Abstract

Neurophysiological evidence suggests that face and object recognition relies on the coordinated activity of neural populations (i.e., neural oscillations) in the gamma-band range (> 30 Hz) over the occipito-temporal cortex. To test the causal effect of gamma-band oscillations on face and object perception we applied transcranial Alternating Current Stimulation (tACS) in healthy volunteers (N = 60). In this single-blind, sham-controlled study, we examined whether the administration of offline tACS at gamma-frequency (40 Hz) over the right occipital cortex enhances performance of perception and memory of face and object stimuli. We hypothesized that gamma tACS would enhance the perception of both categories of visual stimuli. Results, in line with our hypothesis, show that 40 Hz tACS enhanced both face and object perception. This effect is process-specific (i.e., it does not affect memory), frequency-specific (i.e., stimulation at 5 Hz did not cause any behavioural change), and site-specific (i.e., stimulation of the sensory-motor cortex did not affect performance). Our findings show that high-frequency tACS modulates human visual perception, and it is in line with neurophysiological studies showing that the perception of visual stimuli (i.e., faces and objects) is mediated by oscillations in the gamma-band range. Furthermore, this study adds insight about the design of effective neuromodulation protocols that might have implications for interventions in clinical settings.

Keywords: face perception, object perception, face memory, object memory, tACS, neuromodulation

1. Introduction

Human cognition is mediated by the coordinated activity of neural ensembles (i.e., neural oscillations) (Fries, 2005; Uhlhaas & Singer, 2010) that oscillate at different frequencies, spanning from ‘slow-’ (e.g., theta-band oscillations – 4-7 Hz) to ‘high frequency-’ oscillations (e.g., gamma-band oscillations – > 30 Hz) (Buzsaki & Draguhn, 2004). In humans, neural oscillations can be non-invasively recorded via techniques such as electroencephalography (EEG) and magnetoencephalography (MEG), which are sensitive to electric (EEG) or neuromagnetic (MEG) fields generated by neuronal population activity (Buzsaki, Anastassiou, & Koch, 2012; Rivolta et al., 2015). Although there is no evidence for a direct (and strict) correspondence between a spectral band and a specific cognitive skill (Tallon-Boudry, 2009), it is suggested that visual perception is critically mediated by activity in the gamma-band range. For instance, the perception of human faces leads to an enhancement of M/EEG occipito-temporal gamma-band activity (i.e., > 30 Hz), as compared to perception of non-facial stimuli in an oddball paradigm (Gao et al., 2012; Zion-Golumbic & Bentin, 2007; Zion-Golumbic, Golan, Anaki, & Bentin, 2008). This has been related to the potential role of high-frequency oscillations in (face-specific) holistic processing (Anaki, Zion-Golumbic, & Bentin, 2007; Lachaux et al., 2005; Uono et al., 2017), which refers to the ability to perceive faces as a whole rather than the sum of individual features (e.g., eyes, nose, mouth) (McKone & Yovel, 2009; Palermo et al., 2011) (see, however, Bonemei, Costantino, Battistel, & Rivolta, 2018 for a discussion on the face-selectivity of holistic processing).

Brain oscillations are not epiphenomena, since their pharmacological manipulation in animals (Pinault, 2008) and humans (Grent-'t-Jong et al., 2018; Rivolta et al., 2015) causes cognitive and behavioural deficits. In addition, brain oscillations recorded in extrastriate areas (i.e., the fusiform gyrus) have been shown to be reduced during face perception in congenital prosopagnosia (Dobel, Junghöfer, & Gruber, 2011), which is the lifelong impairment of recognising people by their face (Behrmann & Avidan, 2005; Duchaine, 2000; Rivolta, Palermo, Schmalzl, & Coltheart, 2012), and in neurodevelopmental conditions such as autism (Sun et al., 2012) and schizophrenia (Gruetzner et al., 2013). Thus, given the importance of brain oscillations for typical cognition (Uhlhaas & Singer, 2012), the non-invasive modulation of human high-frequency oscillatory activity might be suited to target difficulties in visual cognition.

Neural oscillations can be entrained by the use of a particular form of neuromodulation technique called *transcranial alternating current stimulation* (tACS) (Cabral-Calderin & Wilke, 2019; Polania, Nitsche, & Ruff, 2018). By producing periodic (i.e., sinusoidal) changes of cortical excitability over time with a specific frequency, tACS offers the potential advantage of providing a direct modulation (i.e., entrainment) of ongoing oscillatory brain activity known to be associated with the cognitive process under investigation (Antal & Herrmann, 2016; Herrmann, Rach, Neuling, & Struber, 2013; Polania, Nitsche, & Paulus, 2012). A growing body of evidence shows the efficacy of tACS in the modulation of short-term memory (Feurra, Galli, Pavone, Rossi, & Rossi, 2016), working memory (Polania, Paulus, & Nitsche, 2012) decision making (Yaple et al., 2017), contrast perception (Laczo, Antal, Niebergall, Treue, & Paulus, 2012), fluid intelligence (Santarnecchi et al., 2013), and other cognitive functions (see Schutter & Wischnewski, 2016 for a meta-analysis).

It is known that human face processing relies on a network of cortical and subcortical regions (Haxby, Hoffman, & Gobbini, 2000). In particular, critical areas for face identification are in lateral occipital (i.e., occipital face area – OFA) and fusiform (i.e., fusiform face area – FFA) areas; especially in the right hemisphere (Kanwisher, 2010; Kanwisher, McDermott, & Chun, 1997; Rivolta et al., 2014). Only one tACS study has been performed with respect to face perception so far; results demonstrated an effect of occipital 40 Hz occipital tACS on the recognition of the facial emotion of anger, but did not report an effect on face perception (i.e., identification) skills (Janik, Rezlescu, & Banissy, 2015). This lack of tACS effect on face perception is surprising given the relevance of occipito-temporal gamma-band activity in this cognitive ability (Gao et al., 2012; Zion-Golumbic et al., 2008). Thus, in the present study we targeted the human right occipito-temporal cortex (PO8) with *offline* 40 Hz tACS (i.e., before participants completed face and object perception tasks). Offline tACS has been shown to entrain both slow (Jausovec, Jausovec, & Pahor, 2014; Kasten & Herrmann, 2017; Neuling, Rach, & Herrmann, 2013) and fast (Wischnewski et al., 2018) oscillations (as recorded with electroencephalography, EEG)[1]. We chose offline tACS to avoid potential phosphenes due to tACS on the visual cortex. Furthermore, the choice of offline stimulation might be also informative for the design of rehabilitation protocols. PO8 as target region has been chosen since it allows stimulating face-sensitive regions such as the OFA (and possibly also FFA; see Methods section below). In addition, our previous neuromodulation work with transcranial direct current stimulation (tDCS) (Barbieri et al., 2016) has shown the relevance of PO8 for face (and object) processing.

We included an active control condition with 5Hz tACS and, to ascertain site-specificity of 40 Hz tACS, a control sensory-motor (Cz_40Hz_tACS) condition. Finally, to ascertain whether the potential effect was process specific (i.e., restricted to perceptual processes), we also included memory tasks (for both faces and object stimuli). We hypothesized that only 40Hz tACS would lead to behavioural enhancement, and that this enhancement would be face-specific. In addition, given the relevance of posterior gamma band activity for face perception, we expected the effect to be process (i.e., perception) specific.

2. Materials and Methods

2.1 Participants

Sixty participants (30 females) without any history of psychiatric or neurological disorder and with a mean age of 32.22 years (SD: 7.96; range 18 – 47) participated in this single-blind, sham

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[1] Albeit the offline effects of gamma-band tACS is still largely unexplored

controlled study. Participants were selected if they fulfilled the criteria of: (1) no history or evidence of chronic or residual neurological disease (2) no metal implants in the neck or head area or pacemakers (3) no intracerebral ischemia or history of bleeding, epilepsy, head injury (4) no serious medical conditions, pregnancy or psychiatric illness (5) no alcohol, or drug addiction or participation in a study involving drug intake within the last month, (6) normal or corrected-to normal vision, and (7) at least the last 5 years spent living in the UK.

All participants had normal or correct-to-normal vision and did not report everyday life problems with face and object perception. The study was performed in accordance with The Code of Ethics of the World Medical Association (Declaration of Helsinki) for experiments involving humans and approved by the Ethical Committee of University of East London (UEL). After giving a complete description of the study to the participants, written informed consent was obtained and participants were provided with written information about the study and the procedure.

2.2 Experimental design

Participants were assigned to one of four groups (partial replication from Barbieri et al., 2016): Group-1 ("sham"; N = 16) received fronto-occipital sham stimulation, Group-2 ("5Hz_tACS"; N = 16) received fronto-occipital tACS at theta frequency (5 Hz), "Group-3" ("40Hz_tACS"; N = 16) received fronto-occipital tACS at gamma frequency (40 Hz), and "Group-4" ("Cz_40Hz_tACS"; N = 12) received fronto-Cz tACS at gamma frequency (40 Hz) (Table 1) (see next section for the description of the stimulation protocol). Given that it has been indicated that females show similar cortical excitability to males only during the follicular phase of the menstrual cycle (i.e., progesterone levels are low and oestrogen levels are high) (Inghilleri et al., 2004), we tested female participants only during this phase (see Fertonani, Pirulli, & Miniussi, 2011 for a similar approach). As in Costantino et al. (2017), participants from all three groups performed four tasks: the face perception task (FP), the object perception task (OP), the Cambridge Face Memory Task (CFMT) and the Cambridge Car Memory Task (CCMT). Both the perception and the memory tasks had identical structures for face and object presentation and a similar level of difficulty. All tasks were run on Windows and were administered on a DELL desktop computer with a 17-inch monitor with 1152 x 864 pixels resolution.

In the *Face Perception Task* (FP) (adapted from Barense, Henson, & Graham, 2011), three grayscale images of unfamiliar human faces were presented in each trial. Two of the images were of the same face taken from different angles, whereas the third one belonged to a different face (Figure 1, left). Participants were required to select the face that was different from the other two by pressing a key. In total, 81 trials were presented. For each trial, participants had a time limit of 4 seconds to make a decision (and thus press the button corresponding to the odd face). Accuracy and reaction times (RTs) were recorded. The *Object Perception task* (OP) (adapted from Barense et al., 2011) had the same structure of the FP but objects, rather than faces, were shown (see Figure 1, right). Both the FP and OP were run using E-prime software (Psychology Software Tools, Pittsburgh, PA). The presentation order of the four tasks was counterbalanced across participants.

The *Cambridge Face Memory task* (CFMT; Duchaine & Nakayama, 2006) is a memory task for unfamiliar faces which requires learning of six faces to be recognised in three different viewing conditions: recognition of the same face images; recognition of the same faces in different images (different viewpoint and/or lighting), and recognition of the same faces in different images covered with heavy visual noise. The task is comprised of 72 trials and accuracy (% correct) was recorded. The *Cambridge Car Memory task* (CCMT; Dennett et al., 2011) is identical in structure to the CFMT, but uses cars rather than faces as stimuli. The four experimental tasks were presented in a counterbalanced order, and they took around 45 minutes to complete.

To check for unexpected a priori between-group differences, participants completed the Cambridge Face Perception Test *before* the tACS setup (CFPT; Duchaine, Germine, & Nakayama, 2007). The CFPT involves arranging a set of six faces from the most similar to the least similar relative to a target face. Performance (i.e., number of deviations from the correct sequence) was recorded as a baseline measure of face processing (Figure 1).

2.2.2 tACS

TACS was delivered by a battery driven, constant current stimulator (Neuroelectrics®, Barcelona, Spain) via a pair of surface sponge electrodes (25 cm^2), soaked in saline solution (0.9% NaCl), and applied to the scalp at the target areas of stimulation. Electrodes delivered a constant current of 1.5 mA (peak to peak; current density: 0.080 mA/cm^2). Participants received offline stimulation; that is, tACS (or sham) was applied for 20 minutes *before* any task execution. We chose offline stimulation to be consistent with our previous tDCS work, and because there is evidence for offline tACS effects (Kasten & Herrmann, 2017; Pahor & Jausovec, 2017; Wischnewski et al., 2018). In addition, offline effects have strong clinical relevance since it is important that the behavioural effects outlast the intervention.

We adopted a bilateral bipolar-non balanced montage (Nasseri, Nitsche, & Ekhtiari, 2015). The sites of stimulation were identified using the International 10-20 EEG system, with one of the electrodes placed over PO8 and the other over FP1 (see Willis et al., 2019). The choice of the electrode target site over PO8 was based on prior work which showed that, when using electroencephalography (EEG), the PO8 site ideally records the N170, which strongly reflects face perception-related neural activity within the ventral visual cortex (Navajas, Ahmadi, & Quian Quiroga, 2013; Prieto, Caharel, Henson, & Rossion, 2011). Furthermore, PO8 lies above face- and object- sensitive regions in the right lateral occipital cortex (Gauthier et al., 2000; Malach et al., 1995; Pitcher, Charles, Devlin, Walsh, & Duchaine, 2009; Rivolta et al., 2014). In contrast, no specific face/object-relevant neurophysiological activity is typically recorded under FP1. Overall, the choice of our parameters of stimulation is in line with recent evidence demonstrating beneficiary (cognitive) effects of anterior-posterior tACS montages at >1 mA intensities (Schutter & Wischnewski, 2016).

2.2.3 Statistical analysis

All analyses were conducted using SPSS Statistics software (IBM Corp. Released 2013. IBM SPSS Statistics for Windows, Version 22.0. Armonk, NY: IBM Corp). A one-way ANOVA was conducted to test for potential baseline (i.e., CFPT) between group differences. Two separate 2x4 mixed analyses of variance (ANOVAs) were performed on accuracy scores, with the factors condition (sham, 5Hz_tACS, 40Hz_tACS, Cz_40Hz_tACS) as the between-group factor, and task (perceptual [FP, OP]; and memory [CFMT, CCMT]) as the within group factor. Post-hoc comparisons (Bonferroni-corrected Student´s t-tests) were performed to explore statistically significant main effects and interactions.

3. Results

In this between-subject design, each participant attended only one testing session, which lasted for about 1.5 hours. The participants did not report any discomfort during the three sessions. In addition, participants across the four groups did not differ in their performance on the CFPT [F(3, 59) = 0.31, p = .82, $\eta_P^2 = .00$], thus suggesting an absence of baseline differences across groups.

The ANOVA conducted for the perception tasks revealed a main effect of condition [F(3, 56) = 10.47, p < .001, $\eta_P^2 = .37$], with post-hoc comparisons showing that, with respect to sham (mean = 68%, SEM = 0.014), only the 40Hz_tACS condition (mean = 77.9%, SEM = 0.014) was characterised by enhanced performance (p < .001). There were no differences between sham and 5Hz-tACS (mean = 71.5%, SEM = 0.014, $p = .49$) and between sham and Cz_40Hz_tACS (mean = 68.3%, SEM = 0.016, $p = 1.0$) conditions. In addition, 40Hz_tACS was characterised by higher performance than Cz_40Hz_tACS ($p = .012$). There was also a main effect of task [$F(1, 56) = 9.88$, $p = .003$, $\eta_P^2 = .37$], indicating higher FP (mean = 73.4%; SEM = 0.01) than OP (mean = 69.5%; SEM = 0.010) performance. The condition x task interaction however was not statistically significant [$F(3, 56) = 0.76$, $p = .53$, $\eta_P^2 = .03$] (Figure 2).

The ANOVA conducted on the memory tasks showed a main effect of task [$F(1, 56) = 8.32$, $p = .006$, $\eta_P^2 = 0.014$], with CFMT (mean = 73.3%; SEM = 0.03) showing better performance than CCMT (mean = 67.8%; SEM = 0.014). The main effect of condition [$F(3, 56) = 1.62$, $p = .20$, $\eta_P^2 = .09$], and the condition by task interaction [$F(3, 56) = 0.63$, $p = .60$, $\eta_P^2 = .03$] were not statistically significant.

Overall, these results demonstrate that, with respect to sham, only the entrainment of gamma oscillations enhanced the perception (but not memory) of both faces and objects, thus indicating the frequency-specificity of this effect. In addition, these results demonstrate that the effect of 40Hz_tACS was site specific (i.e., right occipital).

5. Discussion

In the present study we demonstrate for the first time that a single session of (left) fronto-(right) occipital gamma-band (40 Hz) tACS can enhance face and object perception. The effect was “frequency-specific”, that is tACS in theta band (5 Hz) did not modulate behaviour, and “process-specific” (memory was not affected). Furthermore, the effect was “site-specific” since it was caused by right occipital stimulation (i.e., the fronto-Cz setup did not alter perception). These results confirm that tACS can be adopted as a powerful brain stimulation technique capable of interacting with ongoing brain activity and producing tangible behavioural outcomes.

Gamma activity in the lateral occipital cortex enhances visual perception

Human face recognition relies on a network of cortical and subcortical brain regions (Haxby et al., 2000). Over the last decade non-invasive brain stimulation techniques such as transcranial magnetic stimulation (TMS) (Pitcher, Walsh, Yovel, & Duchaine, 2007), transcranial random noise stimulation (tRNS) (Romanska, Rezlescu, Susilo, Duchaine, & Banissy, 2015) and transcranial direct current stimulation (tDCS) (Barbieri, Negrini, Nitsche, & Rivolta, 2016) demonstrated the causal involvement of the human lateral occipital cortex in face-perception skills. In line with this evidence and with EEG/MEG data showing occipital gamma activity during face perception (Gao et al., 2012; Zion-Golumbic et al., 2008), our findings suggest that a single offline session of occipital 40 Hz tACS enhances face perception skills in healthy individuals.

Although previous M/EEG work shows higher gamma-band activity for faces than for objects (Matsuzaki, Schwarzlose, Nishida, Ofen, & Asano, 2015; Zion-Golumbic et al., 2008), also object perception correlates with gamma band activity (Goffaux, Mouraux, Desmet, & Rossion, 2004; Martinovic, Gruber, & Muller, 2007; Tallon-Baudry, Bertrand, Delpuech, & Permier, 1997). This might suggest that gamma-band activity plays a critical role in the general construction of coherent representations based on the integration of visual information (Singer, 2011; Tallon-Baudry, 2009), and explains that 40 Hz tACS, as conducted in the present study, affected both categories of visual stimuli, which are represented in the lateral occipital cortex (Dilks, Julian, Paunov, & Kanwisher, 2013; Grill-Spector, Kourtzi, & Kanwisher, 2001; Pitcher et al., 2009; Rivolta, Palermo, Schmalzl, & Williams, 2012). Since electrophysiological recordings have also demonstrated modulation of gamma-band activity by attention (Engell &

McCarthy, 2010; Fries, Reynolds, Rorie, & Desimone, 2001), a further potential explanation for the present results is that the 40 Hz tACS driven enhancement of both face and object perception is due to a more unspecific mechanism of enhanced attention. Future studies using bimodal tACS-M/EEG recording (Herring, Esterer, Marshall, Jensen, & Bergmann, 2019) could, for instance, clarify the neurophysiological mechanisms behind the behavioural effect we demonstrated in larger detail.

TACS did not affect performance on memory tasks (both faces and objects). Previous M/EEG studies indicate that memory (and learning) is strongly mediated by theta activity (Gruber & Muller, 2006; Lisman & Idiart, 1995), especially in the hippocampus (Burgess & Gruzelier, 1997; Buzsaki & Draguhn, 2004). It is thus likely that the reason for the lack of significant effects of gamma (and theta) tACS on memory in the present study is that memory mostly relies on activity in brain regions which were not targeted by our stimulation protocol.

Online vs. offline effects of tACS: what works better?

The design of an effective intervention protocol should consider various variables, such as the timing of stimulation (i.e., offline vs. online). Many studies using other neuromodulation techniques such as transcranial direct current stimulation (tDCS) underline a preferential cognitive effect of *offline* stimulation on behavioural inhibition (Ditye, Jacobson, Walsh, & Lavidor, 2012), orientation discrimination (Pirulli, Fertonani, & Miniussi, 2013) and face perception/memory (Barbieri et al., 2016). The literature on tACS varies, with positive *online* tACS effects shown, amongst others, on mental rotation (Kasten & Herrmann, 2017), working memory (Polania, Nitsche, et al., 2012) and facial emotion perception (Janik et al., 2015), and *offline* tACS enhancements shown for mental rotation (Kasten & Herrmann, 2017), working memory (Jausovec et al., 2014; Pahor & Jausovec, 2017) and problem solving (Pahor & Jausovec, 2014) (see Schutter & Wischnewski, 2016 for a meta-analysis). Our offline 40 Hz tACS effect on visual perception adds to the growing body of evidence showing *offline* effects of tACS, thus shedding light on potential rehabilitation protocols.

Although online and offline protocols (at different frequencies) have shown promising effects on cognition, the underlying neurophysiological mechanisms causing those effects are not well explored. Studies combining M/EEG and tACS suggest that offline effects are driven by entrainment of neural oscillations (Jausovec et al., 2014; Kasten, Dowsett, & Herrmann, 2016; Neuling et al., 2013; Pahor & Jausovec, 2014). A different view, however, posits that *only* online tACS cause entrainment, whereas offline tACS effects might be mediated by synaptic plasticity (as in tDCS) rather than oscillatory activity (Antal & Paulus, 2013). The current study cannot clarify this issue, and future neuroimaging and computational work is required. However, we believe that it is unlikely that our perceptual results are mediated by neuroplastic (i.e., LTP/LTD-like) effects since (i) previous research has shown absence of neuroplastic effects after gamma tACS (Moliadze, Antal, & Paulus, 2010), and (ii) our tACS effects are seen on perception, but *not* memory tasks (i.e., we would expect neuroplastic effects to also mediate memory; as seen with offline tDCS – Barbieri et al., 2016).

Conclusions and Future directions

In summary, the current findings demonstrate that 40 Hz tACS over the right lateral occipital cortex enhances the perception of both faces and objects. Our results have implications for cognitive neuroscience and potentially also for clinical/therapeutic settings, as they offer insights for the design of effective neuromodulation protocols, and add to the breadth of cognitive processing (perception/memory), and stimuli (faces/objects) that can be modulated by tACS. The present study also serves as a foundation for future studies examining the neurophysiological mechanisms of the effects of tACS. For instance, it would be important to combine tACS and EEG to characterise the oscillatory mechanisms behind the behavioural effects found in this study and/or to localise anatomical regions affected by the intervention.

Our results also raise the interesting possibility of using tACS to modulate occipital gamma activity in conditions in which respective hypo-activity is associated with cognitive difficulties such as in chronic schizophrenia (Grent-'t-Jong et al., 2016), autism (Sun et al., 2012), and congenital prosopagnosia (Dobel, Bolte, Aicher, & Schweinberger, 2007). However, given the likely differences in terms of levels of cortical activity between healthy humans, and patients affected by diseases of the central nervous system (Uhlhaas & Singer, 2012), a one-to-one transferability of results cannot be taken for granted.

Acknowledgments

We wish to thank Dr Morgan Barense for kindly providing stimuli adopted in the face perception task (FP) and in the object perception task (OP). MAN is supported by a grant of the German Federal Ministry of Research and Education (*BMBF, GCBS grant 01EE1403C).*

Tables

Demographic features of the sample indicating the sample size (N), mean age and standard deviation (SD), the ratio between males and females (M/F), and age range.

	Sham	**5Hz_tACS**	**40Hz_tACS**	**Cz_40Hz_tACS**
N	16	16	16	12
Mean age (SD)	32.13 (7.78)	32.06 (6.86)	32.00 (9.33)	32.83 (8.59)
M/F	8 / 8	8 / 8	8 / 8	6 / 6
Range	18-45	19-44	18-47	18-45

Figure legends

Figure 1. Experimental design and examples of trial stimuli. The Cambridge Face Perception Task (CFPT) was administered before tACS (sham or verum). After 20min of stimulation participants completed four tasks: face perception task (FP), object perception task (OP), Cambridge Face Memory Test (CFMT), and Cambridge Car Memory Test (CCMT).

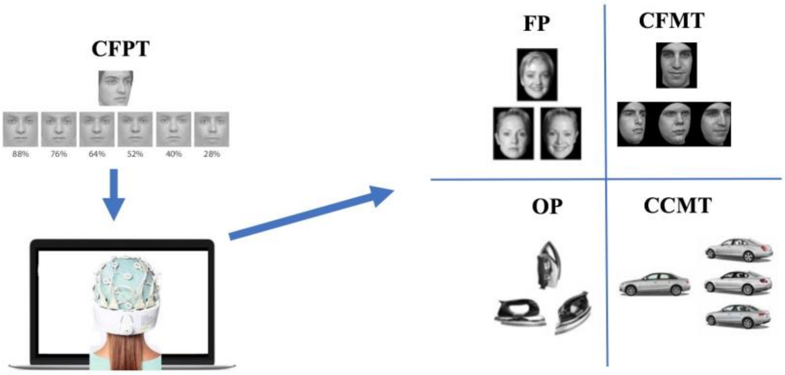
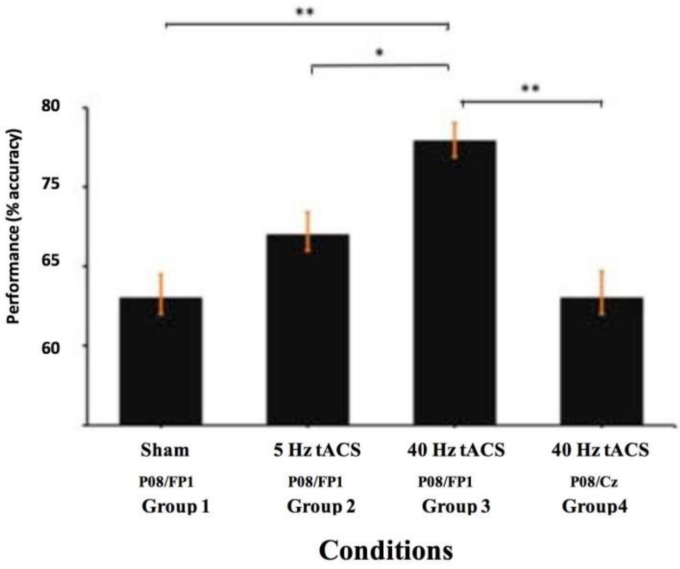


Figure 2. Single-subject accuracy values as averaged across the two perception tasks (FP, OP) in the four experimental conditions (Sham, 5Hz_tACS, 40Hz_tACS, Cz_40Hz_tACS). Average and SEM are indicated (* $p < .001$; * $p < .05$).



References

Anaki, D., Zion-Golumbic, E., & Bentin, S. (2007). Electrophysiological neural mechanisms for detection, configural analysis and recognition of faces. *Neuroimage, 37*(4), 1407-1416. doi:10.1016/j.neuroimage.2007.05.054

Antal, A., & Herrmann, C. S. (2016). Transcranial Alternating Current and Random Noise Stimulation: Possible Mechanisms. *Neural Plast, 2016*, 3616807. doi:10.1155/2016/3616807

Antal, A., & Paulus, W. (2013). Transcranial alternating current stimulation (tACS). *Front Hum Neurosci, 7*, 317. doi:10.3389/fnhum.2013.00317

Barbieri, M., Negrini, M., Nitsche, M. A., & Rivolta, D. (2016). Anodal-tDCS over the human right occipital cortex enhances the perception and memory of both faces and objects. *Neuropsychologia, 81*, 238-244. doi:10.1016/j.neuropsychologia.2015.12.030

Barense, M. D., Henson, R. N., & Graham, K. S. (2011). Perception and conception: temporal lobe activity during complex discriminations of familiar and novel faces and objects. *J Cogn Neurosci, 23*(10), 3052-3067. doi:10.1162/jocn_a_00010

Behrmann, M., & Avidan, G. (2005). Congenital prosopagnosia: Face-blind from birth *Trends in Cognitive Neuroscience, 9*, 180-187.

Bonemei, R., Costantino, A. I., Battistel, I., & Rivolta, D. (2018). he perception of (naked only) bodies and faceless heads relies on holistic processing: Evidence from the inversion effect. *British Journal of Psychology, 109*(2), 232-243. doi:doi: 10.1111/bjop.12271

Burgess, A. P., & Gruzelier, J. H. (1997). Short duration synchronization of human theta rhythm during recognition memory. *Neuroreport, 8*(4), 1039-1042.

Buzsaki, G., Anastassiou, C. A., & Koch, C. (2012). The origin of extracellular fields and currents--EEG, ECoG, LFP and spikes. *Nat Rev Neurosci, 13*(6), 407-420. doi:10.1038/nrn3241

Buzsaki, G., & Draguhn, A. (2004). Neuronal oscillations in cortical networks. *Science, 304*, 1926-1929.

Cabral-Calderin, Y., & Wilke, M. (2019). Probing the Link Between Perception and Oscillations: Lessons from Transcranial Alternating Current Stimulation. *Neuroscientist*, 1073858419828646. doi:10.1177/1073858419828646

Costantino, A. I., Titoni, M., Bossi, F., Premoli, I., Nitsche, M. A., & Rivolta, D. (2017). Preliminary Evidence of "Other-Race Effect"-Like Behavior Induced by Cathodal-tDCS over the Right Occipital Cortex, in the Absence of Overall Effects on Face/Object Processing. *Front Neurosci, 11*, 661. doi:10.3389/fnins.2017.00661

Dennett, H. W., McKone, E., Tavashmi, R., Hall, A., Pidcock, M., Edwards, M., & Duchaine, B. (2011). The Cambridge Car Memory Test: A task matched in format to the Cambridge Face Memory Test, with norms, reliability, sex differences, dissociations from face memory, and expertise effects. *Behavior Research Methods*.

Dilks, D. D., Julian, J. B., Paunov, A. M., & Kanwisher, N. (2013). The occipital place area is causally and selectively involved in scene perception. *J Neurosci, 33*(4), 1331-1336a. doi:10.1523/jneurosci.4081-12.2013

Ditye, T., Jacobson, L., Walsh, V., & Lavidor, M. (2012). Modulating behavioral inhibition by tDCS combined with cognitive training. *Exp Brain Res, 219*(3), 363-368. doi:10.1007/s00221-012-3098-4

Dobel, C., Bolte, J., Aicher, M., & Schweinberger, S. R. (2007). Prosopagnosia without apparent cause: Overview and diagnosis of six cases. *Cortex, 43*, 718-733.

Dobel, C., Junghöfer, M., & Gruber, T. (2011). The role of gamma-band activity in the representation of faces: Reduced activity in the fusiform face area in congenital prosopagnosia. *PLoS ONE, 6*(5), e19550. doi:19510.11371/journal.pone.0019550.

Duchaine, B. (2000). Developmental prosopagnosia with normal configural processing. *Neuroreport, 11*(1), 79-83.

Duchaine, B., Germine, L., & Nakayama, K. (2007). Family resemblance: Ten family members with prosopagnosia and within-class object agnosia. *Cognitive Neuropsychology, 24*, 419-430.

Duchaine, B., & Nakayama, K. (2006). The Cambridge Face Memory Test: Results for neurologically intact individuals and an investigation of its validity using inverted face stimuli and prosopagnosic participants. *Neuropsychologia, 44*(4), 576-585.

Engell, A. D., & McCarthy, G. (2010). Selective attention modulates face-specific induced gamma oscillations recorded from ventral occipitotemporal cortex. *J Neurosci, 30*(26), 8780-8786. doi:10.1523/jneurosci.1575-10.2010

Fertonani, A., Pirulli, C., & Miniussi, C. (2011). Random noise stimulation improves neuroplasticity in perceptual learning. *J Neurosci, 31*(43), 15416-15423. doi:10.1523/JNEUROSCI.2002-11.2011

Feurra, M., Galli, G., Pavone, E. F., Rossi, A., & Rossi, S. (2016). Frequency-specific insight into short-term memory capacity. *J Neurophysiol, 116*(1), 153-158. doi:10.1152/jn.01080.2015

Fries, P. (2005). A mechanism for cognitive dynamics: neuronal communication through neuronal coherence. *Trends Cogn Sci, 9*(10), 474-480. doi:10.1016/j.tics.2005.08.011

Fries, P., Reynolds, J. H., Rorie, A. E., & Desimone, R. (2001). Modulation of oscillatory neuronal synchronization by selective visual attention. *Science, 291*(5508), 1560-1563. doi:10.1126/science.291.5508.1560

Gao, Z., Goldstein, A., Harpaz, Y., Hansel, M., Zion-Golumbic, E., & Bentin, S. (2012). A magnetoencephalographic study of face processing: M170, gamma-band oscillations and source localization. *Hum Brain Mapp*. doi:10.1002/hbm.22028

Gauthier, I., Tarr, M. J., Moylan, J., Skudlarski, P., Gore, J. C., & Anderson, A. W. (2000). The fusiform "face area" is part of a network that processes faces at the individual level. *J Cogn Neurosci, 12*, 495-504.

Goffaux, V., Mouraux, A., Desmet, S., & Rossion, B. (2004). Human non-phase-locked gamma oscillations in experience-based perception of visual scenes. *Neurosci Lett, 354*(1), 14-17. doi:10.1016/j.neulet.2003.09.029

Grent-'t-Jong, T., Rivolta, D., Gross, J., Gajwani, R., Lawrie, S. M., Schwannauer, M., . . . Uhlhaas, P. J. (2018). Acute ketamine dysregulates task-related gamma-band oscillations in thalamo-cortical circuits in schizophrenia. *Brain*. doi:10.1093/brain/awy175

Grent-'t-Jong, T., Rivolta, D., Sauer, A., Grube, M., Singer, W., Wibral, M., & Uhlhaas, P. J. (2016). MEG-measured visually induced gamma-band oscillations in chronic schizophrenia: Evidence for impaired generation of rhythmic activity in ventral stream regions. *Schizophr Res*. doi:10.1016/j.schres.2016.06.003

Grill-Spector, K., Kourtzi, Z., & Kanwisher, N. (2001). The lateral occipital complex and its role in object recognition. *Vision Research, 41*, 1409-1422.

Gruber, T., & Muller, M. M. (2006). Oscillatory brain activity in the human EEG during indirect and direct memory tasks. *Brain Res, 1097*(1), 194-204. doi:10.1016/j.brainres.2006.04.069

Haxby, J. V., Hoffman, E. A., & Gobbini, M. I. (2000). The distributed human neural system for face perception. *Trends in Cognitive Sciences, 4*(6), 223-233.

Herring, J. D., Esterer, S., Marshall, T. R., Jensen, O., & Bergmann, T. O. (2019). Low-frequency alternating current stimulation rhythmically suppresses gamma-band oscillations and impairs perceptual performance. *Neuroimage, 184*, 440-449. doi:10.1016/j.neuroimage.2018.09.047

Herrmann, C. S., Rach, S., Neuling, T., & Struber, D. (2013). Transcranial alternating current stimulation: a review of the underlying mechanisms and modulation of cognitive processes. *Front Hum Neurosci, 7*, 279. doi:10.3389/fnhum.2013.00279

Inghilleri, M., Conte, A., Curra, A., Frasca, V., Lorenzano, C., & Berardelli, A. (2004). Ovarian hormones and cortical excitability. An rTMS study in humans. *Clin Neurophysiol, 115*(5), 1063-1068. doi:10.1016/j.clinph.2003.12.003

Janik, A. B., Rezlescu, C., & Banissy, M. J. (2015). Enhancing Anger Perception With Transcranial Alternating Current Stimulation Induced Gamma Oscillations. *Brain Stimul, 8*(6), 1138-1143. doi:10.1016/j.brs.2015.07.032

Jausovec, N., Jausovec, K., & Pahor, A. (2014). The influence of theta transcranial alternating current stimulation (tACS) on working memory storage and processing functions. *Acta Psychol (Amst), 146*, 1-6. doi:10.1016/j.actpsy.2013.11.011

Kanwisher, N. (2010). Functional specificity in the human brain: A window into the functional architecture of the mind. *Proceedings of the National Academy of Science USA, 107*(25), 11163-11170.

Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: A module in human extrastriate cortex specialized for face perception. *Journal of Neuroscience, 17*, 4302-4311.

Kasten, F. H., Dowsett, J., & Herrmann, C. S. (2016). Sustained Aftereffect of alpha-tACS Lasts Up to 70 min after Stimulation. *Front Hum Neurosci, 10*, 245. doi:10.3389/fnhum.2016.00245

Kasten, F. H., & Herrmann, C. S. (2017). Transcranial Alternating Current Stimulation (tACS) Enhances Mental Rotation Performance during and after Stimulation. *Front Hum Neurosci, 11*, 2. doi:10.3389/fnhum.2017.00002

Lachaux, J. P., George, N., Tallon-Baudry, C., Martinerie, J., Hugueville, L., Minotti, L., . . . Renault, B. (2005). The many faces of the gamma band response to complex visual stimuli. *Neuroimage, 25*(2), 491-501. doi:10.1016/j.neuroimage.2004.11.052

Laczo, B., Antal, A., Niebergall, R., Treue, S., & Paulus, W. (2012). Transcranial alternating stimulation in a high gamma frequency range applied over V1 improves contrast perception but does not modulate spatial attention. *Brain Stimul, 5*(4), 484-491. doi:10.1016/j.brs.2011.08.008

Lisman, J. E., & Idiart, M. A. (1995). Storage of 7 +/- 2 short-term memories in oscillatory subcycles. *Science, 267*(5203), 1512-1515.

Malach, R., Reppas, J. B., Benson, R. R., Kwong, K. K., Jiang, H., Kennedy, W., . . . Tootell, R. (1995). Object-related activity revealed by functional magnetic resonance imaging in human occipital cortex. *Proceedings of the National Academy of Sciences (PNAS), US, 92*, 8135-8139.

Martinovic, J., Gruber, T., & Muller, M. M. (2007). Induced gamma band responses predict recognition delays during object identification. *J Cogn Neurosci, 19*(6), 921-934. doi:10.1162/jocn.2007.19.6.921

Matsuzaki, N., Schwarzlose, R. F., Nishida, M., Ofen, N., & Asano, E. (2015). Upright face-preferential high-gamma responses in lower-order visual areas: evidence from intracranial recordings in children. *Neuroimage, 109*, 249-259. doi:10.1016/j.neuroimage.2015.01.015

McKone, E., & Yovel, G. (2009). Why does picture-plane inversion sometimes dissociate perception of features and spacing in faces, and sometimes not? Toward a new theory of holistic processing. *Psychonomic Bullettin & Review, 16*(5), 778-797.

Moliadze, V., Antal, A., & Paulus, W. (2010). Boosting brain excitability by transcranial high frequency stimulation in the ripple range. *Journal of Phsysiology, 15*(588(Pt 24)), 4891-4904.

Nasseri, P., Nitsche, M. A., & Ekhtiari, H. (2015). A framework for categorizing electrode montages in transcranial direct current stimulation. *Front Hum Neurosci, 9*, 54. doi:10.3389/fnhum.2015.00054

Navajas, J., Ahmadi, M., & Quian Quiroga, R. (2013). Uncovering the mechanisms of conscious face perception: a single-trial study of the n170 responses. *J Neurosci, 33*(4), 1337-1343. doi:10.1523/jneurosci.1226-12.2013

Neuling, T., Rach, S., & Herrmann, C. S. (2013). Orchestrating neuronal networks: sustained after-effects of transcranial alternating current stimulation depend upon brain states. *Front Hum Neurosci, 7*, 161. doi:10.3389/fnhum.2013.00161

Pahor, A., & Jausovec, N. (2014). The effects of theta transcranial alternating current stimulation (tACS) on fluid intelligence. *Int J Psychophysiol, 93*(3), 322-331. doi:10.1016/j.ijpsycho.2014.06.015

Pahor, A., & Jausovec, N. (2017). The Effects of Theta and Gamma tACS on Working Memory and Electrophysiology. *Front Hum Neurosci, 11*, 651. doi:10.3389/fnhum.2017.00651

Palermo, R., Willis, M. L., Rivolta, D., McKone, E., Wilson, C. E., & Calder, A. J. (2011). Impaired holistic coding of facial expression and facial identity in congenital prosopagnosia. *Neuropsychologia, 49*, 1226-1235.

Pinault, D. (2008). N-methyl d-aspartate antagonists ketamine and MK-801 induce wake-related aberrant gamma oscillations in the rat neocortex. *Biological Psychiatry, 63*(8), 730-735.

Pirulli, C., Fertonani, A., & Miniussi, C. (2013). The role of timing in the induction of neuromodulation in perceptual learning by transcranial electric stimulation. *Brain Stimul, 6*(4), 683-689. doi:10.1016/j.brs.2012.12.005

Pitcher, D., Charles, L., Devlin, J. T., Walsh, V., & Duchaine, B. (2009). Triple dissociation of faces, bodies, and objects in extrastriate cortex. *Current Biology, 19*, 319-324.

Pitcher, D., Walsh, V., Yovel, G., & Duchaine, B. (2007). TMS evidence for the involvement of the right occipital face area in early face processing. *Current Biology, 17*, 1568-1573.

Polania, R., Nitsche, M. A., & Paulus, W. (2012). Modulating functional connectivity patterns and topological functional organization of the human brain with transcranial direct current stimulation. *Hum Brain Mapp, 32*(8), 1236-1249.

Polania, R., Nitsche, M. A., & Ruff, C. C. (2018). Studying and modifying brain function with non-invasive brain stimulation. *Nat Neurosci, 21*(2), 174-187. doi:10.1038/s41593-017-0054-4

Polania, R., Paulus, W., & Nitsche, M. A. (2012). Noninvasively decoding the contents of visual working memory in the human prefrontal cortex within high-gamma oscillatory patterns. *J Cogn Neurosci, 24*(2), 304-314. doi:10.1162/jocn_a_00151

Prieto, E. A., Caharel, S., Henson, R., & Rossion, B. (2011). Early (n170/m170) face-sensitivity despite right lateral occipital brain damage in acquired prosopagnosia. *Front Hum Neurosci, 5*, 138. doi:10.3389/fnhum.2011.00138

Rivolta, D., Heidegger, T., Scheller, B., Sauer, A., Schaum, M., Birkner, K., . . . Uhlhaas, P. J. (2015). Ketamine Dysregulates the Amplitude and Connectivity of High-Frequency Oscillations in Cortical-Subcortical Networks in Humans: Evidence From Resting-State Magnetoencephalography-Recordings. *Schizophr Bull, 41*(5), 1105-1114. doi:10.1093/schbul/sbv051

Rivolta, D., Palermo, R., Schmalzl, L., & Coltheart, M. (2012). Covert face recognition in congenital prosopagnosia: A group study. *Cortex, 48*(3), 344-352.

Rivolta, D., Palermo, R., Schmalzl, L., & Williams, M. A. (2012). Investigating the features of the M170 in congenital prosopagnosia. *Frontiers in Human Neuroscience, 6:45.*(doi:10.3389/fnhum.2012.00045).

Rivolta, D., Woolgar, A., Palermo, R., Butko, M., Schmalzl, L., & Williams, M. A. (2014). Multi-voxel pattern analysis (MVPA) reveals abnormal fMRI activity in both the "core" and "extended" face network in congenital prosopagnosia. *Front Hum Neurosci, 8*, 925. doi:10.3389/fnhum.2014.00925

Romanska, A., Rezlescu, C., Susilo, T., Duchaine, B., & Banissy, M. J. (2015). High-Frequency Transcranial Random Noise Stimulation Enhances Perception of Facial Identity. *Cereb Cortex*. doi:10.1093/cercor/bhv016

Santarnecchi, E., Polizzotto, N. R., Godone, M., Giovannelli, F., Feurra, M., Matzen, L., . . . Rossi, S. (2013). Frequency-dependent enhancement of fluid intelligence induced by transcranial oscillatory potentials. *Curr Biol, 23*(15), 1449-1453. doi:10.1016/j.cub.2013.06.022

Schutter, D. J., & Wischnewski, M. (2016). A meta-analytic study of exogenous oscillatory electric potentials in neuroenhancement. *Neuropsychologia, 86*, 110-118. doi:10.1016/j.neuropsychologia.2016.04.011

Singer, W. (2011). Dynamic formation of functional networks by synchronization. *Neuron, 69*(2), 191-193. doi:10.1016/j.neuron.2011.01.008

Sun, L., Gruetzner, C., Bölte, S., Wibral, M., Tozman, T., Schlitt, S., . . . Uhlhaas, P. J. (2012). Impaired gamma-band activity during perceptual organization in adults with autism spectrum disorders: evidence for dysfunctional network activity in frontal-posterior cortices. *Journal of Neuroscience, 32*(28), 9563-9573.

Tallon-Baudry, C. (2009). The roles of gamma-band oscillatory synchrony in human visual cognition. *Front Biosci (Landmark Ed), 14*, 321-332.

Tallon-Baudry, C., Bertrand, O., Delpuech, C., & Permier, J. (1997). Oscillatory gamma-band (30-70 Hz) activity induced by a visual search task in humans. *J Neurosci, 17*(2), 722-734.

Uhlhaas, P. J., & Singer, W. (2010). Abnormal neural oscillations and synchrony in schizophrenia. *Nature Reviews Neuroscience, 11*, 100-113.

Uhlhaas, P. J., & Singer, W. (2012). Neuronal dynamics and neuropsychiatric disorders: Towards a translational paradigm for dysfunctional large-scale networks. *Neuron, 75*, 963-980.

Uono, S., Sato, W., Kochiyama, T., Kubota, Y., Sawada, R., Yoshimura, S., & Toichi, M. (2017). Time course of gamma-band oscillation associated with face processing in the inferior occipital gyrus and fusiform gyrus: A combined fMRI and MEG study. *Hum Brain Mapp, 38*(4), 2067-2079. doi:10.1002/hbm.23505

Wischnewski, M., Engelhardt, M., Salehinejad, M. A., Schutter, D., Kuo, M. F., & Nitsche, M. A. (2018). NMDA Receptor-Mediated Motor Cortex Plasticity After 20 Hz Transcranial Alternating Current Stimulation. *Cereb Cortex*. doi:10.1093/cercor/bhy160

Yaple, Z., Martinez-Saito, M., Awasthi, B., Feurra, M., Shestakova, A., & Klucharev, V. (2017). Transcranial Alternating Current Stimulation Modulates Risky Decision Making in a Frequency-Controlled Experiment. *eNeuro, 4*(6). doi:10.1523/eneuro.0136-17.2017

Zion-Golumbic, E., & Bentin, S. (2007). Dissociated neural mechanisms for face detection and configural encoding: evidence from N170 and induced gamma-band oscillation effects. *Cereb Cortex, 17*(8), 1741-1749. doi:10.1093/cercor/bhl100

Zion-Golumbic, E., Golan, T., Anaki, D., & Bentin, S. (2008). Human face preference in gamma-frequency EEG activity. *Neuroimage, 39*(4), 1980-1987. doi:10.1016/j.neuroimage.2007.10.025