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The causal role of beta band desynchronization: Individualized high-definition transcranial alternating current stimulation improves bimanual motor control

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ABSTRACT

Objective: To unveil if 3 mA peak-to-peak high-definition β transcranial alternating current stimulation (tACS) applied over C4 –the area overlaying the right sensorimotor cortex–enhances bimanual motor control and affects movement-related β desynchronization (MR β D), thereby providing causal evidence for the polymorphic role of MR β D in motor control.

Methods: In this sham-controlled, crossover study, 36 participants underwent 20 min of fixed 20 Hz tACS; tACS individualized to peak β activity during motor planning at baseline; and sham tACS randomized over three consecutive days. Each participant underwent all three conditions for a total of 108 sessions, ensuring within-subject comparisons. Before, during, and after tACS, participants performed a bimanual tracking task (BTT) and 64-channel electroencephalography (EEG) data was measured. Spatiotemporal and temporal clustering statistics with underlying linear mixed effect models were used to test our hypotheses.

Results: Individualized tACS significantly improved bimanual motor control, both online and offline, and increased online MRβD during motor planning compared to fixed tACS. No offline effects of fixed and individualized tACS on MRβD were found compared to sham, although tACS effects did trend towards the hypothesized MRβD increase. Throughout the course of the study, MRβD and bimanual motor performance increased. Exclusively during motor planning, MRβD was positively associated to bimanual motor performance improvements, emphasizing the functionally polymorphic role of MRβD. tACS was well tolerated and no side-effects occurred.

Conclusion: Individualized β -tACS improves bimanual motor control and enhances motor planning MR β D online. These findings provide causal evidence for the importance of MR β D when planning complex motor behavior.

1. Introduction

Motor control is imperative to human behavior. A deeper understanding of it not only advances our fundamental knowledge of the brain but also has the potential to revolutionize therapeutic strategies for neurological conditions, such as stroke and Parkinson's disease (Krakauer, 2006; Nieuwboer et al., 2009). The combination of electroencephalography (EEG) and transcranial alternating current stimulation (tACS) is promising for motor control. While EEG provides real-time monitoring of brain activity, tACS enables noninvasive modulation of neural oscillations, offering a unique opportunity to causally probe brain-behavior relationships (Herrmann et al., 2013; Vosskuhl et al., 2020; Wischnewski et al., 2023). tACS applies weak, oscillatory electrical currents to the scalp. Although incapable of generating action potentials, the resulting time-varying electric fields modulate neural activity by synchronizing endogenous rhythms to the imposed frequency, a process known as entrainment (Fröhlich and McCormick, 2010; Anastassiou et al., 2011). According to the Arnold Tongue Hypothesis, the likelihood of successful entrainment depends on the alignment between the exogenous tACS frequency and the endogenous

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rhythms (Huang et al., 2021). While entrainment is often used to explain the online effects of tACS (i.e., the effects during stimulation), its working mechanisms are more complex and also include neuroplasticity-like effects (Zaehle et al., 2010; Wischnewski and Schutter, 2017; Vossen et al., 2015). These effects also explain why tACS effects do not only occur during stimulation, but also offline, when the stimulation has already been terminated (Vossen et al., 2015; Kasten et al., 2016). Furthermore, when inducing low-intense electric fields, which is typically the case in humans, computational work suggests that tACS may even desynchronize ongoing neural oscillations (Zhao et al., 2024). While tACS can be applied at various frequencies, the β -band (13.5 - 30 Hz) is of particular relevance for motor behavior, as β -tACS has been shown to enhance early motor consolidation (Krause et al., 2016; Pollok et al., 2015), speed up motor performance at the cost of accuracy (Heise et al., 2019), and alter corticospinal excitability (Wischnewski et al., 2019).

While these findings position tACS as a compelling tool to enhance motor control, little is known about its impact on event-related neural processes during and after stimulation. These processes are, however, crucial for cognition and behavior. The few studies that have explored this, indicate event-related neural processes during cognitive tasks are enhanced following tACS (Wischnewski and Schutter, 2017; Kasten et al., 2018; Kasten and Herrmann, 2017).

A key event-related feature for motor behavior is movement-related β desynchronization (MR β D), a transient β power decrease in sensorimotor regions, during the planning and execution of spontaneous, imagined and triggered movements (Barone and Rossiter, 2021; Engel and Fries, 2010; Kilavik et al., 2013; Blanco Mora et al., 2024). The observations that motor planning MR^βD is associated to force production (Stančák et al., 1997), movement direction uncertainty (Tzagarakis et al., 2010) and interlimb motor control (S. Van Hoornweder et al., 2022; S. Van Hoornweder et al., 2022; Alayrangues et al., 2019), and is attenuated in motor disorders (Bizovičar et al., 2014; Heinrichs-Graham et al., 2014), has caused some to perceive MR β D as essential for motor control. However, other work indicates that MR β D might be an epiphenomenon, being insensitive to the used effector (Salmelin et al., 1995) and movement speed (Stancák and Pfurtscheller, 1996) during motor execution. Previously, we brought these contradictory results together by arguing that MRβD is functionally polymorphic, representing movement- and performance-specific features during planning, while predominantly representing more general unspecific processes during execution (S. Van Hoornweder et al., 2022).

There are gaps in our understanding of tACS effects on motor control and MR β D, and the polymorphic role of MR β D in motor control. It's also unclear whether tailoring tACS to individual β frequencies, which concurs with the Arnold Tongue hypothesis, yields neurophysiological and/ or behavioral advantages over conventional fixed-frequency tACS, which is easier to implement.

Therefore, we investigated the online and offline effects of β -tACS on MR β D and the bimanual tracking task (BTT), and probed the association between MR β D and motor control. We hypothesized that tACS increases MR β D magnitude during motor planning, with individualized tACS yielding the greatest enhancement. Likewise, we expected both tACS protocols to improve bimanual motor control compared to sham, with individualized tACS being most effective. We also anticipated that motor performance improvements would relate to MR β D changes, providing further insights into motor control mechanisms and positioning tACS as a potential tool for rehabilitation.

2. Material and methods

This study concurred with the Declaration of Helsinki, and was approved by the ethical committee of Hasselt University (protocol number: B1152020000017).

Thirty-six, healthy right-handed participants, aged between 18 and 30, were recruited via flyers and social media. The sample size

calculations and in- and exclusion criteria are outlined in Appendix 2.

2.1. Procedure

Participants visited the lab for three consecutive days at the same hour. Each day, a different tACS condition was applied in a counterbalanced order to control for carry-over and retention effects. Due to the overt tACS artefacts in the EEG data, only participants were blinded.

Participants were then seated while their head was measured and EEG-tACS was set up. Subsequently, they were introduced to the BTT via a brief familiarization. Next, the protocol outlined in Fig. 1A was followed: a 2 min resting state, followed by a 5 min baseline BTT, and 20 min of tACS, of which 10 min consisted of the BTT. After tACS, a 5 min offline BTT block and 2 min rest block were performed. At the end, participants were asked if they received verum or sham tACS.

2.2. Bimanual tracking task

The BTT assessed bimanual motor control (Fig. 1B) (Sisti et al., 2011). Participants were seated in front of a screen with their forearms resting on a table, holding a fixated handlebar in each hand. Each index finger was placed in a circular groove on a rotatable dial connected to a shaft encoder registering angular displacement at 100 Hz. Participants were instructed to follow a moving target dot on the screen by simultaneously rotating the dials, with left and right rotations corresponding to cursor movements along the y- and x-axes, respectively.

Twenty unique conditions were tested, varying by inter-hand frequency and directional pattern. Five inter-hand frequencies were used; 1:1, 1:2, 2:1, 3:1 and 1:3 indicating the relative speed of the left and right hands. Four directional patterns were used: both hands moving rightward, leftward, inward or outward. Each trial consisted of three phases: rest (1.5 s), motor planning (2 s) and motor execution (4 s). During planning, participants could see the imposed line but were not allowed to move, until an auditory signal signaled the start of the execution phase.

The baseline- and offline BTT blocks consisted of 40 trials, while the online block contained 80. All 20 conditions occurred equally, with the order being randomized per block. The on-screen shown lines were visually offset by -90° and 180° rotations on days 2 and 3, respectively, to minimize retention effects across days (Fig. 1B).

BTT performance was quantified as tracking error (TE), a measure of compliance to the imposed coordination pattern (S. Van Hoornweder et al., 2022; Verstraelen et al., 2021). TE at timepoint t was computed as:

$$TE(t) = \sqrt{(x_c(t) - x_t(t))^2 + (y_c(t) - y_t(t))^2} + \frac{|Ax_c(t) + By_c(t) + C|}{\sqrt{A^2 + B^2}}$$
(1)

Where $[x_c(t), y_c(t)]$ are the coordinates of the participants cursor at timepoint t, $[x_t(t), y_t(t)]$ are the coordinates of the target dot, and *A*, *B* and *C* are the target line's linear equation. Thus, TE informs on the participant's cursor's Euclidean distance to the target dot, and its orthogonal distance to the target line. The data were downsampled to 5 Hz, and TE in the online and offline block were normalized relative to baseline given our focus on TE changes following tACS:

$$TE Change(t)_{b_{2,3}} = \log\left(\frac{TE(t)_{b_{2,3}}}{TE(t)_{b_1}}\right)$$
(2)

2.3. Transcranial alternating current stimulation

tACS was administered via two carbon-rubber ring electrodes connected to a neuroConn DC-Stimulator Plus. The electrodes, centered over C4, were applied using Ten20 paste (Fig. 1C and 1E) (cf., (Tashiro et al., 2020)). The choice for C4 is based on previous literature indicating that β -activity in the non-dominant hemisphere is more



Fig. 1. Overview of the study design and methods. **A)** Study design. Participants received 3 tACS types over 3 consecutive days. The upper part shows the condition counterbalancing, the lower part shows the content of one experimental session. Rest indicates resting-state EEG. Buffer indicates time where researchers set up the bimanual tracking task (BTT), resting-state windows and the EEG-tACS protocol. Fade-in and -out relate to the start and end of tACS. **B)** BTT: Left – Task-setup; Middle – Trial time course; Right – All BTT conditions, with 4 movement patterns (quadrants) and 5 inter-hand frequencies. Single, double- and triple lines denote both hands moving at identical speeds, or one hand moving two or three times faster. Colors denote unique conditions. In sessions 2 and 3, visual offsets were introduced to mitigate learning from the day before. **C)** tACS – EEG setup and paradigms: individualized, fixed and sham high-density tACS were applied over sensor C4. **D)** SimNIBS simulated electric field magnitude at the tACS peak intensity in the MNI head model. **E)** Impedance during fixed and individualized tACS and the initial period of sham. **F)** Histogram of individualized tACS frequencies.

responsive to task complexity (S. Van Hoornweder et al., 2022; Alayrangues et al., 2019; Rueda-Delgado et al., 2017). tACS was delivered for 20 min at 3 mA (peak-to-peak) with a 30 s fade-in and fade-out period (Fig. 1D). Fixed- and sham tACS were applied at 20 Hz, with the latter consisting of only the fade-in and -out. For individualized tACS, frequency was personalized (19.0 \pm 3.0 Hz, Fig. 1G, see Appendix 3 for more information), based on the β peak frequency in terms of power during baseline motor planning (S. Van Hoornweder et al., 2022). Frequencies were rounded to the nearest 0.5 Hz to comply with hardware limitations.

2.4. Electroencephalography

EEG data were recorded using a 64-channel BioSemi ActiveTwo EEG system. The used cap depended on a participants head circumference, and was either small (50-54 cm), medium (54-58 cm) or large (58-62 cm). Signal Gel was used and offsets were kept below $|20| \mu V$. Data were sampled at 2048 Hz. Preprocessing was done via EEGLAB (v2021a) and custom functions (cf., Appendix 3 for the full pipeline). It involved down-sampling to 512 Hz, low-pass filtering, bad channels removal and interpolation, and cleaning tACS artefacts via sine-wave fitting and subtraction matched to the tACS frequency, and Signal-Space Projection (SSP) (Vosskuhl et al., 2020). SSP was applied to all the data to prevent spatial distortions. Data were visually cleaned, re-referenced to the average, and individual component analysis was used to remove bad components. Data were epoched (-2.65 to 5.3 s, 0 s = movement onset), with on average 35.6 \pm 4.4 (block 1), 69.7 \pm 10.6 (block 2), 36.6 \pm 3.5 (block 3) epochs per block. Two datasets were excluded due to insufficient epochs (<20). Time-frequency decomposition (1 – 35 Hz in 1 Hz steps) (Appendix 3) was done using complex Morlet Wavelets per participant, session and block. Power was calculated as the squared sum of the real and imaginary components, and dB normalized with respect to baseline (-2.5 to -2.2 s). A negative dB value in the resultant time-frequency plots in the beta band represents MR β D.

2.5. Statistical analyses

All models were constructed via stepwise backward building, systematically removing non-significant effects. Tukey-corrected post-hoc comparisons were done when applicable. Analyses were performed in MATLAB and RStudio (R Core Team 2021; RStudio Team 2020). Linear mixed effect models (LME) are reported without general- and subject-specific intercepts and error terms for conciseness, although these were present in all models. Alpha was set at 0.05, and all P-values were two-tailed.

2.5.1. The effect of β -tACS on β -band desynchronization The effects of tACS on MR β D were examined in threefold (Fig. 2). All

analyses focused on EEG activity at the tACS frequency \pm 2 Hz. For fixed and sham tACS, this was 20 Hz. For individualized tACS, frequency was personalized.

The first two analyses assessed local and global offline effects, while the third analysis investigated local online effects. Online and offline EEG data were separately analyzed due to tACS artefact removal challenges. While our artefact removal pipeline produced similar neural signatures for the offline and online data, separating the data eliminated the risk of tACS-artefacts affecting conclusions drawn based on the offline data, while still providing the potential of novel insights into the immediate neurophysiological effects of tACS.

2.5.1.1. Local $MR\beta D$ changes at the tACS frequency. This analysis focused on local changes from baseline to the offline block. We applied a temporal clustering approach, fitting an LME per timepoint from 0 to 4 s:

$$\begin{split} \textit{EEG Power}_{ijkl} = & \beta_1 \textit{Stimulation}_{ij} + & \beta_2 \textit{Block}_{ik} + & \beta_3 \bigl(\textit{Stimulation}_{ij} \times \textit{Block}_{ik}\bigr) \\ & + & \beta_4 \textit{ Session}_{il} \end{split}$$

with EEG power, the independent variable, relating to the mean power in the tACS stimulation frequency \pm 2 Hz. All factors right of the equation were the independent variables. F-values were retained and used to calculate threshold-free clustering enhanced (TFCE) values (Smith and Nichols, 2009):

$$TFCE_{ij} = \int_{h} e(h)^{E} h^{H} dh$$
(4)

where *h* is cluster height (F-value cut-off), *e* is cluster extent (the number of temporally adjacent datapoints > *h*), and *E* and *H* are their respective weights, defaulting to E = 0.5 and H = 2. Starting at 0, *h* increased in 0.2 steps until the maximum F-value was reached. Significance was inferred if original TFCE values exceeded the 95th percentile of a surrogate null distribution generated from 800 permutations.

2.5.1.2. Global MR β D changes at the tACS frequency. This analysis explored global offline changes through spatiotemporal clustering. Mean EEG power per timepoint and sensor was fitted via an LME (cf., Eq. (4)), and the resulting F-values were used to calculate TFCE values (cf., Eq. (5)) (Smith and Nichols, 2009). Adjacency was not only temporal, but also spatial, based on neighboring sensors (Fig. 2, middle panel). Significance inference was identical to Section 2.5.1.1.



Fig. 2. The threefold analysis of effects on the tACS frequency band ± 2 Hz. Colored arrows indicate fixed (red), individualized (yellow) and sham tACS (blue). The red circles on the topographic plots represent the tACS montage. Left: A first analysis gauged local offline effects. Middle: A second analysis gauged broad effects using a spatiotemporal clustering approach, with black lines representing spatial adjacency. Right: The third analysis examined local online effects.

2.5.1.3. Online effects of tACS on $MR\beta D$. This analysis examined whether fixed and individualized tACS have different online effects. The sham condition was excluded due to the attenuation of the EEG signal by the tACS-artefact removal pipeline (Fig. 3).



Fig. 3. C4 time-frequency matrices and topographic plots representing MR β D changes across blocks and conditions. Time is locked to movement onset (0 s). Frequency is scaled based on the tACS frequency, which was either individualized or 20 Hz. Topographic plots show mean activity at the tACS frequency \pm 2 Hz in the final second of motor planning and initial 2 s of execution.

Per timepoint, we calculated the change in EEG power by subtracting the baseline block mean from the online block mean. An LME was used to test the effect of stimulation on the change in EEG power per timepoint:

$$\Delta(\text{EEG Power block } 2-1)_{iikl} = \beta_1 \text{Stimulation}_{ii} + \beta_4 \text{ Session}_{il}$$
(5)

Temporal clustering was again used and significance was inferred in line with Section 2.5.1.1.

2.5.2. The effect of β -tACS on bimanual motor performance

We first assessed whether baseline TE was similar across the tACS conditions via an LME, with TE as dependent variable and Stimulation as independent variable.

We then assessed the behavioral effects of tACS via temporal clustering, acknowledging the BTT as time-series data. An LME was fitted per timepoint; Tracking Error Change_{ijklm} = β_1 Stimulation_{ij} + β_2 Block_{ik}

- + $\beta_3(Stimulation_{ij} \times Block_{ik})$
- + $\beta_4 Laterality_{il}$
- + $\beta_5(Stimulation_{ij} \times Laterality_{il})$
- + $\beta_6(Block_{ik} \times Laterality_{il})$
- $+ \beta_7 (Stimulation_{ij} \times Block_{ik} \times Laterality_{il})$
- $+ \beta_7$ Session_{im}

(6)

with laterality referring to whether both hands moved at the same speed ('iso'), or faster rotations were required with the left or right hand. The TFCE procedure and permutation testing were identical to Section 2.5.1.1. In **Appendix 4**, we examined tACS effects on mean TE Change per trial instead of per timepoint. This resembles how previous research analyzed the BTT.

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2.5.3. The link between β -band activity and bimanual motor performance

Our final analysis examined whether MR β D changes during motor planning and/or execution were related to motor control changes, providing mechanistic insights into the polymorphic nature of MR β D. We extracted the 10th percentile MR β D magnitude in C4 during motor planning and execution. The difference in peak MR β D from the offline block to baseline was computed, and an LME was fitted:

Tracking Error Change_{ijklm} =
$$\beta_1 \Delta$$
 peak MR β D_{planning, ij}
+ $\beta_2 \Delta$ peak MR β D_{execution, ik}
+ β_3 Stimulation_{il} + β_4 Session_{im} (7)

2.5.4. Assessing tACS blinding

Blinding effectiveness was assessed using the Chi-Squared test to determine whether participants' responses to the question of whether they believed they received verum, sham or were unsure, were independent of the administered tACS condition (Mangiafico, 2016).

3. Results

3.1. Study sample

Table 1 outlines general sample characteristics. In total, 8 % of the EEG data and 7.4 % of the BTT data were excluded due to tACS bridging (6.5 %) –identified by unstable and impedance values below 1 k Ω –, EEG data removal (0.6 %) due to too few epochs, and study-unrelated illness resulting in a drop-out after session 2 (0.9 %). No tACS side-effects occurred and all participants tolerated three sessions of tACS and sham well. A more thorough investigation of the subjective experiences following tACS is included in **Appendix 5**.

3.2. The effect of β -tACS on MR β D

Fig. 3 shows $MR\beta D$ across blocks and conditions. $MR\beta D$ during motor execution was consistent across blocks, while it emerged during motor planning from block 2 onward.

3.2.1. Local MR β D increases as a result of block and session

A temporal clustering analysis examined tACS effects on MR β D (Fig. 4A). Our findings concerning tACS were in the direction of our

Table 1Sample characteristics.

	Sample (n = 36)
Age (in years)	22.9 \pm 2.2 (Kasten and Herrmann, 2017– (Alayrangues et al., 2019)
Sex	20 women, 16 men
Edinburgh Handedness Inventory	89.6 ± 13.1 [60–100]
Head Circumference (mm)	55.8 \pm 1.5 [(Vergallito et al., 2022; Neri et al., 2020; Wischnewski et al., 2020; Oldfield, 1971; Oostenveld et al., 2011) 58]
Caffeine intake	
Last 24 h (units)	0.6 ± 0.9 [0-4]
Difference across sessions	0.3 ± 0.4 [0–1.6]
Sleep	
Last night (hours)	7.5 ± 1.1 (Wischnewski et al., 2023– (Wischnewski and Schutter, 2017)
Difference across sessions (hours)	$0.5 \pm 0.5 \; [0 - 2.75]$
Alcohol	
Last 24 h	$0.2 \pm 0.7 \; [0-5]$
Difference across sessions	$0.2 \pm 0.5 [0 - 2.22]$
Tobacco use (units)	
Last 24 h	$0 \pm 0 \ [0 - 0]$
Difference across	$0 \pm 0 [0 - 0]$

Mean \pm SD [minimum – maximum] are reported, for all continuous variables.

hypothesis, as mean MR β D during motor planning was enhanced in the fixed and individualized tACS conditions compared to sham. However, both this effect and the stimulation*block interaction were insignificant, as the TFCE value was below the 95th percentile of the null distribution.

Session affected MR β D, with the highest MR β D during both motor planning and execution in session 3, and the lowest in session 1, and differences between sessions 2 and 3 being minor. Three clusters were significant: a transient first cluster (-1072 to -963 ms, peak F_{2,191} = 4.120), followed by longer-lasting clusters 2 (-908 to 2147 ms, peak F_{2,191} = 17.401) and 3 (2225 to 4000 ms, peak F_{2,191} = 7.204).

MR β D increased from baseline to the offline block, during both motor planning and execution. Three clusters were significant: cluster 1 (-1752 to -1674 ms, peak F_{1,191} = 9.753 at -1705 ms), 2 (-1619 to -1533 ms, peak F_{1,191} = 10.168 at -1580 ms), and 3 (-861 ms to 4000 ms, F_{1,191} = 46.19 at 490 ms).

3.2.2. Broad MR β D increases as a result of block and session

Beyond local effects, we analyzed whole-sensor effects through spatiotemporal clustering. No tACS effects or interactions survived multiple comparison correction. Conversely, session and block significantly affected MR β D (Fig. 4B).

MR β D magnitude increased with sessions in the significant spatiotemporal sensors (Fig. 4**B**). The effect was more spatially pronounced during motor planning (Fig. 4**B**, upper left plot), particularly in the right frontocentral, central, centroparietal, and left medial-central sensors. During execution, sensors containing significant effects were mainly restricted to the left and right central sensors (Fig. 4**B**).

 $MR\beta D$ magnitude also increased from baseline to the offline block, with a more spatially extensive effect during motor planning compared to execution, particularly in the midline and right frontocentral, central and centroparietal sensors (Fig. 4B). Significant effects during execution were present in the left and right centroparietal sensors.

3.2.3. Stimulation and session affect the changes in MR β D from block 1 (baseline) to block 2 (online)

We also examined if $MR\beta D$ changes from baseline to the online block were influenced by tACS and session. This analysis focused only on the verum tACS conditions due to the potential impact of the artefact removal pipeline.

Overall, MR β D changes during motor planning from baseline to the online block were most pronounced for individualized tACS (Fig. 4C), with two significant transient clusters: cluster 1 (-1720 to -1705 ms; peak F_{1,60} = 6.0835) and 2 (-751 to -721 ms; peak F_{1,60} = 5.703). The TFCE full-time course of this effect is shown in **Appendix 6**. No significant stimulation effects were present during motor execution, with both groups showing no-to-marginal decreases in online MR β D compared to baseline.

Session also affected MR β D, with the most substantial enhancements from baseline to block 2 in session 1, followed by sessions 2 and 3. The pronounced changes in session 1 align with greater BTT improvements in this session (Section 3.3), supporting the hypothesis that MR β D during motor planning represents processes relevant to motor control. Eight significant session clusters were present (Fig. 4C, lower panel), the three largest being clusters 1 (-752 to -369 ms; peak F_{2,60} = 7.836), 2 (111 to 1787 ms; peak F_{2,60} = 12.027) and 3 (2170 to 2451 ms, peak F_{2,60} = 9.573).

3.3. Individualized β -tACS improves bimanual motor control

Baseline BTT performance was similar across conditions, as the LME found no significant effect of tACS condition ($F_{2,\ 268.42}=0.889,\ p=0.41$).

The temporal clustering analyses yielded significant effects of stimulation, block, laterality and session. However, no interaction effects between stimulation, block and/or laterality were significant, indicating that the effect of stimulation on tracking error did not differ across the





Fig. 4. Effect of tACS on MRβD. **A)** Local offline effects of stimulation (left), session (middle), and block (right) on MRβD in the target sensor, C4. Grey areas denote significance. There was no significant effect of stimulation type. Conversely, session and block affected MRβD, with increases over sessions and blocks. **B)** Global offline effects of session (left) and block (right) on MRβD, the upper plots show the percentage of time during which data in sensors significantly differed across conditions (sessions and blocks) during motor planning and execution. The lower plots show MRβD time course within the sensors with significantly different activity. Whole-sensor session and block effects resembled the local effects discussed in A). **C)** Local online effects of stimulation (upper) and session (lower) on MRβD in the target sensor, C4. Grey areas denote significance. More negative values indicate a greater increase in MRβD in the online block compared to baseline. Concerning stimulation, two transient clusters were significant, with MRβD during motor planning being slightly more enhanced in individualized vs. fixed tACS. The TFCE values associated to these clusters are also shown in Appendix 6. Concerning session, MRβD in the online block vs. baseline increased the most in session 1, and least in session 3.

online or offline block, different laterality conditions.

Stimulation affected TE change, with a significant cluster from 0.6 to 4 s (peak $F_{2,2342} = 18.721$) (Fig. 5). The greatest improvement in BTT performance was present in the individualized tACS condition (estimate = -0.53 ± 0.70), followed by sham (estimate = -0.46 ± 0.66) and fixed tACS (estimate = -0.40 ± 0.62). The traditional, mean-trial, analysis (cf., **Appendix 4**) corroborates this, with Tukey-corrected post-hoc tests showing significant differences between individualized and fixed tACS, and individualized and sham tACS.

The significant effect of block (peak $F_{1,2342}=91.126$) spanned from 0.2 to 4 s, with the improvement in TE with respect to block 1 being greatest in block 3 (estimate $=-0.57\pm0.73$), compared to block 2 (estimate $=-0.36\pm0.57$). However, when interpreting this effect, it is important to recognize that blocks 2 and 3 differed in duration (i.e., 10 versus 5 min). While the observed improvement in TE aligns with expectations, differences in block length may have influenced the magnitude of this effect.

Concerning laterality (peak F_{2,2342} = 31.192, p < 0.05), a cluster from 0.6 to 3 s was present. Improvement in this cluster was largest for the iso(estimate = -0.56 ± 0.86), left (estimate = -0.47 ± 0.54) and right conditions (estimate = -0.44 ± 0.51).

Concerning session (peak $F_{2,2342}=54.930, p<0.05$), a cluster from 2.2 to 4 s was retained. BTT improvement was greatest in session 1 (estimate = -0.70 ± 0.72), followed by session 2 (estimate = -0.50 ± 0.72) and 3 (estimate = -0.48 ± 0.73).

A post-hoc LME (TE Change \sim tACS FREQUENCY * BLOCK * LAT-ERALITY + SESSION) found no significant interaction or main effects of tACS frequency. This suggests that the effectiveness of individualized tACS was not due to stimulation at a fixed frequency that happened to be more effective than 20 Hz, but rather due to its individualized nature.

3.4. The link between β -band desynchronization and BTT performance

We investigated if changes in motor planning and/or execution



Fig. 5. Effect of stimulation, block, laterality and session on tracking error change per timepoint of the BTT task. Tracking error change denotes the change in tracking error relative to the baseline block. Grey areas denote significant timepoints (p < 0.05), colored areas denote 95 % confidence intervals.

 $MR\beta D$ from baseline to the offline block were related to TE changes, when controlling for the effects of stimulation and session.

Consistent with our hypotheses, we found a significant effect of change in MR β D during motor planning (F_{1, 86.088} = 18.721, p < 0.001) but not during motor execution (Fig. 6). Increased MR β D during motor planning from baseline to the offline block was associated to larger BTT improvements from baseline to the offline block. The covariate stimulation was also significant (F_{2, 62.501} = 4.057, p = 0.022), as discussed in Section 3.3.

3.5. tACS blinding effectiveness was limited

There was a significant association between STIMULATION TYPE and tACS beliefs ($\chi^2_4 = 14.391$, p = 0.006), with corrected comparisons



Fig. 6. The relationship between change in tracking error (TE) and motor planning MR β D from baseline to the offline block. Larger MR β D increases were associated to larger bimanual tracking task improvements.

revealing differences between fixed- and sham tACS (p = 0.045) and individualized and sham tACS (p = 0.016), but not between both verum tACS conditions (p < 0.05). While the number of participants believing that they received verum tACS was similar in fixed (58 %) and individualized (63 %) tACS, it was lower for sham (31 %). Conversely, identification as sham was highest in sham (41 %) compared to fixed (12 %) and individualized tACS (9 %). The number of participants uncertain whether they received verum or sham was similar across conditions: 30 % for fixed tACS, 28 % for individualized tACS, and 28 % for sham.

4. Discussion

The current work applied individualized-, fixed 20 Hz- and sham tACS in 36 healthy adults across three days while performing a continuous bimanual motor task. Our main findings are that individualized β -tACS improves bimanual motor performance, that MR β D magnitude is positively associated to bimanual motor control, and that individualized β -tACS seems to enhance online MR β D. Together, these results underscore the importance of personalizing tACS and the relevance of MR β D in motor control.

4.1. The functionally polymorphic nature of MR β D in motor control

MR β D has been described as functionally polymorphic, playing distinct roles during motor planning and execution. In motor planning, MR β D may reflect processes of somatosensory integration and preparation of motor commands (Blanco Mora et al., 2024; Alayrangues et al., 2019; Torrecillos et al., 2015), influenced by factors like motor complexity in interlimb tasks (S. Van Hoornweder et al., 2022; Alayrangues et al., 2019; Rueda-Delgado et al., 2019), directional uncertainty during reaching (Tzagarakis et al., 2010), and effector involvement in grasping (Zaepffel et al., 2013). Conversely, during motor execution, MR β D appears to represent more general motor processes, with findings suggesting insensitivity to motor complexity (S. Van Hoornweder et al., 2022), the speed-accuracy trade-off (Pastotter et al., 2012), and grasp type (Pistohl et al., 2012).

Here, we build on the hypothesis of MRBD's functional

polymorphism, as we found a positive association between MR β D and bimanual motor control during motor planning, but not execution. Moreover, MR β D during motor planning increased as participants became more proficient within and across sessions. The observed MR β D increase during motor execution seems to be driven by heightened MR β D during planning, as illustrated in Fig. 4. This concurs with our previous work, where increased MR β D during motor planning seemed to drive increased MR β D during execution (S. Van Hoornweder et al., 2022).

4.2. Individualized tACS enhances bimanual motor control and online $MR\beta D$

Research into the online effects of tACS on event-related perturbations is limited, primarily due to associated artefacts, especially at intensities such as 3 mA peak-to-peak. The few available studies indicate that tACS at lower intensities (around 1.5 mA) enhances event-related perturbations (Wischnewski and Schutter, 2017; Kasten et al., 2018; Kasten and Herrmann, 2017).

We demonstrate that individualized tACS increases online $MR\beta D$ during motor planning compared to fixed tACS. While a similar trend was observed offline for both individualized and fixed tACS, it was not statistically significant. Notably, individualized tACS improved bimanual motor control compared to sham and fixed tACS. This improvement was not explained by the absolute tACS frequency, supporting the idea that individualized tACS is more effective due to better alignment with participants' endogenous brain activity, consistent with the Arnold Tongue principle (Huang et al., 2021).

A theoretical framework for these findings combines said Arnold Tongue principle with recent computational models, which suggest that low-intensity tACS initially desynchronizes neural firing by disrupting endogenous synchronization, and only starts to induce net synchronization when intensity increases (Zhao et al., 2024). Given that we applied tACS at a low intensity (cf., Fig. 1D and (Zhao et al., 2024)), we may have caused this desynchronization effect. However, due to the baseline correction needed for artifact removal (Engel and Fries, 2010), it is impossible to untangle if our observed MR β D increases resulted from tACS desynchronization (cf., above) or merely reflect a need to cope with increased baseline β -activity as a result of tACS-induced entrainment. More invasive neuroimaging methods which can achieve higher signal-to-noise ratios should investigate this further.

Both tACS conditions appeared to slightly attenuate online MR β D during motor execution (Fig. 4C). As this effect occurred in both conditions, it is likely a result of the artifact removal pipeline, as SSP is known to attenuate neural signals with topographies similar to tACS artifacts (Vosskuhl et al., 2020). If so, this may suggest that the MR β D enhancement during motor planning could be stronger than indicated by the current results or that its topography differed from MR β D during motor execution and the tACS artefact, resulting in less pronounced attenuation due to SSP. Previous research showing distinct β -activity topographies before and after movement provides an argument in favor of the latter (Alayrangues et al., 2019).

The lack of significant offline tACS effects on MR β D may reflect the transient nature of tACS (Pozdniakov et al., 2021). However, offline neuroplasticity-like tACS effects are being increasingly recognized, with previous work showing an offline enhancement of α power following individualized tACS (Wischnewski et al., 2023; Kasten et al., 2016; Wischnewski et al., 2019). Such effects may have occurred in the current study, given that the behavioral effects of individualized tACS did persist, although they would imply that the MR β D did not represent them. Alternatively, data variability and/or the subtlety of post-stimulation effects may have limited detection of such effects. Given that mean offline MR β D trended in the hypothesized direction, this remains a plausible explanation.

4.3. Hemispheric asymmetry in $MR\beta D$

Although we did not directly compare tACS effects between hemispheres, our results concur with the notion that right sensorimotor regions are critical in complex motor control (S. Van Hoornweder et al., 2022; Rueda-Delgado et al., 2017; Gross et al., 2005; Houweling et al., 2008). While the left hemisphere is typically dominant from a movement point-of-view, the right hemisphere provides additional support when complexity increases (S. Van Hoornweder et al., 2022; Alayrangues et al., 2019; Verstraelen et al., 2021; Rueda-Delgado et al., 2017). When comparing MR β D across hemispheres, right sensorimotor MR^βD predicted motor control improvements best (Appendix 7). Likewise, for the global effects of block and session from baseline to the offline block (Section 3.2.2.), particularly during motor planning, data related to the right sensors were predominantly significant. These observations support the importance of the right sensorimotor regions in complex motor behaviors such as bimanual motor control. Consequently, these findings imply that while most β -tACS montages have focused on the left sensorimotor cortex (Wischnewski et al., 2019; Hu et al., 2022), the right sensorimotor cortex may be a viable future target.

4.4. Limitations

Several limitations should be considered. Applying tACS at 3 mA peak-to-peak, in line with (Wischnewski et al., 2019; Alekseichuk et al., 2022), posed challenges in removing tACS artifacts, as the intensity was higher than what is typically used in concurrent tACS-EEG studies. While we recovered genuine neural activity –the online data showed a similar session effect as the offline data, and a tACS effect consistent with our hypotheses–, the online data required more interpolation of channels of interest and was attenuated resulting in the need to separately analyze the offline and online data. Also, the lack of an online sham condition limits our interpretation of online tACS effects.

Another important limitation of the current study is the use of a crossover design with only a one-day washout period. We opted for a crossover design to control for interindividual variability in factors such as anatomy and genetics, ensuring that each participant served as their own control (Vergallito et al., 2022). The one-day washout period was chosen based on the assumption that tACS effects dissipate quickly, while also minimizing variability introduced by factors like hormonal fluctuations (Wischnewski et al., 2023; Vergallito et al., 2022). Although our counterbalanced design ensured that any potential carry-over effects did not systematically bias the results and thus did not compromise the validity of our main tACS findings, we acknowledge that extending the washout period or adopting a between-subjects design in future studies could further mitigate this concern. The latter approach would also help address the subsequent limitation, and seems particularly relevant with respect to motor skill learning.

A significant portion of participants correctly identified the type of tACS they received. This raises concerns about the effectiveness of blinding in tACS studies. While this does not affect the comparisons between fixed versus individualized tACS conditions, which is reassuring for our results, it implies that improvements in conventional sham protocols are needed. Shunting-based sham methods may enhance blinding and strengthen the rigor of future work (Neri et al., 2020).

Lastly, only participants were blinded due to the overtness of artefacts in the EEG data, and the need to individually set-up the tACS parameters in the individualized tACS condition. As the field of transcranial electrical stimulation in general transitions to increasingly individualized approaches, it is becoming increasingly important to consider how these personalized approaches can be effectively doubleblinded.

5. Conclusion

Individualized $\beta\text{-tACS}$ enhances bimanual motor control, with

significant behavioral improvements highlighting the value of personalized neuromodulation. Although the effects on MR β D were subtle and transient, the strong link between MR β D during motor planning and motor task improvements underscores its critical, polymorphic role in motor control. These findings pave the way for individualized tACS in neurorehabilitation, indicate that the right sensorimotor cortex is an interesting tACS target in light of motor control in right-handed individuals, and offer a framework for studying the role of event-related perturbations in neural oscillations in motor control and beyond.

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CRediT authorship contribution statement

Sybren Van Hoornweder: Writing - review & editing, Writing original draft, Visualization, Validation, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. Diego Andres Blanco Mora: Writing - review & editing, Validation, Supervision, Software, Methodology, Investigation, Conceptualization. Marten Nuyts: Writing - review & editing, Conceptualization. Koen Cuypers: Writing - review & editing, Resources, Funding acquisition. Stefanie Verstraelen: Writing - review & editing, Supervision, Project administration, Funding acquisition. Raf Meesen: Writing - review & editing, Supervision, Project administration, Funding acquisition, Conceptualization.

Declaration of competing interest

We formally declare to have no declarations of interest.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2025.121222.

Data availability

Data will be made available on request.

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