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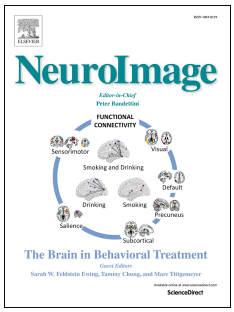

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AG: Investigation, Data curation, Writing- Original draft preparation.
CC: Project administration, Resources, Supervision, Writing- Original draft.
LR: Conceptualization, Methodology, Formal Analysis, Supervision, Writing- Original draft preparation, Visualization, Writing - Reviewing and Editing.

Parietal tACS at beta frequency improves vision in a crowding regime

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ABSTRACT

Visual crowding is the inability to discriminate objects when presented with nearby flankers and sets a fundamental limit for conscious perception. Beta oscillations in the parietal cortex were found to be associated to crowding, with higher beta amplitude related to better crowding resilience. An open question is whether beta activity directly and selectively modulates crowding. We employed transcranial alternating current stimulation (tACS) in the beta band (18-Hz), in the alpha band (10-Hz) or in a sham regime, asking whether 18-Hz tACS would selectively improve the perception of crowded stimuli by increasing parietal beta activity. Resting electroencephalography (EEG) was measured before and after stimulation to test the influence of tACS on endogenous oscillations. Consistently with our predictions, we found that 18-Hz tACS, as compared to 10-Hz tACS and sham stimulation, reduced crowding. This improvement was found specifically in the contralateral visual hemifield and was accompanied by an increased amplitude of EEG beta oscillations, confirming an effect on endogenous brain rhythms. These results support a causal relationship between parietal beta oscillations and visual crowding and provide new insights into the precise oscillatory mechanisms involved in human vision.

Keywords: neurostimulation, perception, vision, tACS, tES

INTRODUCTION

Visual crowding is one of the factors that most impairs visual object recognition and for this reason, it can be considered as a fundamental bottleneck for conscious object perception (Levi, 2008). Crowding can be defined as the deleterious influence of nearby contours on visual discrimination. It is a perceptual phenomenon typical of peripheral vision that limits recognition and it can be observed with simple objects, such as oriented gratings, and also with complex objects, such as letters and faces (Levi, 2008; Pelli, 2008; Whitney and Levi, 2011). For example, crowding limits the perception of elementary contours in the periphery (May and Hess, 2007), the pre-processing of the parafoveal word letters (Moll and Jones, 2013) and limits also the ability to recognize peripheral target in a field of distracting object in demanding tasks such as action videogames (Green and Bavelier, 2007).

Psychophysical studies have greatly contributed to the understating of visual crowding (for reviews see (Herzog and Manassi, 2015; Levi, 2008; Pelli, 2008) by showing, for example, that the main factor that modulates visual crowding is the distance between target and flankers. Moreover, among the main properties of crowding we have eccentricity dependence, size independence, inward-outward anisotropy and radial/tangential anisotropy (Levi, 2008).

Despite the large amount of psychophysical studies on crowding, its neural substrates are still unclear. A better understanding of the neural bases of crowding may help clarifying the mechanisms responsible of crowding and could give important insights for developing neurorehabilitation trainings. In particular, the improvement of perception in a crowding regime is a rehabilitation goal in clinical populations that are associated to excessive crowding, such as developmental dyslexia and amblyopia (Bertoni et al., 2019; Bonneh et al., 2007; Gori and Facoetti, 2015; Zorzi et al., 2012).

Visual crowding is considered as a heterogeneous phenomenon generally occurring because the output of detectors activated by several simple features belonging to the target is inappropriately integrated to the output of detectors responding to non-target features (Chakravarthi and Pelli,

2011). There is general consensus that the more complex the object, the higher the visual area responsible for crowding: excessive integration may occur at an early level of visual processing where binding of elementary contour features occurs (Freeman and Simoncelli, 2010; Pelli, 2008) or at a higher level, for example in ventral area V4, that mediates integration of object contours. Moreover, bottom-up processing in the dorsal stream also contributes to crowding. Contour integration in normal vision is facilitated by coarse representation of visual input achieved by bottom-up dorsal processing. Through recursive feedback from the parietal cortex, the major projection of the dorsal stream, this low-frequency representation drives binding mechanisms towards the stimulus configuration and facilitates attention-demanding identification tasks in the ventral stream (Levy et al., 2010; Vidyasagar, 2004, 1999). In principle, the same re-entrant information from the dorsal stream would promote binding between target and flankers in a crowded regime and would limit segmentation of the target from flankers in the peripheral field (Chakravarthi and Pelli, 2011; Omtzigt et al., 2002). However, when the task needs an uncrowded perceptual solution, the dorsal-to-ventral feedback mediates segmentation of the target letter from the flankers through activation of receptive fields of appropriate size (Lamme and Roelfsema, 2000; Lee et al., 1998).

A promising approach to enlighten the mechanisms of crowding is that of the studies employing electroencephalography (EEG). Recently, EEG studies were performed by using complex stimuli configurations (e.g. Vernier stimuli, letters) found that crowding induced a lower amplitude of a late visual event-related potential (ERP) component (i.e., the N1), peaking around 200/250 ms post-stimulus (Chicherov et al., 2014; Ronconi et al., 2016) . Chen and colleagues (Chen et al., 2014), used simple gratings as target stimuli and showed that the C1 component in the ERPs, reflecting activity in early visual areas (Di Russo et al., 2002), was suppressed in a crowded condition, but also significantly modulated by attention. In a more recent study, Han and Luo (Han and Luo, 2019) employed EEG in combination with a temporal response function (TRF) approach. They showed the presence of two components in the target-specific TRF response: an early component in

occipital channels and a late component (starting from ~200 ms) in fronto-parietal channels. This late fronto-parietal component correlated, as opposed to the occipital component, with target discrimination in the crowded condition. Overall, the picture emerging from these recent studies shows that visual crowding emerges in the EEG (Han and Luo, 2019) and ERPs (Chicherov et al., 2014; Ronconi et al., 2016) (i.e. N1) with timing and scalp distribution that are typically associated with later stages of stimulus processing, or alternatively appears at earlier stages but are influenced by dorsal/attentional feedback modulation (Chen et al., 2014; Peng et al., 2018).

Another fundamental approach to understand the neural mechanisms of crowding is the analysis of its oscillatory correlates. In two recent studies, Ronconi and colleagues (Ronconi et al., 2016; Ronconi and Bellacosa Marotti, 2017) found a relationship between visual crowding and EEG oscillations in the beta band (15-30 Hz). In particular, Ronconi et al. (Ronconi et al., 2016) measured crowding in different conditions of spacing between target and flankers and found a stronger post-stimulus beta power reduction in the strong crowding condition (smaller target-flankers distance) relative to the weak crowding condition. Moreover, stronger beta power reduction correlated to individual task performance that was more disturbed by visual crowding. Ronconi and Bellacosa Marotti (2017) further confirmed the relationship between beta band oscillations and visual crowding, by showing that beta power before the time of the stimulus onset was higher in frontal and parieto-occipital sensors for trials where participants correctly discriminated the target letter among flankers, but only in the strong, not in the weak, crowding condition.

Although there is evidence of a strong relationship between ongoing neural oscillations and crowding phenomenon, a causal relationship can only be found by means of a direct modulation of these neural oscillations. In particular, tACS seems a particularly appropriated method to directly modulate oscillatory signals. Some studies indeed showed that tACS is able to interact with the brain's natural cortical oscillations causing entrainment (Fröhlich and McCormick, 2010; Helfrich et al., 2014) and driving the activity of cortical regions to the frequency imposed by tACS. Moreover, tACS dependent behavioural effects on sensory and cognitive processes have been

shown (Herrmann et al., 2016). In vision for example, Laczo and colleagues (Laczó et al., 2012) showed that tACS at 60 Hz over the visual cortex increased contrast perception compared to tACS at 40 and 80 Hz. In addition, tACS in the gamma frequency has been shown to modulate perception of bistable motion (Strüber et al., 2014). Moreover, tACS at theta frequency over the right parietal cortex increased visual working memory (Bender et al., 2019; Wolinski et al., 2018).

The present study was based on the evidence reviewed above of a relationship between visual crowding and EEG oscillations in the beta band (15-30 Hz) and on the evidence that tACS can be used as a method to modulate perceptually relevant brain oscillations. With these premises, tACS seems appropriate to assess a direct role of beta frequency range (13-20 Hz) in reducing crowding.

tACS was delivered on the right parietal cortex for different reasons. First, previous EEG studies showed that the strongest beta modulation was evident in a cluster of right occipito-parietal channels (Ronconi et al., 2016; Ronconi and Bellacosa Marotti, 2017). Second, the N1 component of the ERPs, which is the main component reflecting crowding as introduced above (Chicherov et al., 2014; Ronconi et al., 2016), originates mainly from cortical sources in the right parietal cortex, as found in previous visual perception studies that did (Chicherov et al., 2014) or did not (Di Russo et al., 2002) directly manipulate the crowding strength. Third, Romei and colleagues (Romei et al., 2012, 2011) used rhythmic TMS over the right and left parietal cortex to entrain oscillatory activity in the theta, beta and alpha band aimed at modulating local and global attention in a Navon task. The authors found that beta stimulation of the right (but not left) parietal cortex (Romei et al., 2011) facilitated local processing. In addition, beta band EEG activity is selectively predictive of parietal cortex excitability when probing TMS-induced phosphene perception (Cabral-Calderin and Wilke, 2019; Samaha et al., 2017). We also reasoned that beta modulation of parietal cortex with consequences on crowding would ultimately confirm a role of dorso-ventral feedback in such task (Lamme and Roelfsema, 2000; Robol et al., 2013). The role of beta tACS (18 Hz) in reducing crowding was compared to that of two control stimulations on the same cortical site: i) a sham (no stimulation) and ii) a 10-Hz tACS (i.e. within alpha band, which has not been shown to affect

crowding (Ronconi et al., 2016; Ronconi and Bellacosa Marotti, 2017). To test the hypothesis that tACS can lead to changes of endogenous brain rhythm (Fröhlich and McCormick, 2010; Helfrich et al., 2014), we recorded the resting-state EEG signal, to test pre- and post-stimulation power differences in the relevant frequency bands (beta and alpha).

METHOD

Participants

Twenty participants (10 male, mean age = 23.05, age range = 18 – 33) took part in this study. They were all students from the University of Padova. They provided informed consent, had normal or corrected to normal vision and normal hearing. All of them met the criteria for the application of Transcranial Alternating Current Stimulation (tACS) (Antal et al., 2017). This experiment has been approved by the Ethics Committee of the Department of General Psychology at the University of Padua (protocol n. 2598).

Stimuli

Participants performed the task in a dimly lit room and viewed stimuli binocularly on a 19" LCD Asus monitor with 60 Hz refresh rate. Stimuli were displayed on a mid-level gray background with 40 cd/m^2 luminance. They were created via Psychtoolbox for Matlab (Brainard, 1997; Pelli, 1997) and consisted of 1.5 x 1.5 deg gaborized H-like and T-like configurations. Gabors that formed each stimulus were obtained through a product of an oriented sinewave grating and a circular Gaussian window according to the following formula:

$$G(x,y) = e^{\frac{-(x^2+y^2)}{2\sigma^2}} \times \cos[\frac{2\pi \times (\cos(\theta x) + \sin(\theta y))}{s+p}]$$

In this equation, the orientation θ could be either 0 deg for vertical and 90 deg for horizontal gabors. The phase of the sinusoid (p) was set on 90 deg. The spatial frequency (s) of the elements

was 2 c/deg and the standard deviation of the Gaussian window (σ) was .12 deg. Stimuli were presented at full contrast (Michelson). On each trial, stimuli were built as follows. We designed a matrix of the size of the stimulus. We divided it into a 5 x 5 grid of equally spaced x,y locations. The gabors were then placed along the path of the letter (H or T). We used 9 patches for the Ts and 13 for the Hs. Centre-to-centre distance between adjacent patches was constant at .3 deg. Patches could be both horizontal and vertical.

Procedure

We implemented an orientation discrimination task with MATLAB Psychtoolbox (Brainard, 1997; Pelli, 1997). The task was structured as follows: a fixation point was displayed for 2 seconds, then the target T was randomly presented for ~50 ms to the left or to the right of the fixation point at 11 degrees of eccentricity (this duration is not enough to execute a saccade towards the stimulus). Ts could have 4 possible orientations (0-270 deg in step of 90 deg) and they were vertically flanked by H letters which could have 7 possible distances from the target (1 = 1.90 deg; 2 = 2.27 deg; 3 = 2.65 deg; 4 = 3.02 deg; 5 = 3.40 deg; 6 = 3.78 deg; 7 = 4.15 deg). A blank screen was shown for 2 seconds and finally a response display showed the 4 possible T rotations and the corresponding response keys. One second after response, a new trial started. Participants were asked to recognize the rotation of the Ts presented in each trial, keeping their fixation on the central point displayed for the entire trial duration.

Each subject repeated the task three times with three different stimulation conditions, which were randomized across participants: 10 Hz, 18 Hz and sham. 10 Hz was chosen as the frequency laying at the center of the alpha band (8-12 Hz). 18 Hz was chosen because it was the frequency reflecting the greatest amplitude modulation (i.e. power decrement) previous EEG study (Ronconi et al., 2016). In the Supplementary Figure 1, we plotted EEG power of channel P4 in the beta range extracted from our previous study in support of our choice of using this precise stimulation frequency.

Each session lasted 45 minutes. The three sessions took place always in three different days. Each session provided two small breaks after 15 and 30 minutes in order to prevent fatigue (tACS, however, was on during the entire session). On average participants completed 512 trials in the sham condition (SD=44; mean left hemifield trials =251; mean right hemifield trials =261), 508 trials in the 10-Hz session (SD=49; mean left hemifield trials =250; mean right hemifield trials =258) and 513 trials in the 18-Hz session (SD=53; mean left hemifield trials =254; mean right hemifield trials =259). All participants were unaware of the specific tACS protocol that was administered on each session, thus resulting in a single blind procedure.

Stimulation setting and EEG recording

tACS was applied through a StarStim8 device, a hybrid wireless neurostimulation system for concurrent EEG/tACS controlled by the software Neuroelectrics Instrument Controller (*NIC 2.0;* http://www.neuroelectrics.com/products/software/nic2/). The system had 8 channels that could be located in 39 possible scalp positions through a neoprene headcap and according to the 10-10 system. We used 5 PISTIM Ag/AgCl electrodes with 1 cm radius both for stimulation and EEG recording and 3 GELTRODE Ag/AgCl electrodes just for EEG recording. The stimulation setting was set as follows: the stimulation electrode was placed in P4, while the 4 return electrodes were placed in C4, Pz, O2 and P8. Stimulation intensity was set at 0.8 mA (*milliAmpere*), with offset set at 0 mA; this value chosen following the most recent guidelines for tACS safety guidelines considering a session duration of 40 minutes (Antal et al., 2017). This montage was chosen after carefully evaluating the electric field distribution with the software NIC 2.0. In particular, this high-density montage centred on P4 was optimal to stimulate the right parietal cortex (see Figure 1). We created three protocols with different stimulation frequencies: 10 Hz, 18 Hz and Sham. It is important to note that none of the participants reported the presence of retinal phosphenes nor with 10-Hz neither with 18- Hz tACS. Moreover, only two participants reported mild skin sensation (see questionnaire in Fertonani et al., 2015) that disappeared after a few seconds of stimulation. All the

other participants did not report skin sensation. All subjects were asked at the end of the experiment whether they could guess the presence of stimulation and were at chance level (see Supplementary Table 1). About the EEG setting, the signal was recorded at a sampling frequency of 500 Hz and with a 24-bit digitization using 8 electrodes positioned on the following scalp locations: C4, Pz, P4, P8, PO8, PO7, Oz, O2. Channels activity was online referenced to Cz and the impedance was kept below 10kΩ. EEG signal was recorded during an eyes-closed resting-state period of 3 minutes immediately before and immediately after tACS application.

Data analysis: behavioural data

We calculated the proportion of correct response as a function of the target-flankers distance. Data were then fitted with a logistic function (maximum likelihood criterion) by using the routines provided by the Palamedes toolbox (Prins and Kingdom, 2018). The psychometric function was created according to the following formula:

$$P(C;\alpha,\beta,\gamma;\lambda) = \gamma + \frac{1-\gamma-\lambda}{1+e^{-\beta(C-\alpha)}}$$

The inferior asymptote γ was set to a probability of 0.25 corresponding to the chance level. The superior asymptote λ was fixed by setting the lapse rate to 0.02. α and β parameters were left free. α corresponds to the threshold, β corresponds to the function's slope. In this study, the threshold is the target-flanker distance (deg) related to a probability of 0.625 to give a correct response. This value lies between the probability of best performance (1=100% of correct response) and the chance level (0.25).

To analyse the effect of tACS on crowding, we performed a repeated measures analysis of variance (ANOVA) on both the slope and threshold values with two within subject factors: Stimulation Condition (10 Hz vs 18 Hz vs Sham) and Target Position (left vs right).

Data analysis: Resting state EEG data

Offline, eyes closed resting EEG data were band-pass filtered between 0.05 and 40 Hz (Butterworth filter, order=2). The continuous data were segmented into 1-sec epochs to obtain a total 180 epochs for both pre- and post- tACS periods. These epochs were visually inspected to remove data segments contaminated by muscular or ocular artefacts (mean ± SD of retained epochs after artefacts rejection were: 177.88 ± 3.54 across all conditions). An independent component analysis (ICA), estimated together for the pre- and post- tACS sessions, was used to correct for electrodes artifacts when needed, resulting in a single ICA component that was removed in 8 out of 60 experimental sessions. The cleaned epochs were then used to extract the FFT spectrum. Zero padding was applied (N=2000 samples) to increase the frequency resolution and data were baseline normalized (dB) to the average epoch power. Finally, the individual power values in the frequency range of interests were averaged for each participant and separately for the pre- and post-stimulation sessions.

Hereafter, we will refer to 'alpha power' to indicate the average of power values extracted in the frequency range between 8 and 12 Hz. Similarly, we will refer to 'beta power' to indicate the average of power values extracted in the frequency range between 15 and 25 Hz. Differences in alpha and beta power before and after tACS were tested at the channel P4 with paired samples t-tests. Bonferroni correction was applied to account for the multiple comparisons (i.e. number of channels). Data analysis was performed using Matlab (MathWorks, Inc., Natick, MA) and EEGLAB (Delorme and Makeig, 2004).

Data analysis: relationship between tACS phase and perception

In order to study how the phase of the external stimulation influences crowding accuracy, we used the tACS sinewave to extract with a Hilbert transform the phase points (in radian) for each temporal point during the stimulation session. This allowed us to obtain a phase value corresponding to the presentation of the target in each trial. We created then six bins, evenly sized and non-overlapping, ranged as follows: $[-\pi; -2/3\pi], [-2/3\pi; -1/3\pi], [-1/3\pi; 0], [0; 1/3\pi], [1/3\pi; 2/3\pi], [2/$

$3\pi;\ \pi]$ (in radians). Each bin contained on average 42.6 trials for the 18-Hz condition (SD=3.7) and 43.3 trials for the 10-Hz condition (SD=3.8).

The analysis above, however, does not evaluate whether the modulation of performance as a function of tACS phase has a sinusoidal shape as predicted by a true neural entrainment effect. Thus, we performed a second analysis where we first averaged the data across participants and then we calculated the best fitting sinusoidal function separately for target hemifield (left vs. right) and tACS frequency (10 vs. 18 Hz). The sinusoidal function used a fixed frequency (i.e. one cycle across the datapoints) but free amplitude and phase, similarly to other previous studies (e.g. Stonkus et al., 2016). The goodness of fit (R^2) of the resulting best fitting function for the observed data was compared with a null distribution obtained with 1000 permutations of the real data. Specifically, for each individual dataset we calculated 1000 permutations by randomizing the phase bin label. Permuted data were averaged across participants and the 1000 measures of goodness of fit obtained from these permuted data constituted the null distribution against which we could compare the goodness of fit obtained from the real data and extract the p-value.

[Figure 1 about here]

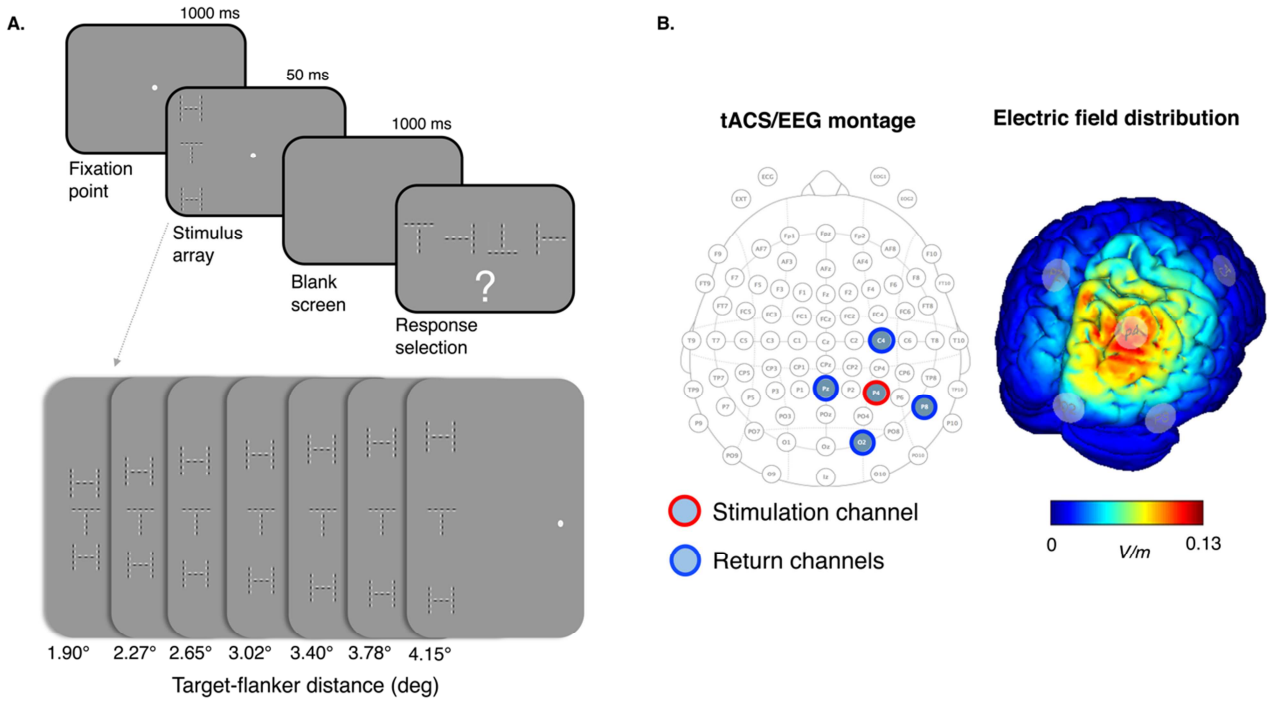

Figure 1. (A) Illustration of a trial example and of the different target-flankers distances used in the crowding task. (B) tACS/EEG montage and the electric field distribution on the cortical surface; as it can be seen, the maximum current density was induced on the right parietal cortex.

RESULTS

18-Hz tACS diminished the effect of crowding on perception

The individual fitting of the psychometric function[1] provided the following goodness-of-fit measures (pDev; Kingdom and Prins 2016) in terms of mean±SD: left hemifield target with sham tACS=0.52±0.27, right hemifield target with sham tACS=0.59±0.24, left hemifield target with 10 Hz tACS=0.53±0.32, right hemifield target with 10 Hz tACS=0.52±0.35, left hemifield target with 18 Hz tACS=0.47±0.29, right hemifield target with 18 Hz tACS=0.53±0.28.

[1] Raw data that were fitted with psychometric functions contained only 2 outliers out of 840 data points (> 3 standard deviations). Additional analysis taking into account outliers and further explanation about the Palamedes fitting routines can be found in the Supplementary Material).

Threshold values were submitted to a repeated measures ANOVA with two within subject factors: Stimulation Condition (10 Hz *vs* 18 Hz *vs* Sham) and Target Position (left *vs* right). The ANOVA did not show a significant main effect of the Stimulation Condition ($F_{(2,38)} = 1.71$, $p = .19$; $\eta^2_p = .08$) and Target Position ($F_{(1,19)} = 1.32$, $p = .26$; $\eta^2_p = .06$). Importantly, a significant interaction Stimulation Condition × Target Position was found ($F_{(2,38)} = 6.70$, $p = .003$; $\eta^2_p = .26$). Post hoc comparison (t-test Bonferroni corrected) revealed lower threshold value (shorter distance target-flankers at 0.625 proportion of correct response) for stimuli presented in the left visual hemifield (contralateral to the stimulation) during the tACS session at 18 Hz compared to 10 Hz ($t_{(19)} = 3.03$; $p_{corr} = .02$; Cohen's d=0.67) and sham session ($t_{(19)} = 2.70$; $p_{corr} = .042$; Cohen's d=0.6) (Figure 2). On the contrary, for stimuli presented in the right visual hemifield (ipsilateral to the stimulation) no effects of tACS was evident (all *ps* > .99).

The ANOVA on slope values, on the contrary, did not reveal main effects of Stimulation Condition ($F_{(1.28,24.4)} = 0.95$, $p = .39$; $\eta^2_p = .05$) or Target Position ($F_{(1,19)} = 3.56$, $p = .07$; $\eta^2_p = .16$), nor a significant interaction ($F_{(1.22,23.19)} = 1.38$, $p = .36$; $\eta^2_p = .07$).

[Figure 2 about here]

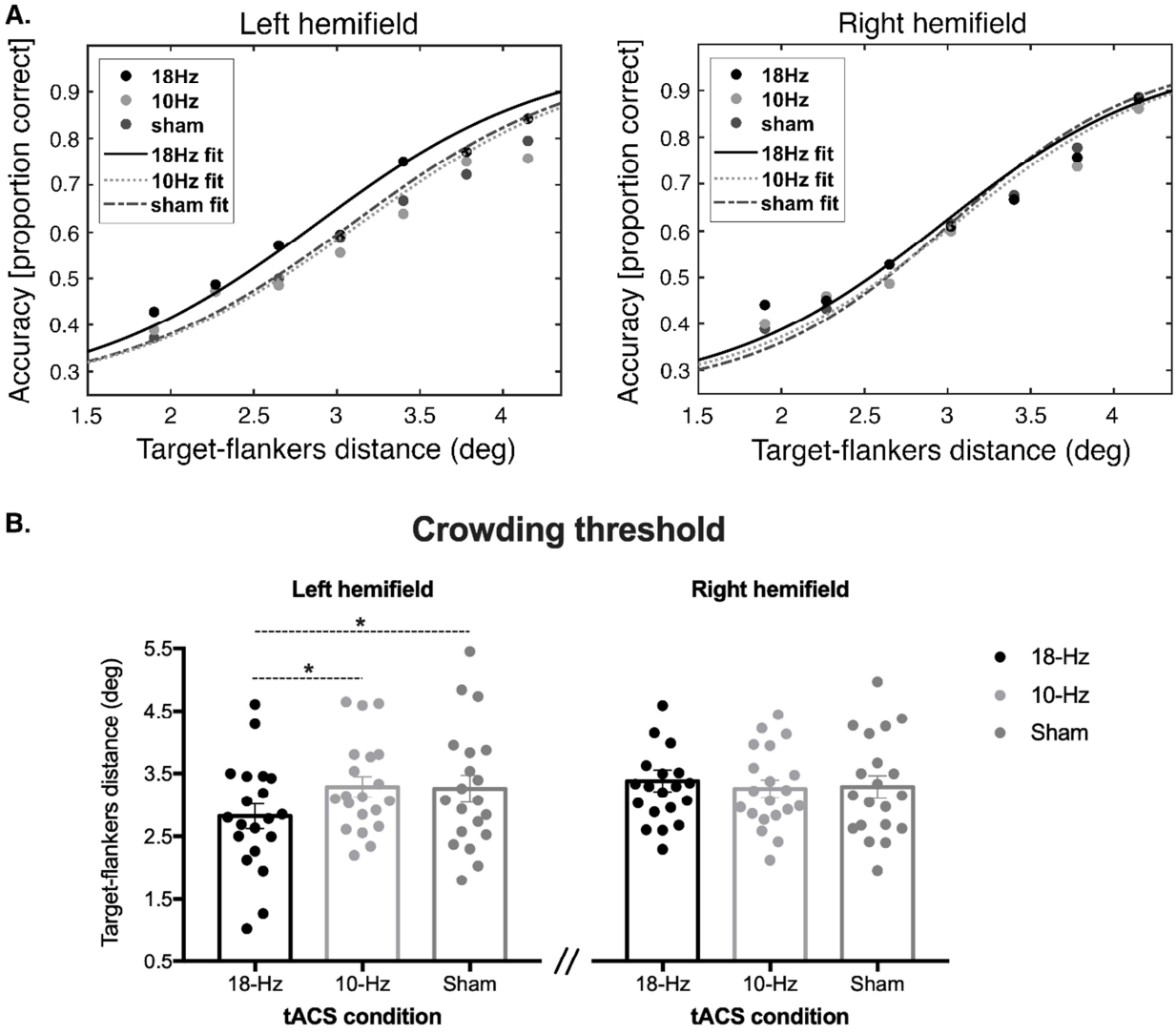

Figure 2. Beta tACS improved crowded perception. (A) Psychometric functions obtained from the mean data with 18-Hz tACS (black line), 10-Hz (grey dotted line) and sham (dark grey broken line). Dots represent mean accuracy as a function of target-flanker distance (18-Hz tACS: black dots, 10-Hz tACS: grey dots, sham: dark grey dots). (B) threshold values obtained with 18-Hz, 10-Hz tACS and sham for the left and right hemifield. * indicates pvalue < 0.05 (Bonferroni corrected). Bars represent standard error of the mean and dots represent individual values.

Relationship between tACS phase and perception during visual crowding

Two participants were excluded from the phase analysis due to technical problems that made the tACS data unavailable. Mean accuracy rates for each phase bin (Supplementary Figure 2), divided for left and right hemifield, were analysed with a repeated measures ANOVA with two factors within subjects: Stimulation Condition (10 Hz *vs* 18 Hz) and Phase Bin (6 levels). Mean accuracy

rates for each phase bin when the stimulus was presented in the right hemifield were not affected by the stimulation or tACS phase: indeed, we did not find a significant main effect of the Stimulation Condition ($F_{(1,17)}$ = 07, p = .79; η^2_p = .004) and Phase Bin ($F_{(5,85)}$ = .8, p = .55; η^2_p = .045) and the interaction was not significant ($F_{(5,85)}$ = .21, p = .96; η^2_p = .01). Mean accuracy rates for each phase bin when the stimulus was presented in the left hemifield showed a significant effect of Stimulation Condition ($F_{(1,18)}$ = 10.2, p = .005; η^2_p = .38) indicating higher performance with 18-Hz tACS, but the factor Phase Bin ($F_{(5,85)}$ = 1.18, p = .33; η^2_p = .07) and the interaction ($F_{(5,85)}$ = 1.8, p = .1; η^2_p = .1) were not significant (see Supplementary Figure 2).

Also the second analysis, which was conducted in order to see whether tACS phase modulated performance according to a sinusoidal function, did not reveal any significant effects (all permutation tests p-values>.08; see Supplementary Figure 3).

Effects of tACS on EEG activity

Comparing EEG oscillatory power before and after each stimulation session, we observed a significant increment in beta power after 18-Hz tACS ($t_{(19)}$=-3.58, p_{corr}=.008). On the contrary, no significant differences in beta power were observed after 10-Hz tACS ($t_{(19)}$=-0.67. p_{uncorr}=.255) and after sham stimulation ($t_{(19)}$=-0.30, p_{uncorr}=.385) (see Figure 3).

When we compared EEG oscillatory variations in the alpha band, we observed a significant increment only after the sham condition ($t_{(19)}$=-2.85, p_{corr}=.041). On the contrary, no differences in alpha power were observed after 18-Hz tACS ($t_{(19)}$=-1.74, p_{corr}=.39) and after 10-Hz tACS ($t_{(19)}$=-1.43, p_{uncorr}=.085) (see Figure 3).

Finally, we performed additional analyses to check whether the power of delta (0.5-4 Hz), theta (4-7 Hz) and low-gamma (25-40 Hz) frequency bands changed after 18 Hz tACS. We did not find any significant increment of the power in these other frequency bands (all ps>0.26).

[Figure 3 about here]

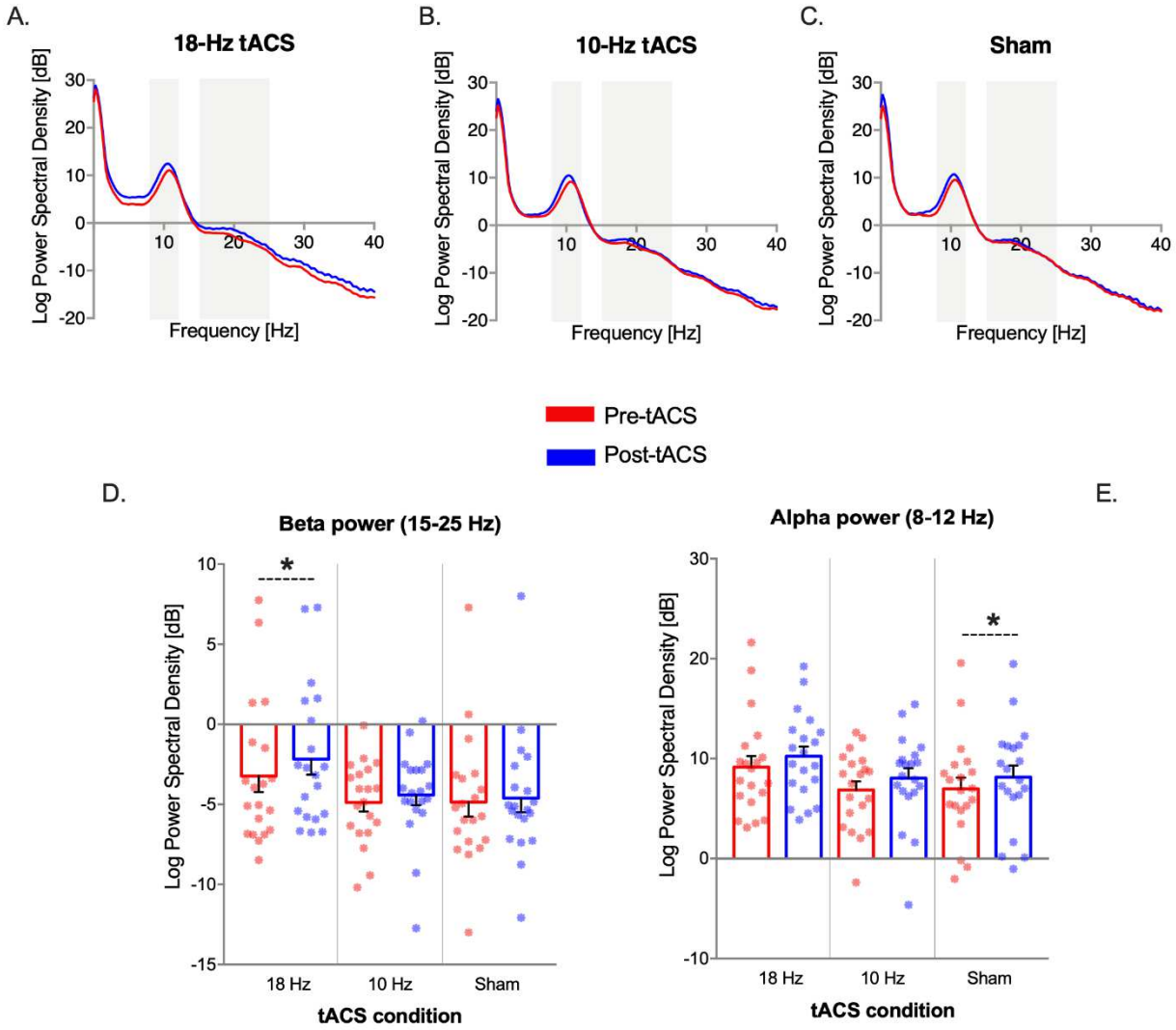

Figure 3. Effect of tACS on resting-state neural oscillations showing a selective increment of parietal beta (15-25 Hz) oscillations after 18-Hz tACS. Power spectrum of resting-state EEG before and after 18-Hz (A), 10-Hz (B) or sham (C) tACS from the channel P4. The frequency band of interest (alpha and beta) are highlighted by the shaded gray areas. The average power values obtained from these power spectrums are shown in the plots below as a function of the type of stimulation (i.e. tACS condition) and time of recording (Pre- vs. Post-tACS), separately for the beta (D) and alpha (E) frequency band. *=p<.05 (Bonferroni corrected). Dots represent individual values. Error bars indicate SEM.

Discussion

Visual crowding is a primary bottleneck for conscious object recognition. In this study we conducted an investigation of possible ways to modulate visual crowding with tACS at different frequencies. Our aim was to enrich our comprehension of the neural mechanisms of visual

crowding. We started from the relationship between visual crowding and beta oscillatory activity (Ronconi et al., 2016; Ronconi and Bellacosa Marotti, 2017) and from the fact that tACS can be a method to shape perceptually relevant brain oscillations (Cecere et al., 2015; Helfrich et al., 2014; Neuling et al., 2012; Stonkus et al., 2016; Wolinski et al., 2018). We hypothesized that tACS within the beta frequency band (18 Hz) would improve the performance in a visual crowding task compared to a control frequency (10 Hz) or to a no stimulation (sham) condition, and tested this hypothesis using a classical crowed letter orientation discrimination paradigm.

Our results showed a lower threshold for stimuli presented in the contralateral hemifield and when participants were stimulated with right parietal 18-Hz tACS, as compared to 10-Hz tACS and to the sham stimulation on the same cortical area. The specificity of 18-Hz tACS (vs. 10-Hz tACS) speaks in favour of a precise oscillatory frequency characterizing the activity of the right parietal cortex in crowding tasks. Importantly, the specificity of the effect for the contralateral hemifield was wanted and often used (Battaglini et al., 2017; Bender et al., 2019; Wolinski et al., 2018) to exclude a tACS effect due to participants' differential feeling of sham from real stimulation that would have shown an effect on both visual hemifields.

The central aspect of the present findings is a threshold modulation observed for the 18-Hz parietal tACS, whereas stimulation at 10-Hz did not show any effect. This indicates the specificity of the tACS in the beta band applied over the right parietal cortex in resolving crowding. This result is in line with previous EEG studies that showed that beta power, but not alpha, is modulated by the strength of crowding (Ronconi et al., 2016; Ronconi and Bellacosa Marotti, 2017). Moreover, in our study, analysing the resting state EEG activity, we observed that beta parietal tACS was able to induce a significant power increment in the corresponding frequency band, whereas the same effect was not observed with alpha parietal tACS. This evidence is in line with previous findings about the fundamental role of beta oscillations in the excitability of the parietal cortex, as opposed to alpha oscillations that seem to be more related to the occipital cortex excitability (Cabral-Calderin and Wilke, 2019; Samaha et al., 2017).

All these results corroborate the link between the beta frequency in the parietal cortex and the visual crowding previously reported in the literature (Ronconi et al., 2016; Ronconi and Bellacosa Marotti, 2017). Since in these previous studies visual crowding was found to be related to both event-related beta desynchronization and pre-stimulus beta power, one potential target of the 18-Hz tACS protocol used here could be the interplay between pre-stimulus beta power and event-related beta desynchronization. Indeed, in the literature looking at the behavioural and neurophysiological effects of tACS in the alpha band, there are studies showing that continuous tACS applied during a task is capable of enhancing event-related alpha desynchronization likely by boosting pre-stimulus alpha power (Kasten et al., 2018; Kasten and Herrmann, 2017).

One critical aspect of the current finding that needs to be mentioned is that we could not find a significant variation of EEG alpha power over and above the variation observed in the sham condition which has been reported in some previous studies (e.g. Zaehle et al. 2010; Neuling et al. 2013; Vossen et al. 2015; Kasten et al. 2016; Kasten and Herrmann 2017). Beyond an intrinsic limit of our experimental design, which did not calculate individual alpha frequency which might have led to different results, we can identify at least three possible reasons for this null effect. First, one major difference that might explain this discrepancy could be that resting EEG has been obtained during eyes-closed condition, and several studies indicate that tACS may not modulate alpha oscillations during eyes-closed states (Neuling et al., 2013; Ruhnau et al., 2016). Second, contrarily to the present study where we used a high-density montage that delivered the electrical current selectively on the right parietal area, some previous studies that found a significant effect of alpha tACS on perception have employed a standard montage with larger stimulation electrodes (e.g. Helfrich et al. 2014; Cecere et al. 2015). Those montages can cause change in activity in many cortical areas at the same time (e.g. occipital and parietal) and thus, it remains to be evaluated whether previously reported behavioural modulation induced by alpha tACS are ultimately due to the stimulation of occipital or parietal areas. Third, we might have targeted a brain region that is not one of the main sources of the alpha activity. At this proposal, recent TMS-EEG evidence support

the idea that alpha is the main rhythm of the occipital cortex and beta is the main rhythm of parietal areas. Samaha and colleagues, in particular, found that phosphene perception induced by occipital TMS was influenced by the power of the prestimulus/ongoing EEG in posterior (occipital) regions, while phosphene perception induced by parietal TMS was modulated by the power of EEG beta oscillations (Samaha et al., 2017). Moreover, other TMS studies showed that the dominant EEG oscillatory response evoked by TMS to occipital cortex is within the alpha band, whereas the dominant response after parietal TMS is within the beta band (Rosanova et al. 2009; Ferrarelli et al. 2012; for similar findings see Kundu et al. 2014). Overall, these TMS-EEG findings support the existence of partially distinct neural mechanisms that are responsible for alpha and beta activity with influence on perception.

Modulation of beta oscillations is often associated to an endogenous perceptual reorganization (Belitski et al., 2008). Indeed, modulation of beta-band power has been associated to the perceptual switch in bi-stable pictures (Ehm et al., 2011; Kornmeier and Bach, 2012; Okazaki et al., 2008), binocular rivalry (Piantoni et al., 2010) and bi-stable motion (Zaretskaya and Bartels, 2015). Beta band power has also been related to other perceptual tasks such as visual form-motion integration (Aissani et al., 2014), perceptual binding of ambiguous visual motion (Costa et al., 2017) and perceptual grouping (Zaretskaya and Bartels, 2015), phenomena that may underlie crowding (Chakravarthi and Pelli, 2011; May and Hess, 2007; Strappini et al., 2017).

Consistent with the view that beta oscillations are associated to an endogenous perceptual reorganization, which also occurs when perception switches from crowded to uncrowded, is the hypothesis that the perceptual reorganization promoted by tACS during a crowding task consists in an increase of the efficiency of the mechanism underlying uncrowded perception. But what mechanism would be made more efficient by beta tACS? There is general consent that to perceive an uncrowded visual world the output of detectors activated by several simple features belonging to a target has to be combined into an integrative receptive field of appropriate size for isolating the target from the background (not too large not too small). Fast and automatic feedforward processing

in the dorsal stream is inadequate because it only provides information on undetailed basic features (Hochstein and Ahissar, 2002; Jehee et al., 2007) and their spatial location (Vidyasagar and Pammer, 2010). Figure-ground segmentation mechanisms need to be activated in the ventral stream or in lower level areas in order to select the appropriate (smaller) receptive fields (Lamme and Roelfsema, 2000; Lee et al., 1998) for isolating the target from flankers. There is general consent that interactions between higher and lower visual areas through activation of feedback would be needed in order to activate these visual filters with small, high-resolution receptive field and obtain a detailed representation of visual images (Hochstein and Ahissar, 2002; Jehee et al., 2007; Lamme and Roelfsema, 2000; Lee et al., 1998).

We speculate that, by synchronizing the activity of parietal areas with the tACS at the appropriate frequency, it is possible to promote long-range synchrony between bottom-up and top-down processing involved in visual perception (Costa et al., 2017) and the dorso-ventral feedback might become more efficient and facilitate local information processing, thus inducing a good discrimination of target from flankers and inducing active disambiguation. Some studies might support our speculation. For example, it has been shown that beta band connectivity is the preferential rhythm for communication within the right fronto-parietal network (that gives top-down feedback to ventral areas for selecting spatial location for further processing) during spatial attention tasks (Siegel et al., 2008). Patterns of rhythmic beta TMS stimulation in frontal right areas lead to greater entrainment of local oscillations and to higher conscious detection of contralateral stimulus compared to random patterns (Vernet et al., 2019) and visual alertness processes correlate with a prestimulus beta band activation (Britz et al., 2011). Interestingly, 18-Hz tACS facilitation was found especially when the target-flanker distance was at threshold level, suggesting that dorso-ventral feedback becomes more effective in local information processing when the stimulus configuration is ambiguous (in our task, close H flankers can make ambiguous the orientation of the T target).

Given that the effects of 18-Hz tACS was found with tACS applied to parietal cortex, we suggest that the parietal cortex activation contributes to the changes from global (crowded) to local (uncrowded) perception mediated by dorso-ventral feedback. These perceptual changes are not exogenously driven but rather endogenously driven by the task, and possibly mediated by feature-based attention (Vidyasagar and Pammer, 2010). This suggestion is consistent with previous studies showing that switches in perception have been related to the parietal cortex activation (Britz et al., 2011, 2009; Carmel et al., 2010; Kanai et al., 2010). Our results therefore confirm the suggestion that the parietal beta-band activity plays a role in internally, rather than externally driven changes in perceptual processing (Zaretskaya and Bartels, 2015).

Resting state EEG activity showed that only beta parietal stimulation was able to induce a significant power increment in the corresponding frequency band in line with previous studies that showed that beta activity is predictive of the excitability of the parietal cortex (Cabral-Calderin and Wilke, 2019; Samaha et al., 2017). On the contrary, we did not observe a comparable significant alpha power increment after the 10-Hz tACS, but we observed only an alpha power enhancement after sham, which might be caused by tiredness after the task (Benwell et al., 2019).

We also tested whether there was an association between specific 18-Hz tACS phase and performance when the stimulus was presented in the left hemifield, or if the modulation of performance followed a sinusoidal function as it would be predicted by a true neural entrainment effect. In both analyses, we did not find a significant modulation of task accuracy as a function of tACS phase. There is a growing number of studies showing the importance of tACS phase at the onset of the stimulus. Polanía and colleagues (Polanía et al., 2012) showed a decrease of reaction time during a working memory task during a specific phase of 6Hz theta tACS delivered over the frontal and parietal areas. Helfrich and colleagues (Helfrich et al., 2014) using a visual oddball paradigm showed that the phase of the tACS modulates target detection performance. Similarly, Neuling et al. (Neuling et al., 2012) showed that the perception of auditory stimuli embedded in noise was modulated by the phase of tACS delivered within the alpha frequency. Most of the

studies targeting theta/alpha oscillations with tACS suggest that a stimulus can be elaborated better during a specific phase of the alpha wave that is associated to higher neural excitability. However, at present there is no neurophysiological evidence of a clear relationship between the phase of beta oscillations and neural excitability. Thus, applying the same logic of 'duty cycle' (i.e. the one half of the alpha cycle associated to a better perception and higher neural activity) to beta oscillations may be misleading (Samaha et al., 2017). The majority of previous studies looking at the relationship between theta/alpha tACS phase and perception/cognition interpreted the observed effects as the consequence of the entrainment of endogenous neural oscillations, based on behavioural (Neuling et al., 2012), EEG (Stonkus et al., 2016) or both (Helfrich et al., 2014) evidence. In the present study, on the one hand we found a significant modulation of EEG beta band power after tACS, which is one of the criteria to establish the presence of neural entrainment; indeed, an increased post-tACS EEG power is supposed to reflect a large population of neurons that become phase aligned to the tACS frequency and resonate at this frequency even after the end of the stimulation (Hanslmayr et al., 2019; Romei et al., 2011). Another evidence would be the presence of phase alignment of the population activity to the entraining tACS frequency during the stimulation itself (Hanslmayr et al., 2019). In our study however, we cannot test this second criterion because we did not record EEG data during the stimulation. It is important to note, however, that these data would be massively contaminated by tACS artefacts and, at present, there is no agreement in the literature on what is the best approach to remove them (e.g. see Noury et al., 2016; Noury and Siegel, 2017). A third sign of entrainment of brain oscillation would be a significant modulation of task accuracy by tACS phase, especially if such modulation follows a sinusoidal function. In our data, however, we did not find evidence of a phasic modulation of accuracy. This could be possibly attributable to the limited number of trials going into each phase bin (for a recent discussion of different phase analysis approaches see Zoefel et al., 2019), and future studies are needed to better address this question with appropriate statistical power.

In conclusion, we found that 18 Hz electrical stimulation of the parietal cortex enhanced perceptual discrimination in conditions of visual crowding. Our results showed a hemifield-specific effect and a frequency-specific effect, which constitute two important internal controls for this study.

The demonstration that parietal tACS at beta frequency not only impacts on behaviour but also significantly affects endogenous oscillatory dynamics suggest, more broadly, that the efficiency of the right dorsal fronto-parietal network can be modulated by tACS at relevant frequencies, with potential applications in many other aspects of perception and cognition, such as reading (Barollo et al., 2017; Bertoni et al., 2019; Zorzi et al., 2012). Our findings constitute the first demonstration that visual crowding can be reduced through the application of beta neurostimulation in the parietal area and contributes to enlighten the neural mechanisms and the oscillatory fingerprint of a fundamental aspect of human vision.

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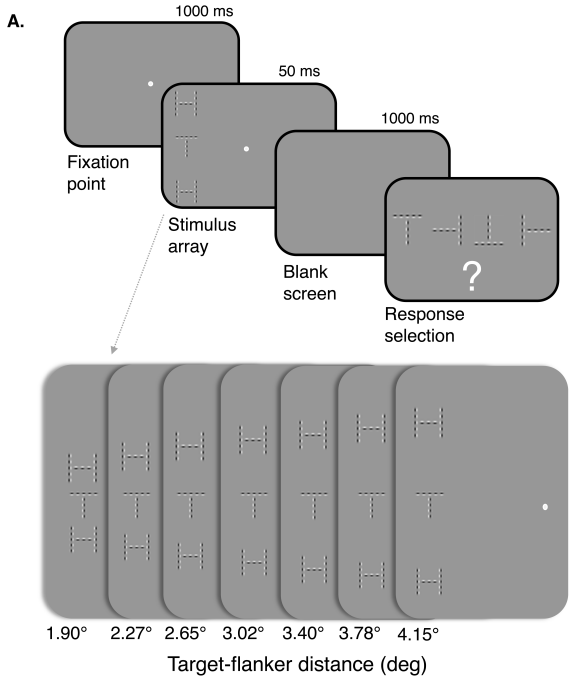
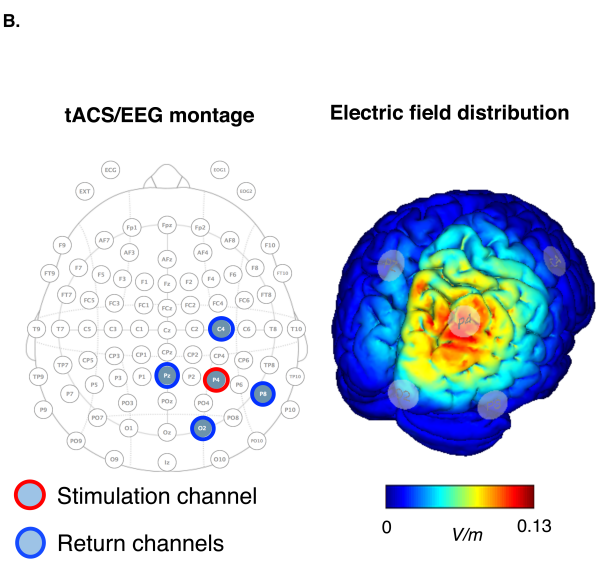
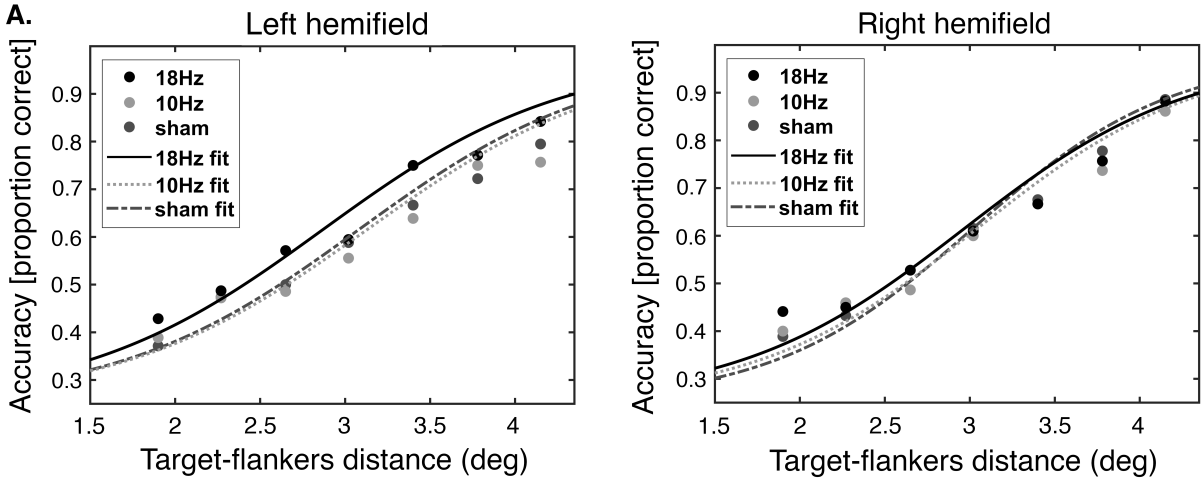
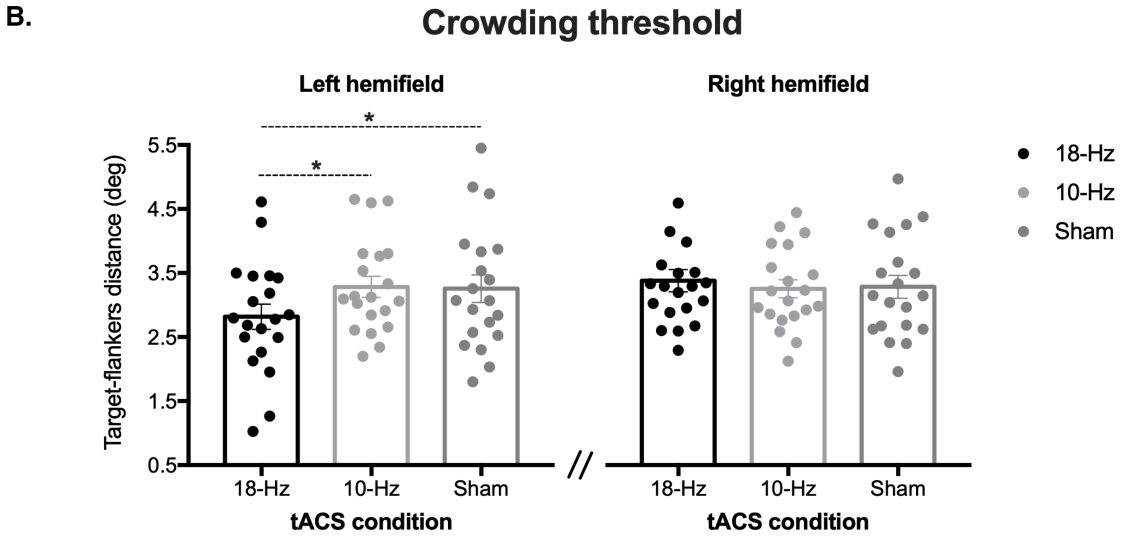
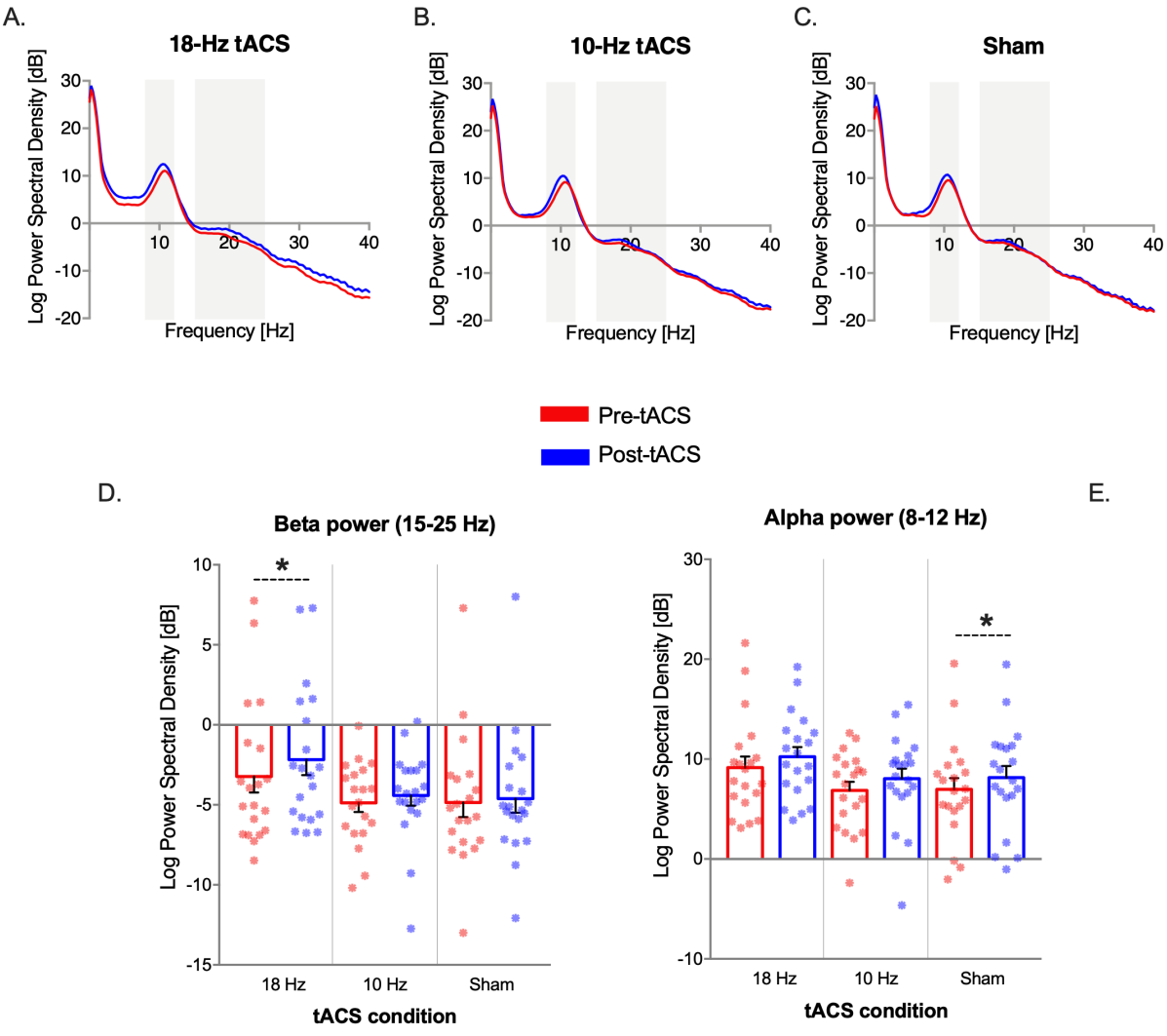

A.
1000 ms
50 ms
1000 ms
Fixation point
Stimulus array
Blank screen
Response selection
1.90°
2.27°
2.65°
3.02°
3.40°
3.78°
4.15°
Target-flanker distance (deg)


B.
tACS/EEG montage
Electric field distribution
Stimulation channel
Return channels
0
V/m
0.13


A.
Left hemifield
Right hemifield
18Hz
10Hz
sham
18Hz fit
10Hz fit
sham fit
Accuracy [proportion correct]
Target-flankers distance (deg)


B.
Crowding threshold
Left hemifield
Right hemifield
Target-flankers distance (deg)
18-Hz
10-Hz
Sham
tACS condition


A.
18-Hz tACS
B.
10-Hz tACS
C.
Sham
Log Power Spectral Density [dB]
Frequency [Hz]
Pre-tACS
Post-tACS
D.
Beta power (15-25 Hz)
E.
Alpha power (8-12 Hz)
*
18 Hz
10 Hz
Sham
tACS condition