

Neuromodulation Special Issue

Midfrontal-occipital θ -tACS modulates cognitive conflicts related to bodily stimuli

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Abstract

Neurophysiological studies show that during tasks tapping cognitive control (like the flanker task), midfrontal theta (MF θ) oscillations are associated with conflict and error processing and neural top-down modulation of perceptual processing. What remains unknown is whether perceptual encoding of category-specific stimuli (e.g. body vs letters) used in flanker-like tasks is modulated by theta oscillations. To explore this issue, we delivered transcranial Alternating Current Stimulation (tACS) in the theta frequency band (6 Hz) over the medial frontal cortex (MFC) and the extra-striate body area (EBA), whereas healthy participants performed two variants of the classical flanker task, one with stimuli representing human hands (i.e. hand-flanker) and the other with stimuli representing coloured letters (i.e. letter-flanker). More specifically, we aimed at investigating whether θ -tACS involving a body-related area may modulate the long-range communication between neuronal populations underlying conflict monitoring and visuo-perceptual encoding of hand stimuli without affecting the conflict driven by letter stimuli. Results showed faster correct response times during θ -tACS in the hand-flanker compared with γ -tACS (40 Hz) and sham. Importantly, such an effect did not emerge in the letter-flanker. Our findings show that theta oscillations over midfrontal-occipital areas modulate bodily specific, stimulus content-driven aspects of cognitive control.

Key words: theta oscillations; transcranial alternating current stimulation (tACS); cognitive control; conflict monitoring; perceptual processing

Introduction

Coordinated neural systems are needed for optimizing the cognitive control through which one can process different levels of information and minimize occurrence of errors (Botvinick et al., 2001; Ullsperger and von Cramon, 2001). The mechanisms underpinning conflict and error monitoring are crucial for implementing the control that is needed when the activation of two or more representations compete and create a mismatch between the intended and actual responses (Holroyd and Coles,

2002; Yeung et al., 2004). Compelling evidence from electrophysiological studies confirm the presence of characteristic signals in the time (e.g. N2 and ERN) and the time-frequency (e.g. theta oscillations) domains recorded along the frontal electrodes (and indexing neural activity in frontal regions) that are associated with conflict processing, error detection and behavioural adaptation (Luu et al., 2004; Folstein et al., 2008; Cavanagh et al., 2012; Heil et al., 2000; Cohen and Donner, 2013a; Pavone et al., 2016; Pezzetta et al., 2018; Spinelli et al., 2018; Özkan et al., 2019). Con-

Received: 28 May 2020; Revised: 21 July 2020; Accepted: 8 September 2020

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conflict monitoring plays a pivotal role in making salient the need for top-down control. In particular, conflict monitoring allows to adjust the performance and minimize errors when the activation of task-relevant or irrelevant information induces response competition (Carter et al., 1998; Botvinick et al., 2001; Kerns et al., 2004; Yeung et al., 2004). One of the neuro-computational hubs orchestrating cognitive control is the medial frontal cortex (MFC), a higher-order region that interacts with neural systems involved in sensory, emotional, motivational and social processing to guarantee optimal goal-directed behaviours (Ridderinkhof et al., 2004). Recent studies show that oscillatory activity in theta band (θ) recorded over the MFC may represent an electro-cortical signature or biomarker of conflict and error processing that correlates with increased need for control (Cavanagh et al., 2012; Cohen and Donner, 2013a; Cohen, 2014). In turn, midfrontal theta (MF θ) appears related to the temporal dynamics of several brain areas reflecting the attempt to achieve top-down control through the synchronization of frontal structures (Nigbur et al., 2011; Cavanagh and Frank, 2014). Transcranial alternating current stimulation (tACS) studies suggest that delivering frequency-specific and low-amplitude sinusoidal current in the theta band over the frontal cortex may modulate cognitive and behavioural processing during tasks that require top-down control (Sela et al., 2012; Vosskuhl et al., 2015; van Driel et al., 2015; Chander et al., 2016; Wischniewski et al., 2016; Fusco et al., 2018; Lehr et al., 2019). tACS is an emerging, non-invasive brain stimulation (NIBS) technique that has the potential to influence the endogenous patterns of oscillatory activity in a frequency- and phase-dependent manner, by acting on the cortical networks that underpin behavioural performance (Antal and Walter, 2013; Tavakoli and Yun, 2017).

It is worth noting that theta rhythm is a widespread activity that may ground other top-down mechanisms in the domain of perception (Güntekin and Başar, 2014), memory (Backus et al., 2016), attention (Clayton et al., 2015), decision-making (Lin et al., 2018) and sensorimotor integration (Bland and Oddie, 2001). These results support the view that theta rhythm is a communication code widely used by different neuronal cortical populations and raise the issue about whether MF θ might be considered as a general electro-cortical signal evoked for requesting cognitive control or just epiphenomenal to complementary neural computations not exclusively related to conflict and error monitoring. Among the different NIBS techniques, tACS may represent the optimal one for testing apart one hypothesis from the other. Although the underlying mechanisms of its functioning are not completely clear (Thut et al., 2017), this technique may have the potential to modulate the endogenous activity of cortical areas involved in two related but distinct stages of information processing, like, for example, perceptual encoding and conflict monitoring that are both associated with oscillatory patterns in theta rhythm. A well-established experimental paradigm that easily elicits conflict is the classical Eriksen flanker task (Eriksen and Eriksen, 1974) where responses to a central letter are interfered when it is flanked by different ones. More specifically, each target stimulus is 'flanked' on each side by distractor stimuli that can be similar (congruent condition [CC]) or dissimilar (incongruent condition [IC]) to the target, thus creating a string of elements in which the target occupies the central position. The rapid co-activation of different response representations associated with the target and flankers processing may induce incorrect performance. Indeed, cognitive conflicts arise mostly during IC in which reaction times (RTs) are expected to be higher and the error rate lower rather than during CC (i.e. the flanker congruency effect) in which the activated representations are the same. The activation of

competing responses is not only reflected in the behavioural performance, but it also evokes MF θ (Cohen et al., 2008; Nigbur et al., 2012).

The flexible nature of the flanker task allowed scholars to employ stimuli with different degrees of visual complexity: from basic lines shaping arrows or letters (Miller, 1991; Nieuwenhuis et al., 2006) to more structured and sophisticated representations like faces and bodies (Mondloch et al., 2013; Petrucci and Pecchinenda, 2017; Oldrati et al., 2019). Interestingly, recent Electroencephalography (EEG) studies reported oscillatory synchronization in theta rhythm over the occipito-temporal electrodes corresponding to the extra-striate body area (EBA) contingent upon the simple presentation of hands images (Moreau et al., 2018, 2020a). EBA is a brain region located in the occipito-temporal cortex that is activated during static or dynamic images processing of body and body parts (Downing et al., 2001; Urgesi et al., 2004; Moro et al., 2008). When this area is stimulated with transcranial magnetic stimulation (TMS), the visual perception of body stimuli might be altered (Urgesi et al., 2004, 2007a, 2007b; Downing and Peelen, 2016; Gandolfo and Downing, 2019).

To explore whether θ -stimulation modulates conflict processing *per se* or also by acting on the type of stimulus used for creating a conflict, we developed a new version of the flanker task by using stimuli representing human hands or letters. In particular, we delivered tACS simultaneously over the MFC and EBA in neuro-typical participants who performed, in a balanced order and separate sessions, two variants of the task, namely the letter-flanker (LF) and the hand-flanker (HF). We reasoned that if the exogenous midfrontal oscillations lead to a generic modulation of conflict monitoring regardless the nature of the stimuli administered in the flanker, we would observe similar behavioural effects in both versions of the task. Alternatively, if θ -tACS improves neuronal computation of categorial-specific stimuli (i.e. the hands) during the early 'perceptual' and late 'conflict' stages of information processing and promotes the communication between MFC (conflict related) and EBA (body processing related), we would affect the behavioural performance selectively in the HF task. Specifically, we hypothesized that targeting a region involved in body processing may lead to a boosting of hands visual representation (i.e. target identification) and therefore, to an improvement of the response selection mechanism compared with the LF performance. Exploring the effects of alternating current injection may highlight the role of theta frequency in processing content-specific, body-related perceptual components of conflict monitoring and resolution.

Material and methods

Participants

Thirty-two healthy, right-handed participants (15 F; mean \pm SEM.; 25.84 \pm 0.74) took part in the study. None of the participants reported a history of epilepsy, implanted metal devices, neurological or psychiatric diseases and consumption of any medication. All participants had normal or corrected-to-normal visual acuity in both eyes and were naïve as to the purposes of the study. The experimental protocol was approved by the ethics committee of the Fondazione Santa Lucia and was carried out in accordance with the ethical standards of the 2013 Declaration of Helsinki. All participants gave their written informed consent to take part in the study.

Body- and non-body-related conflict tasks

Participants were asked to complete two modified versions of the flanker task (Eriksen and Eriksen, 1974), namely the HF and the LF. The tasks required participants to respond as accurately and as quickly as possible to central targets that were embedded in a string of distractors (i.e. flankers), by pressing one out of two possible buttons on the keyboard (the order of the two keys was counterbalanced across participants). The targets (palm or back of the hand for the HF, letters H or S for the LF) were flanked by two distractors on each side, which could be the same or different with respect to the target. The four possible target-distractor combinations produced two CCs and two ICs. To increase response conflict, the flankers appeared 100 ms before the onset of the central target. The full stimulus (100 ms flankers + 50 ms target) lasted 150 ms (see Figure 1). In both HF and LF, the stimuli could be coloured in pink or brown (Figure 1). Participants were required to answer only when the target stimulus had a specific colour (e.g. 'press the key on the left only when the back of the hand/ the letter S is pink and the key on the right when the palm of the hand/the letter H is brown'). The entire stimuli (visual angle of 9.31° horizontally and 2.32° vertically) appeared on a grey background of a 47×30 cm computer monitor. Participants were asked to respond in a time window of maximum 750 ms. When responses were given after 500 ms, a headphone beep sound warned participants to respond faster

in the subsequent trials. If participants failed to press the key during the available time, a visual feedback was provided on the screen, reporting the non-response (i.e. 'You did not answer'). A fixation cross was visible for 200 ms before the presentation of each stimulus (see Figure 1 for a timeline of each trial). To make more demanding the tasks, we added to the flanker trials (60 ICs and 60 CCs) 40 no-go flanker trials (20 CCs and 20 ICs). In the no-go flanker trials, participants were required to withhold the motor response when the central target differed from the instruction (e.g. a pink palm/H or a brown back/S). When participants pressed the response key in the no-go flanker trials, a 'false alarm' visual feedback was provided on the screen. A training session of 16 trials (6 CCs, 6 ICs, 2 CCs no-go flanker and 2 ICs no-go flanker) was administered before the experimental phase and could be repeated at most twice in case the instructions were not understood. The task was developed through E-prime 2.0 professional software (Psychology Software Tools Inc., Sharpsing, PA, USA).

Transcranial alternating current stimulation

Electrical sinusoidal current was delivered by means a rechargeable battery-operated system included in the Starstim device (Starstim/Enobio, Neuroelectronics, Barcelona, Spain) and controlled by a Bluetooth connection. Two circular sponge-

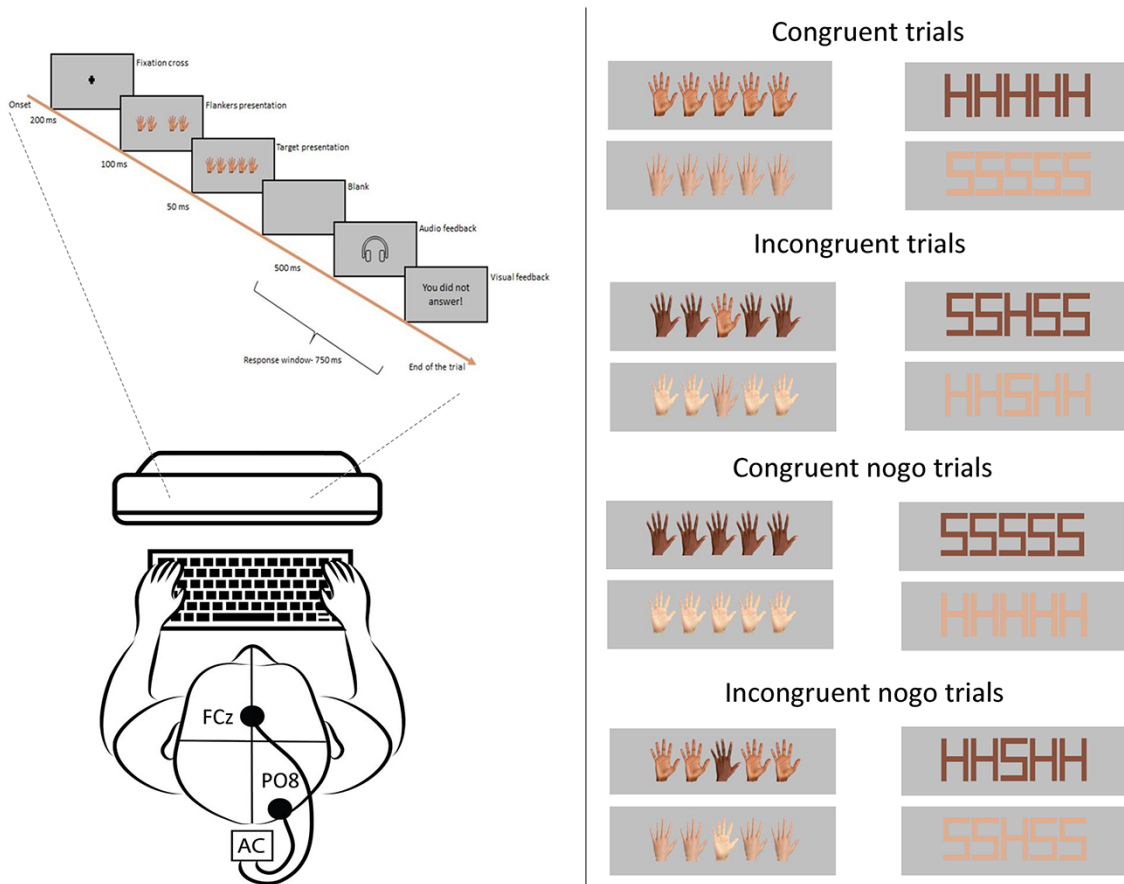


Fig. 1. Left panel: timeline of a representative trial and electrode montage for tACS (International 10–20 Standard System: FCz channel for the medial frontal cortex modulation and PO8 for the extra-striate body area modulation). Right panel: representation of the stimuli used in the two versions of the flanker task (left: hand-flanker; right: letter-flanker).

conductive-rubber electrodes (25 cm², Sponstim, Barcelona, Spain) soaked in physiological solution (NaCl) and connected via wires with the current deliver module, were fixed in an EEG-like cap. To maximize the impedance reduction and then the current flow passage through the scalp, a further electro-conductive gel was applied on both surfaces of the electrodes. One electrode was placed in correspondence of the MFC (FCz channel of the International 10–20 Standard system, Vosskuhl *et al.*, 2015; Fusco *et al.*, 2018), whereas the second electrode was positioned over the right EBA (PO8 channel of the International 10–20 Standard System, Taylor *et al.*, 2010; Moreau *et al.*, 2018, 2020a). The computational model of the electric field distribution (Realistic vOlumetric Approach to Simulate Transcranial Electric Stimulation [ROAST], Huang *et al.*, 2019) is shown in Figure 2. The electrical modulation was administered at 2000 μ A (peak-to-peak) intensity and at different frequencies adopted separately in the two sessions: 6 Hz for the theta band (θ , Cavanagh and Frank, 2014; Cohen, 2014) and 40 Hz, as a control frequency, for the gamma band (γ). The two frequency-tACS were delivered in two separate sessions, performed 5 to 7 days apart to reduce carry-over effects. For the sham stimulation, tACS was delivered for the first 30 s and then it was interrupted by the experimenter. The waveform of the current was sinusoidal without Direct current (DC) offset and 0° relative phase while the impedance was kept below 5 k Ω . The alternating current was applied throughout the behavioural task (\sim 3 min for each block, for a total of \sim 12 min of stimulation in each session) following 5 s of ramp-up and

lasted until the participants ended the task, when 5 s of ramp-down were provided. During the familiarization procedure, tACS was administered at 1000 μ A and at 13 Hz for 30 s. The alpha frequency was selected to induce visual percepts (e.g. flickering, flashing) and thus expose participants to subjective effects of tACS (Fertonani *et al.*, 2015; Fusco *et al.*, 2018) that could also be experienced in the experimental sessions (see Procedure).

Procedure

Prior to the experiment, participants were asked to read and complete the form detailing the criteria to be included in the tACS study (Antal *et al.*, 2017). The experimental sessions were conducted in a quiet, semi-dark room. Participants seated on a chair, 90 cm distant from the PC monitor, frontally set on a desk. First, in order to place the electrodes, the scalp was measured and FCz and PO8 localized, using the International 10–20 system and an EEG-cap. The defined area was cleaned with a cotton soaked in ethyl alcohol to reduce skin's resistance and then marked by a sign. The two electrodes were placed into the EEG-cap and then stabilized over the head of the participants. To familiarize with the sensations induced by tACS, a 30 s stimulation (including 5 s ramp-up and 5 s ramp-down) at intensity of 1000 μ A and frequency of 13 Hz was delivered to participants. Then, participants were required to start the training session. Half of the sample started with the

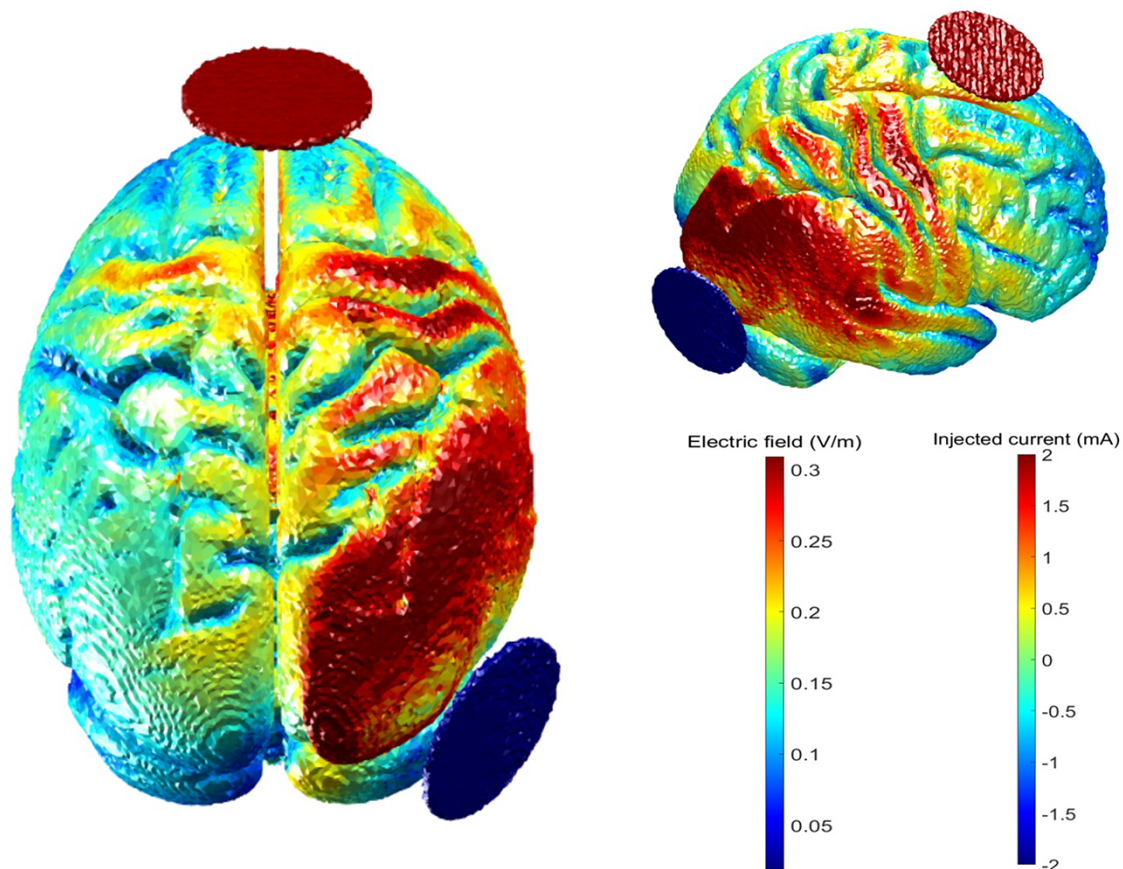


Fig. 2. Axial and lateral view of 3D cortical maps representing the electric field intensity distribution simulated through the open-source software: ROAST (<https://www.parralab.org/roast/>; Huang *et al.*, 2019). The computational model shows how the strength of the electric field is maximal (between 0.2 and 0.3 V/m) in correspondence of the right occipito-temporal cortex.

training session of HF and the other half with LF with the aim of counterbalancing the order of the two tasks. After familiarization with the stimuli, the experimental phase began. For each block, 160 stimuli (60 CCs, 60 ICs, 20 CCs no-go flanker and 20 ICs no-go flanker) were presented on the centre of a PC monitor following a random order. The target central stimulus corresponded to the central fixation cross presented at the beginning of each trial. In each session, tACS was delivered while participants performed three blocks of each version of the flanker task. Each block lasted around 3 min, with an inter-block interval of around 5 to 7 min. During the first and the last block of each session, the sham stimulation was performed. The other four blocks were administered at one of the two bands: half of the participants started with session in theta and half in gamma (the tACS sessions were counterbalanced across the participants). Moreover, at the end of each block, participants were asked to report any tACS-induced discomfort and any other sensation that might have occurred in the block. Previous studies highlighted that during electrical NIBS, perceptual and physical effects might occur due to the propagation of the current on the scalp, skin, retina and nerves (Fertonani et al., 2015; Fusco et al., 2018). In order to assess these sensations, participants were asked to rate on a 0 to 100 scale (where 0 represented no sensations at all and 100 a very strong sensation) the occurrence of: cutaneous sensations (itching, heating, tingling, burning and prickling); visual sensations (flickering, flashes and bright dots), taste sensations (metalling feeling in the mouth) and general physical feelings (fatigue, dizziness, head heaviness, nausea, headache and sleepiness). Although different scales are used to evaluate the subjective quality of the discomfort caused by transcranial electric stimulation (tES; see, for example, the questionnaire proposed by Fertonani et al., 2015), our procedure was developed to explore associations with the behavioural performance and control for possible attentional biases induced by the electrical neuro-modulation (see the Supplementary data for the raw data and analysis). Between the two sessions, participants were asked to fill out through an online procedure, questionnaires assessing affective processes that might have an influence on participants' conflict and error monitoring. Specifically, participants filled out the State Trait Anxiety Inventory form (STAI-Y, Spielberger, 2010), the Behavioural Inhibition and Activation Scales (BIS/BAS, Carver and White, 1994), the 16 items reduced form of the Need for Closure Scale (NCC, Roets and Van Hiel, 2011) and the Barratt Impulsiveness Scale (BIS-11, Barratt, 1959). At the end of the second session, participants were further required to perform a version of the Implicit Association Test (IAT; Greenwald et al., 2003) aimed at measuring possible implicit race bias that may have modulated response strategies during the HF (see Table 1 for raw data).

Data handling

Data normally distributed (Shapiro–Wilk test $P > 0.05$), were analysed by means Analyses of Variance (ANOVAs) for repeated measures in a 2 TASK (hands, letters) \times 3 BAND (theta, gamma, sham) \times 2 CONG (congruent, incongruent) factorial within-subject design. Main effects and significant interactions were further analysed with the Newman–Keuls (NK) *post hoc* test. Correlation analyses were computed through the Pearson product-moment correlation test (r^2). For data not normally distributed (Shapiro–Wilk test $P < 0.05$), a logarithmic (log10) transformation was applied. In the case the distribution remained not Gaussian, data were analysed by means the Friedman non-parametric ANOVA(s) for the within-group design. Significant effects were compared with the Wilcoxon Matched Pair Test. The

Table 1. Scales, Questionnaires and I.A.T. Sample raw data for (from left-to-right): the State-Trait Anxiety Inventory (STAI-trait, STAI-state); the Barratt Impulsiveness Scale (BIS-11); the Behavioural Inhibition and Activation Scales (BIS/BAS), the Need for Closure Scale (NCC). In the last column are reported the d' scores obtained from the Implicit Association Test (IAT).

Participants	STAI-trait	STAI-state	BIS11	BISBAS	NCC	IAT
1	47	51	58	62	50	0.32
2	31	51	57	55	47	0.32
3	35	52	56	47	48	0.13
4	49	48	63	56	51	-0.25
5	74	45	66	47	45	0.57
6	67	45	68	46	59	0.5
7	38	50	60	50	38	-0.07
8	58	51	69	44	43	0.2
9	33	48	48	52	49	0.81
10	33	48	60	50	30	0.41
11	30	56	70	56	51	-0.18
12	58	51	66	46	52	-0.09
13	37	44	48	48	33	0.4
14	62	49	72	52	42	0.2
15	57	51	48	52	43	0.59
16	38	49	51	62	55	0.24
17	50	41	50	38	51	0.41
18	43	52	53	49	54	0.61
19	49	47	64	46	40	0.62
20	36	50	62	41	63	0.84
21	45	48	65	48	52	0.23
22	43	47	79	48	60	0.94
23	50	51	60	51	45	0.23
24	51	54	55	46	60	0.7
25	35	48	59	53	41	0.7
26	40	54	54	62	54	0.19
27	33	46	66	48	66	0.66
28	29	53	43	55	46	0.42
29	30	48	63	36	45	0.8
30	41	50	47	55	39	0.64
31	28	50	52	49	58	0.86

Bonferroni correction was adopted for the planned within-group comparisons. One participant was excluded from all the analyses because of the poor performance in the HF task (more than ± 4.0 s.d. respect to the sample mean; accuracy for correct responses $< 27.5\%$). Therefore, the analysis was computed on 31 participants. The behavioural variables analysed in the study were: the RTs in correct trials (RTs in msec), the accuracy (percentage of correct responses), the RTs/accuracy ratio, the post-error slowing (PES) and the false alarms (% error rate and RTs). Since the RTs analysis of the flanker trials was crucial for the study, these results are reported below in the following section. Raw data and analyses of other variables are reported in the Supplementary data.

Results

Reaction times (msec)

Mean scores of RTs for the flanker correct trials were normally distributed. Values < 200 msec (0.97% of trials) were considered as automatic responses and were removed from the analysis together with the post-error RTs (i.e. the response times of correct trials that followed errors; in total 12.3% of trials). The ANOVA showed a main effect of CONG ($F(1,30) = 453.491$; $P < 0.001$; $\eta^2 = 0.937$). In particular, the CC produced faster

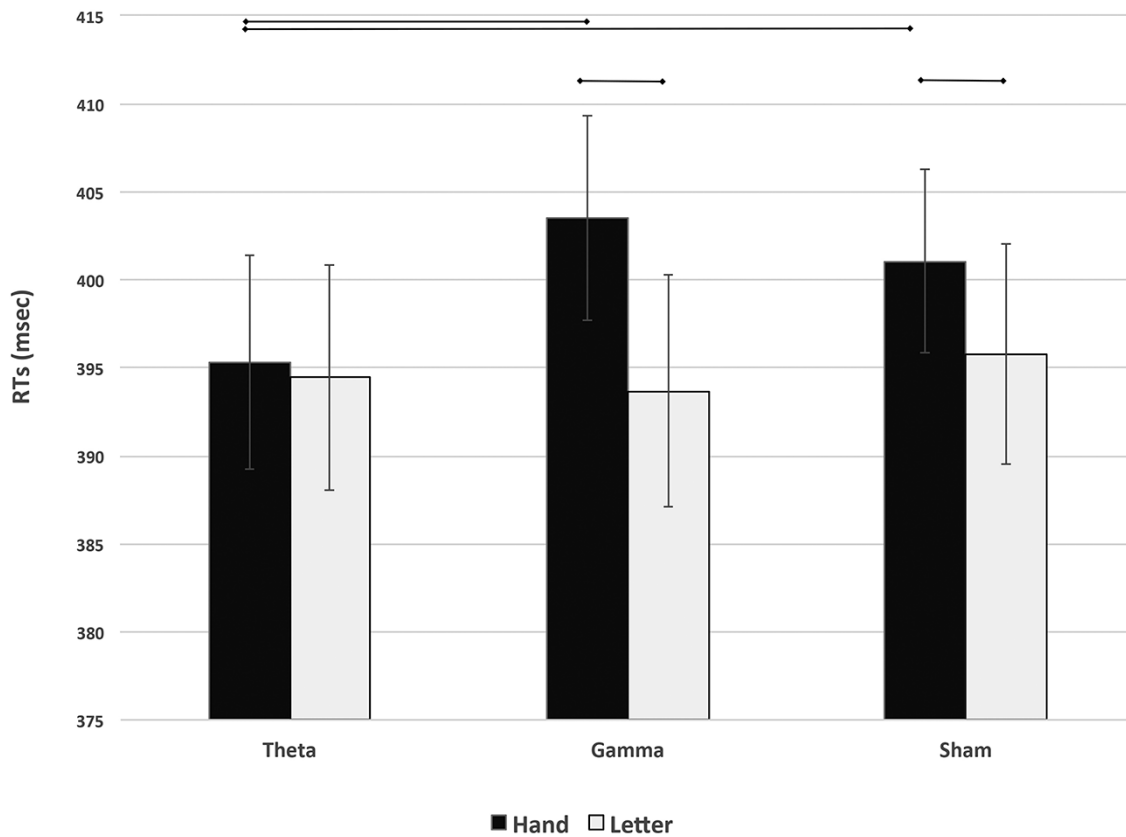


Fig. 3. Correct trials RTs (means) in the different tasks and frequency stimulation conditions. θ -tACS (6 Hz) significantly reduced the temporal responses in the hand-flanker compared with γ -tACS (40 Hz; $P = 0.005$) and sham ($P = 0.047$; Newman-Keuls *post hoc* comparisons, bars denote standard measurement errors).

responses (366.63 ± 2.64) compared with the IC (427.95 ± 2.70) regardless the different shape of stimuli presented in the tasks.

The significance of the $TASK \times CONG$ ($F(1,30) = 81.13$; $P < 0.001$; $\eta^2 = 0.730$) clearly showed the flanker congruency effect in both the versions of the flanker. Indeed, the interaction was accounted for by faster RTs in the CC of LF (357.82 ± 5.47) respect to the other conditions (incongruent LF: 431.46 ± 5.89 ; $P < 0.001$; congruent HF: 375.45 ± 6.25 ; $P < 0.001$; incongruent HF: 424.44 ± 6.35 ; $P < 0.001$). Similarly, the CC of the HF was significantly faster than the ICs of the HF ($P < 0.001$) and LF ($P < 0.001$). Moreover, the ICs of the two tasks resulted significantly different from each other ($P = 0.027$).

Importantly, the interaction $TASK \times BAND$ was significant ($F(2,60) = 3.626$; $P = 0.032$; $\eta^2 = 0.107$). The *post hoc* test indicates that during θ -tACS the response time in the HF was faster (395.31 ± 6.90) rather than during γ -tACS (403.50 ± 6.81 ; $P = 0.005$; Figure 3) and sham (401.03 ± 5.96 ; $P = 0.047$), which did not differ from each other ($P = 0.298$). In the LF task, θ -tACS, γ -tACS and sham did not result significantly different. The RTs recorded in the γ -tACS condition of the HF were significantly slower than in the γ -tACS (393.68 ± 6.25 ; $P < 0.002$) condition of the LF. In the same line, the RTs measured in the sham of the HF were significantly slower than in the sham (395.78 ± 5.59 ; $P = 0.029$) condition of the LF. In turn, while θ -tACS did not affect response time during the processing of letter stimuli, it clearly boosted the ability to process conflicting hand stimuli. Moreover, the *post hoc* analysis revealed that participants were significantly slower during γ -tACS and sham in performing the HF rather than LF, suggesting that processing the former requires higher

cognitive load with respect to the latter. No other main effects nor significant interactions were found.

Discussion

Performance monitoring is fundamentally important for optimizing behaviour in challenging environments. However, highly demanding actions that overload the computational systems for cognitive control (e.g. action selection under time-constrained circumstances) may in turn lead to behavioural errors. Here we delivered transcranial non-invasive band-specific electrical stimulation to modulate conflicting stimuli processing and neuronal computations during actions with different cognitive demands. Specifically, we applied tACS in participants performing two versions of the flanker tasks in which the congruent or incongruent stimuli could be letters or human hands. Alternating current in theta or gamma frequency were delivered over two cortical areas namely, the EBA involved in the perceptual processing of body-related stimuli and the MFC typically involved in conflict monitoring. Sham stimulation sessions were also used. Results indicate a selective theta-related improvement of the RTs associated with correct trials processing only in the hand version of the flanker. Importantly, faster responses indexed an improvement of performance as no change in speed-accuracy trade-off was found.

The functional activity of specialized neurons located within the MFC contribute to regulate the temporal dynamics of frontal structures by generating rhythmic oscillations in theta

frequency (i.e. the MF θ) during conflict monitoring and cognitive control processing (Cohen, 2014; Cavanagh and Frank, 2014; Töllner et al., 2017). Van Driel and colleagues (2015), for example, applied tACS either in theta or alpha individual frequency over the MFC while participants were required to perform a colour-location Simon task. The results showed a behavioural temporal slowing in responding to low-conflict trials during theta-tACS, suggesting that a modulation of conflict processing may have occurred (van Driel et al., 2015). In a previous study, we reported the effects of 6 Hz-tACS in modulating the behavioural performance during the LF (Fusco et al., 2018). Specifically, participants received alternating current over the MFC and medial parietal cortex (MPC). Different frequency for each oscillatory band (i.e. 2 Hz delta, 6 Hz theta, 11 Hz alpha, 21 Hz beta, 60 Hz gamma) and sham stimulation were delivered in six separate blocks. We found that only θ -tACS was able to speed up the temporal responses needed to process congruent trials following error execution (i.e. less PES) compared with the sham stimulation. Therefore, we speculate that cognitive control may have benefited from the exogenous theta alternating current, reflecting a possible improvement of the inter-regional communication between neuronal populations placed along the fronto-parietal network ultimately optimizing the behavioural adjustment (Fusco et al., 2018). It is worth noting that in resting-state conditions, 6 Hz-tACS is effective in modulating the functional connectivity (e.g. the reduced efficiency of the dorsal anterior cingulate cortex [dACC] to orchestrate signals in a hub-like manner) within the frontal networks following bilateral stimulation of the dorsolateral prefrontal cortices (DLPFCs; Onoda et al., 2017). When the DLPFC is stimulated during task performance, however, the electrical modulation seems to affect the interplay between frontal areas. Indeed, it has been reported that the application of high-definition tACS in theta frequency over the left DLPFC may alter the neural transmission with the dACC during the performance of a Stroop colour-word task causing a reduced Stroop effect (i.e. the different cognitive demand requested for responding to incongruent or congruent trials) in response time processing (Lehr et al., 2019). Although the above investigations varied in some methodological aspects (e.g. task, electrodes placement, tACS parameters, the stimulated brain areas) that may lead to heterogeneous outcomes, the administration of midfrontal θ -tACS seems to be an exploitable procedure to investigate the link between endogenous frontal theta rhythms and cognitive control processing. Moreover, in these studies (van Driel et al., 2015; Fusco et al., 2018; Lehr et al., 2019), the temporal dimension of behaviour was affected by tACS, suggesting that the exogenous alternating current in theta rhythm might have induced a computational advantage that facilitated information coding. Such a facilitation may partially explain the effect that we found during θ -tACS in which we observe a reduction of the RTs while participants processed hand conflicting stimuli. Compared with previous studies, however, we have adopted a bipolar montage placing one of the two stimulation electrodes over the right EBA, an occipito-temporal region that is specialized in processing body and body-related visual stimuli (Downing et al., 2001; Urgesi et al., 2007a; Downing and Peelen, 2016; Gandolfo and Downing, 2019). Interestingly, using EEG Moreau and collaborators (2018) showed that passive observation of categorical-specific stimuli (body vs plant parts), brought about an increase of theta synchronization under the electrodes corresponding to EBA that was selective for arm and hand images processing (Moreau et al., 2018). The same pattern

of results has been also confirmed in a subsequent EEG study during the performance of a matching-to-sample task. In their paradigm indeed, when hand images were presented to healthy participants, an increment of theta power was observed over the EBA region, leading the authors to postulate that theta rhythm might be a possible electro-cortical biomarker reflecting selective neuronal computations for the early encoding of hand-related representations (Moreau et al., 2020a). In turn, we speculate that in our study the endogenous modulation of EBA-related theta oscillations may have facilitated the processing of the perceptual properties of the hand stimuli thus contributing to improve the performance in the hand-driven rather than in the letter-driven conflict.

Midfrontal theta as a neural computational code for top-down perceptual modulation

Our theoretical assumption that while MFC may map conflict *per se*, EBA is more concerned with stimulus content-specific modulation remains somewhat speculative. We admit that one possible limitation of the present study is that we do not have conditions where EBA or MFC are modulated independently using tACS. It is worth noting that we did not find any θ -tACS-related significant modulation in the LF compared with γ -tACS or sham, and therefore, we cannot support the view that MF θ tACS was sufficient to modulate the processing of letter conflicting representations. However, our pattern of results may suggest that EBA-related theta oscillations may represent a necessary condition for the conflict resolution. One may submit that θ -tACS may have induced only a facilitation of the visual processing of the hand stimuli properties. However, we did not observe any other behavioural index of performance (e.g. PES or false alarms) that benefited from a better visual recognition of hand stimuli during the HF task. Unfortunately, we do not have data to suggest that tACS over the areas more concerned with letter processing, like, for example, the left angular gyrus (Seghier, 2013), may modulate the performance more in LF than in the HF tasks. Perhaps, it would be interesting to test this hypothesis in future studies.

It is also worth noting that a recent review questioned the effectiveness of θ -tACS in affecting visual perception following occipital modulation, highlighting a specific influence of the exogenous current in modulating auditory perception (Cabral-Calderin et al., 2020). Here, as a potential explanation of the results, we hypothesize that θ -tACS, rather than affecting the activity of neuronal populations underlying either MFC or EBA, might modulate the informational exchange between these two distal and functionally different cortical areas that, however, were both called into play during task performance. It may be relevant that previous studies showed an increment of the fronto-occipital connectivity in tasks requiring top-down control (Pessoa et al., 2003; Scerif et al., 2006; Bressler et al., 2008; Paneri and Gregoriou, 2017; Moreau et al., 2020b). In a functional Magnetic Resonance Imaging (fMRI) study, for example, Egner and Hirsch (2005) investigated the role of the extra-striate fusiform face area (FFA) in processing visual face stimuli during a variant of the Stroop task and reported an enhanced functional connectivity between this region and the DLPFC especially under higher control conditions (Egner and Hirsch, 2005). In a similar vein Cohen and colleagues (2009) recorded the oscillatory cortical activity while participants were asked to perform a revised Go-No Go paradigm and found a stronger synchronization

mediated by low-frequency oscillations between the frontal-medial and occipital electrodes following error execution. The authors hypothesised that one important mechanism by which the MFC adjusts the online performance is that of biasing top-down signals towards a specific sensory area so as to favour the processing of task-relevant information (Cohen et al., 2009). Notably, follow-up EEG results confirmed theta directed synchrony from MFC towards the occipital cortex as a possible top-down regulating mechanism of perceptual processing (Cohen and Van Gaal, 2013b). It is in principle possible to submit that the modulation of task-related theta oscillations found in our study may be due to modulation of long-range communications between EBA and MFC that lead to improved processing of visual body-related stimuli and ultimately to facilitated information processing during conflict monitoring. We also speculated that the entire process might be due to feed-forward mechanisms during cognitive control (Basso and Belardinelli, 2006). However, only specific tACS protocols adopting three or more electrodes may have the potential to explore the neuronal computation underlying the interplay between cortical areas through manipulations of the alternating current phase (see, for example, in-phase and anti-phase tACS studies, Polanía et al., 2015; Tseng et al., 2018). Unfortunately, because of the lack of any EEG recording we cannot provide any direct evidence about changes in the communication between EBA and MFC. Future neurophysiological and behavioural studies are needed to explore the neural mechanisms underlying the effects of θ -tACS on the endogenous cortical activity.

Conclusion

Within the family of NIBS techniques, tES are gaining momentum in neuroscience and clinical neurophysiology for they seem to highlight the causal relationship between physiological and cognitive processes and the functioning of specific brain areas (Paulus, 2011). Within the tES family, tACS is the one that is attracting special attention for its peculiarity to interact with the endogenous oscillatory activity and thus influence neuronal membrane potentials depending on its frequency and phase (Antal and Walter, 2013). By applying tACS in theta frequency over the fronto-occipital network, we have been able to affect two interactive processes relying on theta oscillations (i.e. conflict monitoring and perceptual processing) and fundamental to achieve optimal performance in a flanker-like task. We observed that θ -tACS over the MFC and the EBA modulated top-down control and improved the temporal ability to solve conflicts driven by hand rather than letter stimuli. Importantly, understanding the role of theta oscillations in modulating the visuo-perceptual components of conflicting body-related representations may have translational impact for clinical conditions characterized by dysfunctions of bodily perception and representation (e.g. anorexia nervosa).

Funding

Ministero della Salute (Ricerca Corrente 2020) and Ministero dell'Università e della Ricerca, PRIN grants (Progetti di Ricerca di Rilevante Interesse Nazionale, Edit. 2017, Prot. 2017N7WCLP) awarded to SMA.

Supplementary data

Supplementary data are available at SCAN online.

Conflict of interest

The authors certify that they have no affiliations with or involvement in any organization or entity with any financial interest in the subject matter or materials discussed in this manuscript.

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