta frequency band over
25 fronto-mesial regions in the rhythmic task compared to the non-rhythmic task. Interestingly, increased
26 frontal theta synchronization was reported in response inhibition paradigms such as stop signal and
27 go/no-go tasks (for a review, see [80]) and could reflect executive processes such as conflict and errors
28 monitoring or updating of the response program [79,80,118]. The increased theta power in the

1 rhythmic task found in the present study could thus reflect a need for higher-level executive control to
2 select the appropriate action (*i.e.*, strictly unilateral contractions) and prevent the emergence of MM
3 [79,80]. As for attentional activations, this increased executive control could be related to the higher
4 cognitive effort required to perform the rhythmic task. Thus, available attentional and executive
5 resources to prevent MM could be reduced, leading to an increase of MM especially during rhythmic
6 movements with the left non-dominant hand.

7

8

9 **Conclusions**

10 To our knowledge, the present study is the first to highlight a behavioural and cerebral motor
11 asymmetries of MM specific to a rhythmic task **involving low-force contractions** in right-handed
12 healthy young and middle-aged adults. We propose that behavioural and cerebral motor asymmetries
13 of MM are related to the higher cognitive effort required to perform the rhythmic motor task as
14 suggested by greater attentional and executive control engaged during the rhythmic task compared to
15 the non-rhythmic task. Surprisingly, few differences were found between the young and middle-aged
16 adults. For future investigations, we could extend this research **to other higher force levels but also to**
17 older adults to investigate attentional and executive correlates related to the increase of MM in this
18 population. Finally, another interesting perspective would be to explore the role of inhibitory
19 interhemispheric interactions between the motor areas in the emergence of MM in these two motor
20 tasks and age groups.

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FIGURES AND CAPTIONS

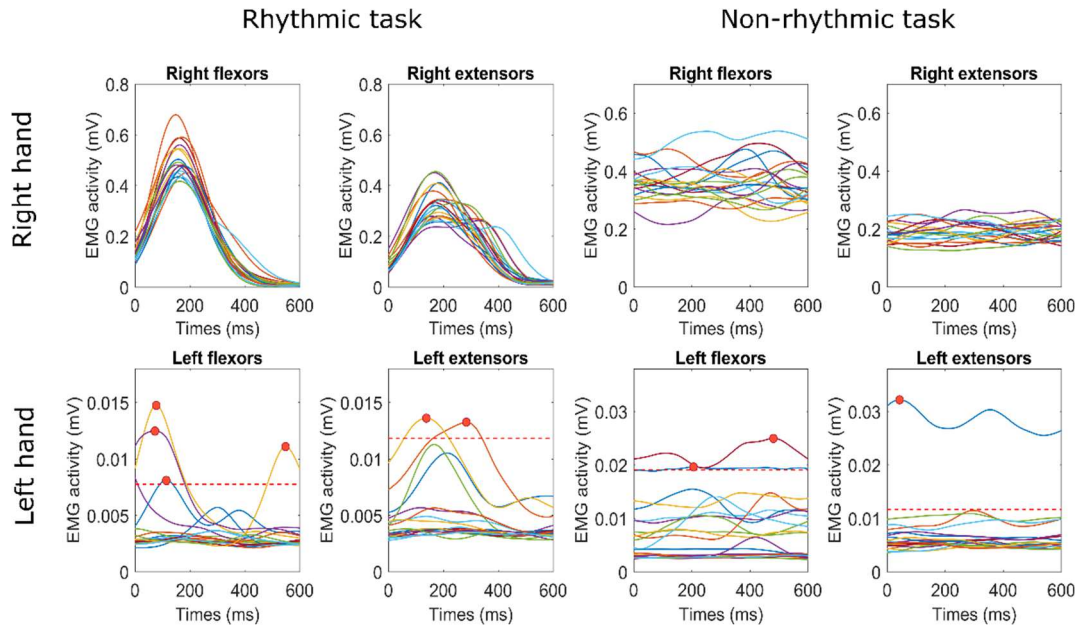
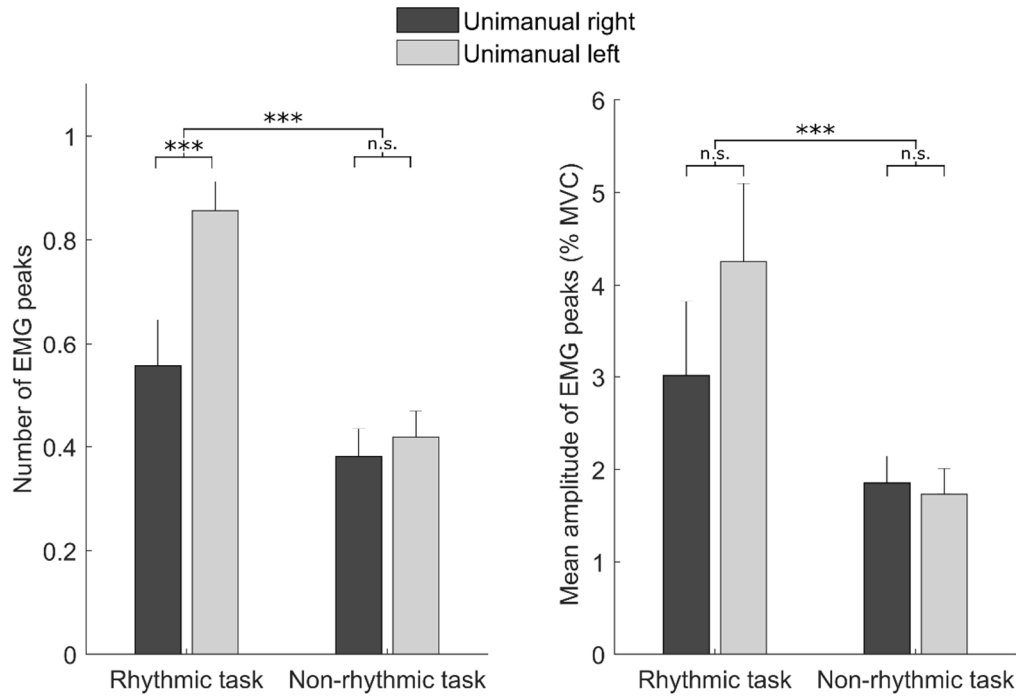


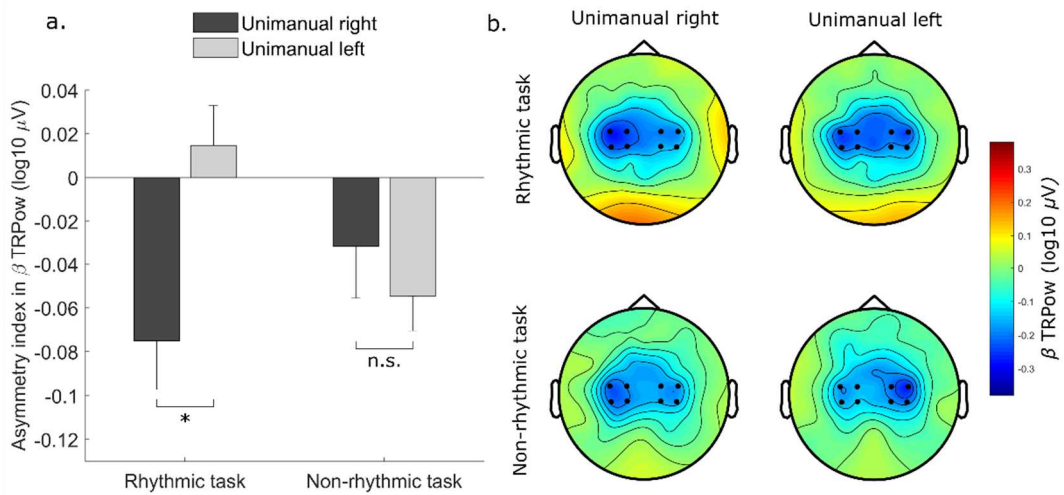
Figure 1. Illustration of EMG peak detection on the left hand (bottom panel with the flexors and extensors muscles) during the unimanual right contraction condition in the rhythmic and non-rhythmic tasks (left and right four subplots respectively) in one middle-aged participant. Multiple colored traces correspond to the linear envelope of the denoised and full-wave rectified EMG in each contraction (20 rhythmic unimanual right power grip contractions in the rhythmic task and 20 prolonged unimanual right power grip contractions in the non-rhythmic task). The horizontal dashed red lines indicate the threshold value set at two standard deviations above the mean value of EMG envelope recording during all corresponding control trials. The filled red circles represent detected EMG peaks above the corresponding threshold.

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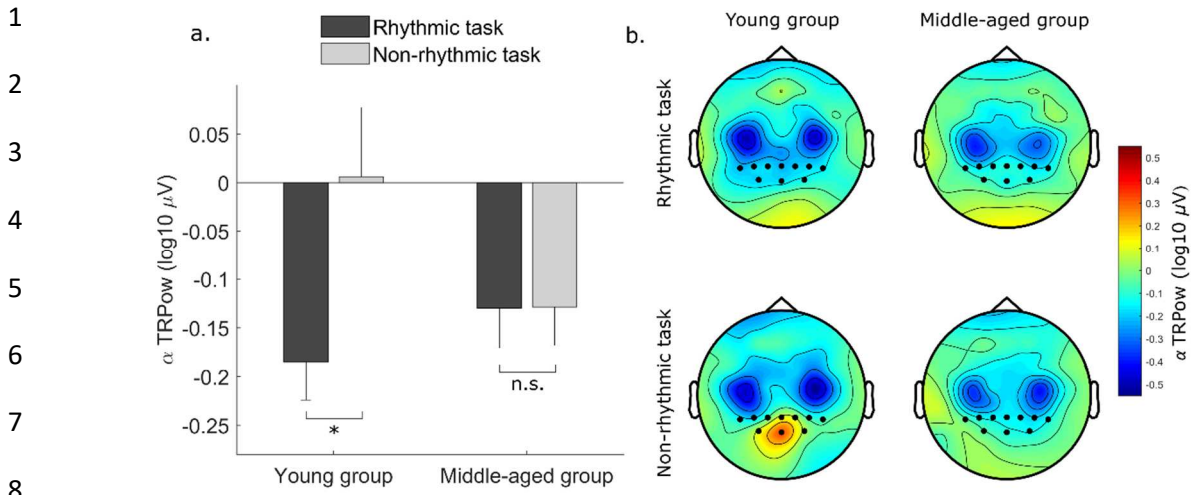


12 **Figure 2.** Bar plot of the number and mean amplitude of EMG peaks (left and right panels
13 respectively) during right and left unimanual movement (black and gray bars respectively) in rhythmic
14 and non-rhythmic tasks **in all young and middle-aged participants (pooled data)**. *** indicates
15 significant difference ($p < .001$). Vertical bars represent standard error of the mean.

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10 **Figure 3. a.** Bar plot of the asymmetry index of β TRPow in sensorimotor ROI during right and left
11 unimanual movement (black and gray bars respectively) in rhythmic and non-rhythmic tasks (left and
12 right panels respectively) **in all young and middle-aged participants (pooled data)**. * indicates
13 significant difference ($p < .05$); 'n.s.' indicates not significant. Vertical bars represent standard error of
14 the mean. **b.** Scalp topography of β TRPow during right and left unimanual movement (left and right
15 panels respectively) in rhythmic and non-rhythmic tasks (top and bottom panels respectively) **in all**
16 **young and middle-aged participants (pooled data)**. Black dots represent right and left sensorimotor
17 ROI. TRPow decreases (area of activation) are coded in blue and TRPow increases are coded in red.



9 **Figure 4. a.** Bar plot of α TRPow parieto-occipital ROI during rhythmic and non-rhythmic tasks
 10 (black and gray bars respectively) in young and middle-aged groups (left and right panels
 11 respectively). * indicates significant difference ($p < .05$); 'n.s.' indicates not significant. Vertical bars
 12 represent standard error of the mean. **b.** Scalp topography α TRPow during rhythmic and non-rhythmic
 13 tasks (top and bottom panels respectively) in young and middle-aged groups (left and right panels
 14 respectively). Black dots represent parieto-occipital ROI. TRPow decreases (area of activation) are
 15 coded in blue and TRPow increases are coded in red.

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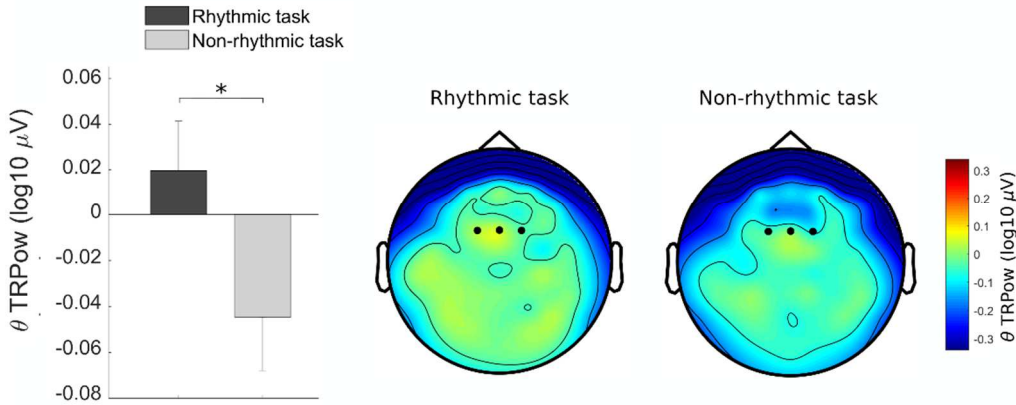


Figure 5. Scalp topography of θ TRPow during rhythmic and non-rhythmic tasks (left and right panels respectively) in all young and middle-aged participants (pooled data). Black dots represent fronto-mesial ROI. TRPow decreases are coded in blue and TRPow increases (area of activation) are coded in red.