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Transcranial direct current stimulation over right posterior parietal cortex changes prestimulus alpha oscillation in visual short-term memory task ☆

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ABSTRACT

Alpha band activity changes accompanied with the level attentional state, and recent studies suggest that such oscillation is associated with activities in the posterior parietal cortex. Here we show that artificially elevating parietal activity via positively-charged electric current through the skull can rapidly and effortlessly change people's prestimulus alpha power and improve subsequent performance on a visual short-term memory (VSTM) task. This modulation of alpha power and behavioral performance, however, is dependent on people's natural VSTM capability such that only the low performers benefitted from the stimulation, whereas high performers did not. This behavioral dichotomy is accounted by prestimulus alpha powers around the parieto-occipital regions: low performers showed decreased prestimulus alpha power, suggesting improvement in attention deployment in the current paradigm, whereas the high performers did not benefit from tDCS as they showed equally-low prestimulus alpha power before and after the stimulation. Together, these results suggest that prestimulus alpha power, especially in low performers, can be modulated by anodal stimulation and alter subsequent VSTM performance/capacity. Thus, measuring alpha before stimulus onset may be as important as measuring other VSTM-related electrophysiological components such as attentional allocation and memory capacity related components (i.e. N2 posterior-contralateral, N2pc, or contralateral delay activity, CDA). In addition, low VSTM performers perhaps do not suffer not only from poor VSTM capacity, but also from broad attentional mechanisms, and prestimulus alpha may be an useful tool in understanding the nature of individual differences in VSTM.

Introduction

Oscillation is an intrinsic property of neuron activity (Buzśaki and Draguhn, 2004; Hsieh and Ranganath, 2014). Ever since the strongest electrophysiological signal, alpha oscillations were measured from human waking brain, and alpha activity has been interpreted as the state of "cortical idling" for a long time (Pfurtscheller et al., 1996). This interpretation was based on the finding that alpha activity recorded from parieto-occipital areas would increase when subjects are awake but not engaged in any task. Recent studies, however, suggest that the function of alpha activity is much more than "cortical idling" (for a review, see Klimesch et al., 2012). For example, the state of alpha activity preceding the target stimuli strongly correlates with the performance of the following visual detection task and discriminability of threshold-level stimuli (Ergenoglu et al., 2004; Hanslmayr et al., 2007; Linkenkaer-Hansen et al., 2001; Romei et al., 2008a,b; van Dijk et al., 2008). Thus, the increased alpha oscillations have been suggested to either reflect active processing related to task relevant information (Palva and Palva, 2007) or inhibit the regions that are not required for the task (Jokisch and Jensen, 2007; Klimesch et al., 2007). In addition, decreased alpha band oscillations have also been found to be highly correlated with performance of subsequent tasks. For instance, trial-by-trial variability in alpha oscillation at baseline covaries with the variability of forthcoming stimuli processing in a visual discrimination task (Babiloni et al., 2006; Ergenoglu et al., 2004; Gonzalez Andino et al., 2005; Hanslmayr et al., 2007; Romei et al., 2008a,b; Thut et al., 2006; van Dijk et al., 2008; Womelsdorf et al., 2006). Similar results also were found by van Dijk et al. (2008), where participants were required to detect different contrast stimuli at detection threshold: trials were sorted according to the level of prestimulus alpha power and divided into four quartiles, and the hit rate in the first quartile (i.e. low alpha power) was found to be significantly higher than that in the fourth quartile (i.e. high alpha power). This important observation of an increase in hit rates with decreased alpha power strongly

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suggests that prestimulus alpha power is highly correlated with subsequent contrast-discrimination ability in a simple visual task. Electrophysiological evidence supported these arguments by showing an inverted-U relationship between prestimulus alpha power and stimulus evoked P1 amplitude (Rajagovindan and Ding, 2011). Converging evidence therefore implies that prestimulus brain rhythm seems to be important for subsequent perceptually tasks.

Perhaps the most well-known function of alpha power is its relationship with changes of attentional state (Fries et al., 2008; Payne et al., 2013; Sauseng et al., 2005; Thut et al., 2006; Worden et al., 2000). One notable evidence comes from a visual attentional study in which a central cue was presented to direct participants' attention to the location of a subsequent target. The topographic distribution of alpha-band activity changed depending on the loci of attention. That is, the alpha activity showed retinotopically organized pattern depending on where attention was allocated. Alpha activity increases contralaterally for the unattended space (Rihs et al., 2007). Moreover, alpha oscillation not only changed with the state of ongoing visual attention, the anticipatory attention during prestimulus period, but also altered prestimulus alpha oscillations and influenced subsequent behavioral performance (Rajagovindan and Ding, 2011; Rohenkohl and Nobre, 2011). This influence of prestimulus alpha oscillations on subsequent performance was examined by transcranial magnetic stimulation (TMS) study. Rhythmic TMS was applied over the posterior parietal cortex (PPC) immediately before visual target onset. It was found that only 10 Hz TMS without any delay would affect perception. When the target was presented contralateral to the 10 Hz TMS site, performance was significantly impaired relative to the 5 Hz and 20 Hz TMS. Conversely, when 10 Hz TMS was administered ipsilateral to the target, participants' performance would be significantly enhanced compared to 5 Hz and 20 Hz TMS (Romei et al., 2010). These interesting results suggest that low prestimulus alpha power, at least around the PPC area, may play a critical role in inhibiting irrelevant visual information/influence from other unrelated brain regions in order to regulate the attentional state for the forthcoming information. Indeed, PPC has been implicated to be the key region in biasing spatial attention in perception through an interaction between dorsal frontoparietal cortex and occipital visual regions (Corbetta and Shulman, 2002; Kastner and Ungerleider, 2000; Lane et al., 2011, 2013; Serences and Yantis, 2007). Importantly, it is also the entrance point of attentional anticipation on prestimulus alpha oscillations (Bressler et al., 2008; Capotosto et al., 2009, 2012; Romei et al., 2010; Taylor and Thut, 2012; Thut et al., 2011).

In visual short-term memory (VSTM), fMRI studies have strongly suggested that right posterior parietal cortex (rPPC) mediates the capacity of VSTM. The activity of rPPC increases with increasing number of items encoded in VSTM. Furthermore, rPPC activation in BOLD signals and VSTM capacity from behavioral performance are highly correlated (Gillebert et al., 2012; Todd and Marois, 2004; Vandenberghe and Gillebert, 2013; Xu and Chun, 2006). To further test the functional role of rPPC, noninvasive stimulation technique such as TMS (e.g. Beck et al., 2006; Tseng et al., 2010) and transcranial direct current stimulation (tDCS) has also been used. The neurophysiology of tDCS, in short, is that anodal (positively charged) stimulation should selectively increase neural spike levels beyond baseline activity by modulating GABAergic activity (e.g., Utz et al., 2010), and vice versa for cathodal stimulation (negatively charged), and the two usually elicits improved or impaired behavioral performance, respectively (e.g. Dayan et al., 2013; Hsu et al., 2011; Miniussi and Thut, 2010; Miniussi et al., 2012; Nitsche et al., 2008). Recently, Tseng et al. (2012) found that anodal tDCS over rPPC could alter low-performers' VSTM capacity and its corresponding ERP component, the amplitude of N2pc and SPCN. Therefore, the aforementioned evidence converges to indicate that rPPC may play a crucial role on memory capacity. Tseng et al. (2012) study, however, did not rule out the potential possibility that rPPC anodal stimulation may modulate attention anticipatory on prestimulus alpha oscillations. That is, it remains possible that participants' performance improved not only because of improved memory maintenance and comparison, but also due to better anticipation, or focused attention. Therefore, the current study aims to investigate, via the use of anodal tDCS, whether the modulation of rPPC activity could influence attention and, if so, exhibits such effect on prestimulus alpha power. If anodal stimulation on rPPC could modulate attention, reduced prestimulus alpha power and increased memory performance will be expected.

Moreover, many studies have suggested that alpha oscillations could vary widely across individuals (van Dijk et al., 2008). Similar patterns of individual differences were also observed in ERP (Tseng et al., 2012; Vogel and Machizawa, 2004) and fMRI (Todd and Marois, 2004). Therefore, we also expect to observe a wide range of individual differences in prestimulus alpha power: that is, high performers should have lower prestimulus alpha power than the low performers do.

Methods

Participants

Twenty neurologically normal college students with normal or corrected-to-normal vision participated in the experiment (7 males, 13 females; mean age = 22). All gave informed consent prior to participation. All experimental and tDCS procedures were approved by the Institutional Review Board of the Chang Gung Memorial Hospital, Linkou, Taiwan. The study used a within-subject design, thus each person participated on 2 different days for offline anodal and sham tDCS sessions. The order of all the sessions was counterbalanced across all participants. Since one participants EEG data was missing (due to unintended machine malfunction), only nineteen participants were included and analyzed in time–frequency analysis.

tDCS protocol

To test the functional role of rPPC, anodal tDCS was applied over rPPC, located as P4 according to the International 10–20 System, for EEG electrode placement. Since tDCS requires two electrodes that simultaneously stimulate P4 and inhibit another, the reference electrode was placed on the left cheek (Berryhill et al., 2010; Hsu et al., 2011) to avoid any confounding effect from other brain regions. The current was applied for 15 min, excluding the total duration of fade in and fade out time (15 s each, 30 s total), with an intensity of 1.5 mA, which can create an excitatory effect for up to 90 min (Nitsche and Paulus, 2001). The duration of the sham tDCS condition is the same as the anodal tDCS condition. However, sham stimulation only included 15 s of fade in and fade out time (30 s total), and in the remaining 15 min the tDCS stimulator was inactive. This fade in and out times in the sham condition allowed participants to feel the slight tinkling sensation of the current passing through the skin (but without actual stimulation), so that the participants were unaware of which session they were participating in (single blind design). tDCS sessions were conducted using a Neuroconn Eldith DC-stimulator and a pair of electrodes housed in 4 × 4 cm saline-soaked sponge coverings.

The asymmetrical effect induced by anodal and cathodal stimulation has been reported in previous tDCS studies (Berryhill et al., 2010; Nitsche and Paulus, 2001). To identify which polarity would affect participants' performance, one pilot study was done to test the effects of anodal, cathodal and sham on VSTM performance. Anodal (or cathodal) stimulation was applied over rPPC for 15 min, excluding the total duration of fade in and fade out of 30 s (15 s each), with an intensity of 1.5 mA. After stimulation, participants performed the change detection task (please refer to the Experimental design section for details). Ten participants were recruited in the pilot study and they all received anodal, cathodal and sham conditions on different days. The results showed significant tDCS modulation over K value ($F(2,18) = 6.778$, $MSE = .347$, $p = .006$). The simple main effect showed that the significant difference was coming from the comparisons of sham vs. anodal

($p = .001$) and cathodal vs. anodal ($p = .004$), but not cathodal vs. sham ($p = .55$). Since the pilot experiment did not reveal a reliable effect of cathodal stimulation, the present study focused on the facilitating effects of anodal stimulation to see if VSTM performance and alpha band activity could be improved with increased rPPC activity.

EEG protocol

EEG activity was recorded with Ag/AgCl electrodes mounted in an elastic cap (Electrocap International) using a 64-electrode arrangement following the International 10–20 System, online reference adopted typical reference electrode site, sitting between Cz and CPz. Offline referenced to the left and right mastoid. Vertical and horizontal electro-oculograms were also recorded. Electrode impedances were kept below 5 kΩ for all electrodes, and amplifier bandpass was 0.05–70 Hz. Data were recorded with Neuroscan 4.2 software, with a sampling rate of 1000 Hz.

EEG data with time–frequency analysis

All data analysis was performed off-line using SPM8 for MEG/EEG (Wellcome Department of Cognitive Neurology, London, UK; www.fil.ion.ucl.ac.uk/spm/) and custom MATLAB (MathWorks) scripts. The continuous EEG data were stimulus-locked to the onset of memory array, from 1000 ms prior to and 1600 ms following the memory array. Trials containing artifacts exceeding ±150 μV were excluded from the time–frequency analysis. Each epoch was analyzed with a Morlet wavelet transform (i.e., $mf_0\sigma_t = 6$) from 2 to 45 Hz (Roach and Mathalon, 2008). Oscillatory power, defined as the square of the modulus of the resulting complex number, was then averaged across trials. The averaged oscillatory power for each condition for each participant was estimated from 400 to 0 ms before the fixation offset (i.e. 600th to 1000th ms after fixation onset.). This was defined as prestimulus period. The range of prestimulus alpha power was defined 8–13 Hz from posterior sites (PO3, POZ, PO4, O1, OZ, O2). Two trial types, anodal and sham trials, were subjected to statistical analysis with all trials averaged according to their trial type. A two way mixed-effect ANOVA was conducted to test whether prestimulus alpha power has changed between groups (low vs. high) and tDCS (anodal vs. sham) conditions. To further address where and how strong was the effect of anodal stimulation on prestimulus alpha oscillation within low and high performance groups, in addition to the analysis of alpha power within specific electrodes, whole brain electrodes were recruited to test the modulation of anodal stimulation over whole brain prestimulus alpha power. T-test (Jacobson et al., 2012) was conducted to test the difference of prestimulus alpha power between anodal and sham condition within each group. The results are plotted as T-maps for each group by time (Fig. 4).

Experimental design

Participants were required to perform a change detection task. Each trial began with a 1000 ms fixation cross, followed by a 200 ms memory array, 900 ms retention interval, and a 2200 ms test array (Fig. 1).

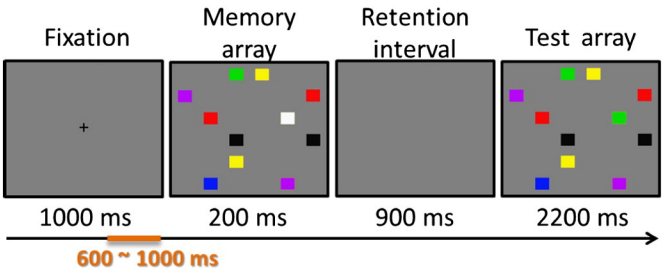

Fig. 1. Trial procedure. On half of the trials, one square would change color. The orange bar indicates the time window selected for analysis of prestimulus alpha power.

Participants were required to use their right hand to press number '1' on the keyboard when there was a change, or to press number '2' for no change.

The entire display extended approximately 31° × 24°, which is bigger than most change detection studies in order to increase task difficulty and avoid ceiling effects (note that an even bigger version has been used before successfully in a change detection paradigm by Tseng and Bridgeman (2011)). Therefore, the improvement in VSTM performance here may be underestimated due to the bigger display. All trials consisted of 11 rectangles of different colors, sized at 1.6° visual angle wide and 1.3° visual angle tall. All rectangles were kept at least a vertical distance of 1° visual angle and a horizontal distance of 2.4° visual angle apart. Each rectangle was randomly selected from a pool of 7 highly discriminable colors (red, blue, violet, green, yellow, black, and white), and each color could not repeat more than twice within each trial.

Participants received tDCS stimulation first. Once the stimulation was complete, the experimenters sat up the formal behavioral session with concurrent EEG recording.

Statistical analysis

d′ and Cowan's K were used to measure sensitivity to change and assess VSTM performance, respectively. The estimation of d′ followed the signal detection theory (Macmillan and Creelman, 1991). The rationale of d′ is that the better sensitivity, the greater difference between hit and false alarm rate. In order to compare hit rate and false alarm rate fairly, both measures were transformed to z-scores. Therefore, the formula is d′ = z(hit rate) − z(false alarm rate). On the other hand, the Cowan's K (Cowan, 2001) assumes that an individual can hold K items in memory out of an array of S items such that K = set size ∗ (hit rate − false alarm rate). This equation accounts for guessing by subtracting incorrect guesses from the correct responses.

Results

A two-way mixed-effect ANOVA was conducted to investigate the effects of tDCS (anodal vs. sham) and VSTM capacity (high vs. low). The behavioral indexes were d prime and K, and the electrophysiological index was alpha power during the prestimulus time window.

Behavioral results

In terms of behavioral data, the group of 20 participants varied widely in their VSTM performance, with K ranging between 1.2 and 5.6. To examine whether the effect of tDCS interacted with preexisting individual differences in VSTM performance, we sorted the 20 individuals by their K estimates in the sham condition (range: 1.2 to 5.6 items), and split them by the median score (~3.7 items) (Fukuda and Vogel, 2011). This divided the participants into a high-performing ($n = 10$; mean $K = 4.6$) and low-performing ($n = 10$; mean $K = 2.3$) group based on their natural VSTM capability without tDCS, and the performance ratio between the two groups happened to be 2:1 for K. When we took the variance of individual differences in VSTM into account, we observed a significant interaction in a 2 × 2 ANOVA for tDCS (anodal vs. sham) and groups (high vs. low) in d prime and K. From mixed two-way ANOVA in d′, there was a significant group difference in main effect ($F(1,18) = 38.745$, MSE = 0.107, $p < .001$, $\eta^2 = 0.683$) and an interaction between tDCS and groups ($F(1,18) = 5.847$, MSE = 0.051, $p < .05$, $\eta^2 = 0.245$). However, post hoc analysis did not reveal significant difference between sham and anodal within low ($p = .067$) or high performers ($p = .158$). No tDCS main effect was found ($F(1,18) = .113$, MSE = 0.051, $p = .741$, $\eta^2 = 0.006$). Similarly, mixed two-way ANOVA was also used to analyze K. A significant effect of groups ($F(1,18) = 33.677$, MSE = 0.941, $p < .001$, $\eta^2 = 0.652$) and an interaction ($F(1,18) = 7.78$, MSE = 0.445, $p < .05$, $\eta^2 = 0.302$) were also observed in K. Interestingly, subsequent multiple comparisons showed that anodal tDCS was only facilitative in the low-

performing group ($p = .008$), and tDCS was not helpful in the high-performing group ($p = .344$; please refer to Fig. 2). Again, no tDCS main effect was observed in K value ($F(1,18) = 1.998$, MSE = 0.445, $p = .175$, $\eta^2 = 0.100$).

Time–frequency decompositions with Morlet wavelets

Since one EEG data in the low capacity group was missing, due to unintended machine malfunction, the rest of the EEG data from the same two groups of participants were analyzed using time–frequency analysis to see whether there was an underlying physiological difference between high- and low-performing individuals that could explain their different receptivity to anodal tDCS. The subject number in following the analysis of prestimulus alpha power is 9 (low-performing group) vs. 10 (high-performing group). Behaviorally, d prime and K were both showing a significant difference between groups. Electrophysiologically, prestimulus alpha power was selected from posterior sites (PO3, POZ, PO4, O1, OZ, O2) to test the difference between high- and low-performing individuals. No significant group main effect ($F(1,17) = .188$, MSE = 78.048, $p = .670$, $\eta^2 = 0.011$) and no tDCS main effect ($F(1,17) = .939$, MSE = 3.385, $p = .346$, $\eta^2 = 0.052$) were found, but there was a marginally significant interaction in the two-way mixed ANOVA ($F(1,17) = 4.34$, MSE = 3.385, $p = .053$, $\eta^2 = 0.203$; Fig. 3). The low-performing group showed a marginally significant difference between sham and anodal tDCS stimulation ($p = .05$). The high-performers, on the other hand, showed no difference between sham and anodal stimulation ($p = .429$). A contrast of the low-performing group and high-performing group was also conducted within the sham and anodal conditions. The differences between the low-performing group and high-performing group did not reach significance for the sham ($p = .417$) or the anodal condition ($p = 1$). Whole-brain prestimulus alpha power was further examined by group where low performers showed significant differences between the anodal and sham conditions (marked by red circles; $p < .05$; Fig. 4). After anodal stimulation, prestimulus alpha power was significantly reduced in low-performers. Consistent with our previous findings on N2pc and SPCN (Tseng et al., 2012), the amplitude of both indexes was significantly different under tDCS manipulation in low-performers rather in high-performers. The low-performers showed a decline to their preexisting prestimulus alpha power as a consequence of anodal tDCS, whereas high-performers, who were slightly affected by external stimulation since they had lower prestimulus alpha power to begin with, were not strongly affected by external stimulation as low-performers were.

Discussion

The current study focused on whether prestimulus alpha oscillation would be affected by anodal tDCS, and how such effect would be reflected in one's behavioral VSTM performance. Our results showed a coupling between decreased alpha oscillation during the prestimulus time window and improved memory capacity. The topographic distribution of prestimulus alpha power suggested that the largest difference is concentrated in the occipital region. In contrast, when the prestimulus alpha power was high, poor performance is observed.

Furthermore, the current study employed anodal tDCS stimulation to modulate the neural activity at P4, the entrance point of our observed alpha oscillation. These results showed that anodal stimulation affects the activity of prestimulus alpha frequency band. However, like our behavioral results, the low-performers showed a decrement in alpha power after anodal stimulation. The high-performers, on the other hand, already had a low prestimulus alpha band power to begin with, and their activity of prestimulus alpha oscillation was not strongly affected by external stimulation. Therefore, the effect of anodal stimulation may be more or less state dependent.

Alpha power, visual attention, and cortical inhibition

The main issue of the present study focused on whether anodal stimulation over rPPC could modulate the activity of prestimulus alpha oscillation and further affect subsequent VSTM performance. The results suggest that prestimulus alpha power was strongly modulated by anodal tDCS in low performers during the prestimulus period. Prestimulus alpha oscillation has been suggested to be highly correlated with one's attentional state (Ergenoglu et al., 2004; Hanslmayr et al., 2007; Linkenkaer-Hansen et al., 2001; Romei et al., 2008a,b; van Dijk et al., 2008). Thus, the modulation of prestimulus alpha oscillation may indicate a change in the state of attention, which can explain the improvement in VSTM capacity. Specifically, low alpha power implies strong anticipatory attention (Rohenkohl and Nobre, 2011), therefore the significant decrement in prestimulus alpha power after anodal tDCS seems to suggest enhance anticipatory state of visual attention in our low performers. This account would also be consistent with studies that demonstrated a link between prestimulus alpha oscillation and visual perception (Babiloni et al., 2006; Ergenoglu et al., 2004; Gonzalez Andino et al., 2005; Hanslmayr et al., 2007; Romei et al., 2008a,b; Thut et al., 2006; van Dijk et al., 2008; Womelsdorf et al., 2006).

Another potential explanation that can account for the present findings is the idea of inhibition or disengagement (Cooper et al., 2003; Jensen et al., 2002; Klimesch et al., 2000, 2007; Ray and Cole, 1985; Tuladhar et al., 2007; Vanni et al., 1997). Strong alpha power has been shown to serve an inhibitory role in preventing task-irrelevant visual stream into the brain area that is involved in target processing (Klimesch et al., 2000, 2007). Alpha power has also been shown as a reflection of a state of inhibition or suppression, by those brain regions that are relevant to the current task (Jokisch and Jensen, 2007; van Dijk et al., 2010). This can also explain why low performers had high prestimulus alpha power under the sham condition; because at least one critical locus for VSTM (rPPC, or P4) was highly inhibited, or underutilized. In sum, the prestimulus alpha oscillation is not only a good index to measure the level of attentional involvement for

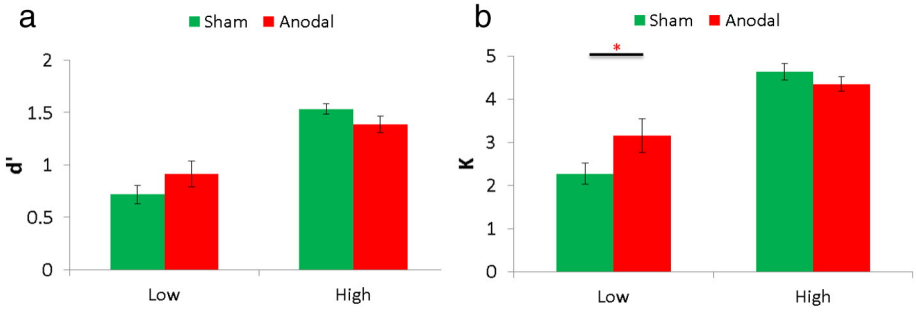

Fig. 2. tDCS-induced improvements in signal detection (d′) and Cowan's K in low performers. (a) d prime shows significant difference between low and high performers. Increment of d′ was found when anodal was applied in low performers. (b) Similar results were also obtained in K. The low-performing group received significant improvement from tDCS. Error bars represent 95% confidence intervals (* for $p < .05$).

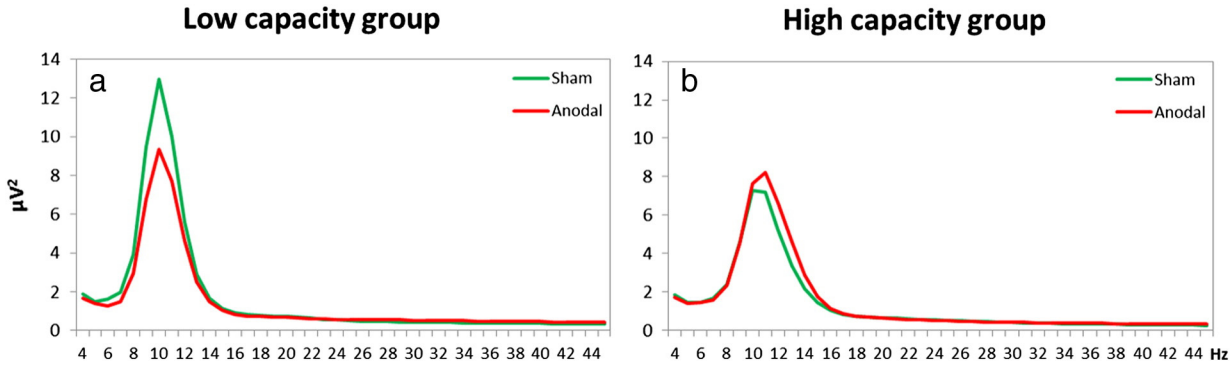

Fig. 3. Anodal tDCS increases alpha power in low performers. (a) Low capacity group shows a different response to anodal stimulation. After anodal stimulation, alpha power dramatically drops to the level closer to high performers. (b) In contrast, high performers show no difference between sham and anodal stimulation.

subsequent visual perception processing, but also capable of explaining the present behavioral results. To our knowledge, this is the first study that demonstrates a rPPC anodal stimulation modulation of prestimulus alpha power and subsequent VSTM performance in low performers.

Alpha power in prestimulus and maintenance stage

The current findings appears to contradict with previous studies that found a positive correlation between alpha activity during the retention interval and memory load in a traditional Sternberg task (Hamidi et al., 2009; Jensen et al., 2002; Palva and Palva, 2007; Scheeringa et al., 2009; Tuladhar et al., 2007). The opposite findings can be explained from two aspects: first, the time window in which the current study measured was obviously different from other studies. Previous studies have focused on the retention period of the Sternberg task, which is an important time window for maintaining information between the memory array and the test array. In contrast, the present was concerned with the stimuli processing up until the encoding stage. Based on the inhibitory filter hypothesis (Klimesch et al., 2007), alpha power reflects inhibitory processes that prevent irrelevant stimuli from interfering with target processing. Consistent with this hypothesis, our results showed a tendency for low prestimulus alpha power to come with better memory performance.

Second, the current task is a change detection paradigm. Although it examined the short-term memory, the nature of the visual change detection task is different from that of a verbal Sternberg task. In a change detection task, performance is highly dependent upon VSTM. From fMRI and TMS studies (Harrison and Tong, 2009; Silvanto and Soto, 2012), it has been found that the occipital cortex strongly contributes to VSTM processing. Thus, it is not surprising that the strong difference of alpha power is observed from those electrodes above the occipital brain region in current study. In contrast, the verbal Sternberg task is concerned with the verbal short-term memory, which does not involve the occipital brain region much. According to Klimesch et al.'s hypothesis (2007), alpha power is stronger in brain regions that are not relevant to the current task set. Klimesch et al. (2007) found that alpha power was stronger in those electrodes right above frontal and parietal areas, which are more involved in visual spatial information processing rather than verbal stimuli. This may explain the discrepancy between our results and prior studies using a Sternberg task.

Individual differences in VSTM capacity and its interaction with tDCS

Individual difference is a critical issue in understanding the nature of VSTM (Luck and Vogel, 2013). It has been demonstrated that VSTM capacity is highly correlated with scores of broad cognitive tasks (Fukuda et al., 2010; Johnson et al., 2013). Vogel et al. (2005) suggested that the underlying cause of individual differences may be attributed to differences in attentional and inhibitory processes. As such, low-capacity performers tend to have less control over which information, relevant and irrelevant alike, to encode into VSTM. High-capacity performers, in contrast, are able to encode only relevant information by successfully

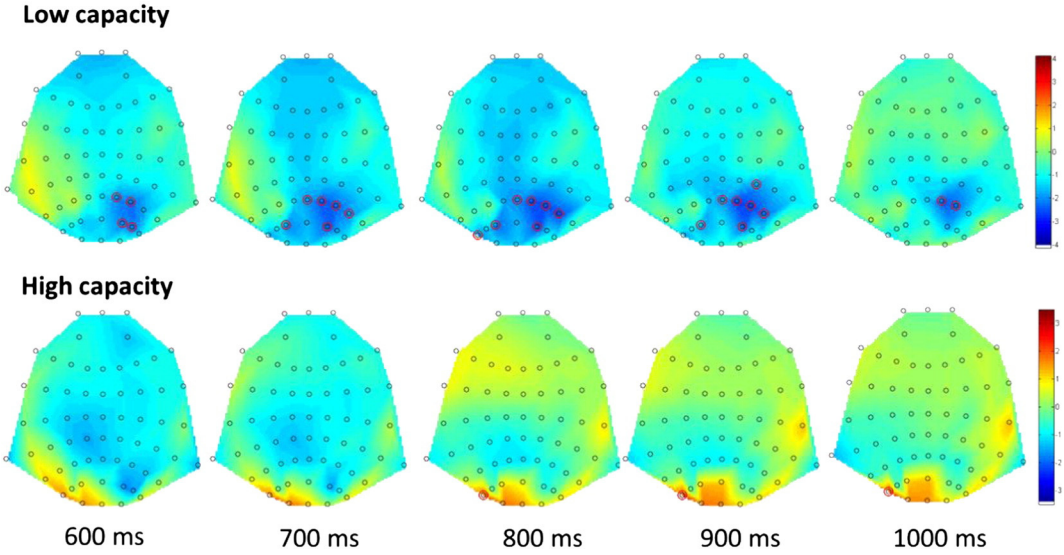

Fig. 4. Contrast of anodal and sham condition in low and high capacity performers. T-maps show that prestimulus alpha power is significantly lower in anodal than sham condition in low capacity performers. Such difference is absent in high capacity performers.

blocking out the irrelevant ones. Furthermore, differences in attentional and inhibitory processes observed in a different amplitude of ERP components are possibly consequences of changes in brain state during the prestimulus period, as indexed by oscillatory activity neurophysiological evidence (Mazaheri and Jensen, 2008). Our findings support this finding and extend the importance of attentional processes to an even earlier time window: the prestimulus period. The general trend of prestimulus alpha power in low capacity performers was for it to be higher than that in high capacity performers in the sham condition. This possibly suggests that the level of alpha power contributes to the subsequent VSTM performance. Also, low capacity performers may have poor broad attentional or inhibitory processes that are reflected on prestimulus alpha power. However, it is also important to highlight the fact that anodal stimulation is only effective in decreasing alpha activity when the initial alpha power is high. Recent studies have suggested that the effect of anodal tDCS seems to be highly interactive with individual capacity and task difficulty, with stronger effects when the level of difficulty is high (Jones and Berryhill, 2012). Therefore, it is possible that the task in the present study was at the optimal level of difficulty for the low performers, but not for the high performers (though our high performers' K measures were far from ceiling). Furthermore, the selectivity of tDCS that targets alpha power is also supported by a recent study using the resting-state paradigm (Spitoni et al., 2013), which observed an effect for tDCS that was limited to alpha oscillations. Interestingly, only anodal stimulation affected alpha oscillations, whereas cathodal stimulation did not elicit any perturbation on spontaneous EEG. Together, these studies may help explain why only low capacity performers were affected by anodal stimulation in terms of alpha power. The individual differences in electrophysiology are not restricted within the timeframe of the task; it can be observed a few hundred milliseconds before the trial. In addition to individual differences in the sham condition, tDCS also induced a different effect in each individual. State-dependency is an important concept in explaining the interaction between the effects of brain stimulation such as TMS and the initial state of stimulated regions. To investigate such state-dependency nature of brain stimulation, researchers have used the transcranial magnetic stimulation adaptation (TMSA) paradigm (Cattaneo et al., 2010; Silvanto et al., 2008) to apply TMS over neurons of a different activation threshold. Interestingly, it was found that the behaviorally facilitating effect of TMS was mostly contributed by the population of adapted neurons, compared with nonadapted ones, within the same stimulated brain area. Specifically, TMS was particularly effective on neurons that were less active, presumably because they had a greater range for firing rate to be increased. Applying these observations to the current context, although the current study did not use TMSA, the state dependent effect of brain stimulation techniques may explain the group difference in memory performance after anodal tDCS. That is, low performers may have less-activated neurons prior to stimulation, thus greater stimulation effects in return. The opposite could be true for high-performers, where highly active neurons have less range for the effect of anodal tDCS to take place. This slight drop of performance induced by tDCS was indeed what we observed in the high performers, although without a statistically significant difference. Furthermore, state-dependent effect may also account for the different findings between the current study and the Berryhill et al. (2010) study, which used a Sternberg working memory task. Since the nature of rPPC is sensitive to spatial configuration of the stimuli, the emphasis on spatial configurations in the present study may activate rPPC differently from those studies using non-spatial stimuli (Berryhill et al., 2010).

Alpha oscillation and physiological evidence

Regarding the reduction of prestimulus alpha oscillation by anodal stimulation in low-performers, the precise effect that anodal stimulation elicits within the cortical layers still needs further investigation. From a physiological standpoint, it has been shown that brain regions that share similar laminar organizations also share similar alpha current distribution as well as the origin of local alpha pacemaker. For example, structurally-similar areas such as V1, V2, and V4 also share similar alpha currents in all layers, including the supragranular (SG), granular (G), and infragranular (IG) layers. Due to these similarities, these brain regions also have identical source of local alpha pacemaker, originating from the IG and G layers in this case. In contrast, structurally-dissimilar areas tend not to share the same laminar organization of alpha current generator or local alpha pacemaker. For example, the source of alpha current generator and local alpha pacemaker of the inferior temporal cortex is situated at the SG layer, which is quite different from the V1, V2, and V4 examples above due to the structural dissimilarity between the two (Bollimunta et al., 2008). But most importantly, all cortical layers can show reduced alpha power, coherence, and Granger causality when they are modulated by attention (Bollimunta et al., 2011). As such, the artificial anodal stimulation may work as in similar ways as internally-generated attention, equally but temporarily exciting each neuron throughout different layers. Such cortical excitability may have contributed to the cortical alpha reduction and enhanced processing of perceptual information. However, one caveat of this account is that it predicts a simple performance improvement in all individuals regardless of their innate ability. Therefore, any account of the effect of brain stimulation would need to consider the context, or the state of the neurons at the moment of the task, in order to fully address the complex results in the literature or the current study. This echoes the state-dependency idea argued by Silvanto et al. (2008) regarding brain stimulation. From the present study, the prestimulus period may be the state during which participants prepares for forthcoming VSTM task. How strong the modulation by anodal stimulation may depend how well each participant prepares for the task.

Limitations

Although the estimate of Pashler's K and Cowan's K is derived from the same discrete-slot working memory model, the choice of K estimate and appropriate task design should be carefully considered. Rouder et al. (2011) suggested that it is principle to report Pashler's K for the whole display design, or Cowan's K for single display design. However, because the design of the present study was derived from the Vogel and Machizawa (2004) study in order to directly compare our behavioral and electrophysiological results with their findings, we opted for the same experimental design (i.e. whole display), procedure, and measure. One point here worth mentioning is that the set size in the present study is 11. No published study so far has assessed which K estimate is appropriate for whole display task with this large set size. On the other hand, we piloted with smaller set sizes (i.e. 6, 8, and 10), and some participants' performance would be quite high, making it difficult to assess the tDCS effect. Therefore, Cowan's K was reported here. These reasons may restrict the extended explanations from the results of the present study. In light of this limitation, systematic manipulations of task, set size, and K estimate are critical for follow-up studies.

Conclusion

The present study demonstrates that prestimulus alpha oscillation is affected by rPPC anodal stimulation and forthcoming VSTM performance, especially in low-performers. The different prestimulus alpha band activity may suggest a different attentional state in each individual. After the application of tDCS over rPPC, decreased alpha oscillation was observed in low-performers, which may account for their improved VSTM performance. Although prestimulus alpha oscillation is not the only factor that contributes to VSTM capacity, our results here suggest that increased alpha during this early time window before stimulus onset and memory maintenance can already have an important impact on subsequent memory performances. Together, the current study

reveals rPPC anodal stimulation modulation of prestimulus alpha power and subsequent VSTM performance in low performers.

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Conflict of interest

The authors declare no conflict of interest.

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