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# Changes in BOLD adaptation and functional connectivity induced by transcranial alternating current stimulation

Kohitij Kar, Takuya Ito, Jessica Wright, Michael W. Cole, and Bart Krekelberg

**Correspondence To:**

Kohitij Kar

Center for Molecular and Behavioral Neuroscience

Rutgers University

197 University Ave

Newark, NJ 07102

E: [kohitij@vision.rutgers.edu](mailto:kohitij@vision.rutgers.edu)

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## Conflict of Interest

A patent application has been ﬁled on subject matter disclosed in this manuscript.

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# Abstract

Transcranial alternating current stimulation (tACS) is used as a non-invasive tool for cognitive enhancement and clinical applications. The physiological effects of tACS, however, are complex and poorly understood. We have previously shown that tACS applied over the motion sensitive area hMT+ in humans, attenuates the behavioral aftereffects of visual motion adaptation. This led to our hypothesis that tACS attenuates adaptation of motion selective neurons. Here we tested this hypothesis using concurrent tACS and fMRI and found that, indeed, tACS attenuated BOLD signal adaptation in the human motion area (hMT+). Beyond BOLD amplitude changes, tACS also resulted in an increase in correlation (i.e. functional connectivity) between hMT+ in the stimulated and non-stimulated hemispheres. Taken together these findings support our hypothesis that tACS attenuates sensory adaptation.

# Introduction

Transcranial alternating current stimulation (tACS) can modulate human behavior when applied over certain brain regions (Cohen Kadosh et al., 2010; Polania et al., 2012; Sela et al., 2012; Struber et al.) and tACS is being established as a potentially powerful neuromodulatory tool. The underlying mechanisms, however, are poorly understood. This lack of understanding stands in the way of the rational development of tACS protocols. We aim to bridge this gap by testing neurophysiological predictions inferred from behavioral measures.

We have previously shown that tACS applied over posterior parietal cortex during the presentation of motion stimuli, attenuates the motion aftereffect (MAE) in human subjects {kar 2014}. Because the MAE is thought to result from the adaptation of direction selective neurons { }, we hypothesized that tACS attenuates adaption. Our intracortical recordings in nonhuman primates provided the first direct neural evidence that, indeed, spike-frequency adaptation in individual neurons of the middle temporal area is reduced by tACS {kar 2016}. Here we pursued this same question in the human brain using simultaneous fMRI and tACS.

Previous neuroimaging studies have identified an area in the human brain (hMT+) that, just as the middle temporal area in the macaque, is highly selective for visual motion (Tootell et al., 1995). (Huk et al., 2001) convincingly showed that neural activity in hMT+, as reflected in the BOLD signal, is reduced after the prolonged presentation of visual motion. Hence, based on our hypothesis that tACS attenuates neuronal adaptation, we predicted that tACS through electrodes positioned over hMT+ in one hemisphere should reduce BOLD adaptation relative to the unstimulated hemisphere.

Our experiments confirmed the prediction; tACS was applied over left hMT+ reduced adaptation in the BOLD responses of the left hemisphere more than the right hemisphere. This provides direct evidence based on human neural activity to support our hypothesis that tACS attenuates adaptation.

# Methods

## Subjects

Ten subjects (5 female) participated in the study. Subjects gave written consent and all had normal or corrected to normal vision. This study was conducted according to the principles expressed in the Declaration of Helsinki and approved by the Institutional Review Board of Rutgers University.

## tACS

We combined transcranial electrical stimulation with MRI acquisition, which has previously been shown to be safe, and result in minimal artifacts and loss of signal to noise (Holland et al., 2011; Antal et al., 2012)(Antal et al., 2011). The stimulus generator was in the control room and connected to the MR compatible, shielded cables (custom CBL200, Biopac) in the scanner room via wall-mounted radio frequency (RF) filters (MRIRFIF, Biopac). The electrode leads were equipped with a 5.6 kOhm resistor to limit RF heating of the head. In addition, we placed each lead in a plastic covering to avoid overlapping wires and wire loops, and thus limit current induction (Brocke et al., 2008; Stagg et al., 2009). The leads were passed out through the side of the head coil and then led along the bore towards the back of the scanner.

We applied tACS using an STG4002 stimulus generator (Multi Channel Systems, Reutlingen, Germany). The circular stimulating electrodes were cut from conductive rubber (7.6 cm diameter), and attached to the scalp using electrode gel (Signa). One electrode was placed above the canonical location of left hMT+; PO7-PO3 in the 10-20 system. The other electrode was placed on the vertex (Cz). The current intensity was 0.5 mA, frequency of tACS was 10 Hz.

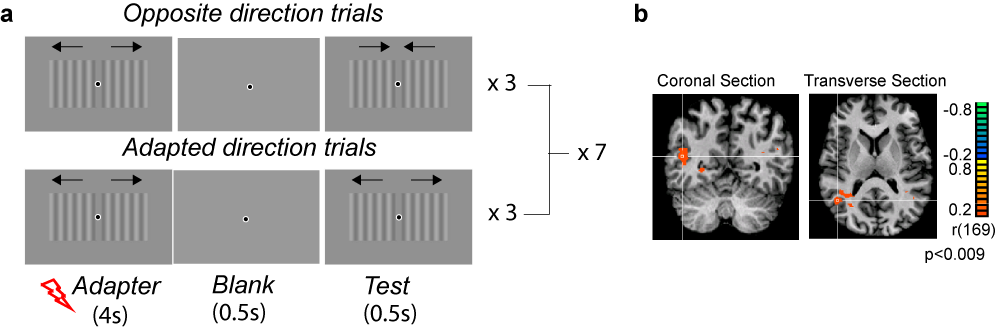
## Apparatus

A Canon REALiS SX80 Mark II LCOS projector back-projected the stimuli onto a screen located at the end of the MRI bore at a refresh rate of 60 Hz. Subjects viewed the stimuli via a mirror attached to the head coil. The combined distance of the screen to the mirror and the mirror to the subjects’ eyes was 103 cm. The display measured 22° (width) by 12° (height) and had a resolution of 1920 x 1080 pixels. Stimulus presentations and the triggering of stimulation were under the control of in-house, OpenGL software. All eye movements were monitored and recorded using an eye tracker (Eyelink II V 2.2) at 500 Hz.

## Motion adaptation paradigm

We adopted the visual motion adaptation paradigm from Huk et al. (2001) to quantify direction-selective motion adaptation in the BOLD signal. Subjects fixated a dot at the center of the screen while we presented two moving gratings on either side of the dot (XX° xYYY° centered on +\- ZZZ°) . For each experimental run, both gratings initially moved inward for 30s (l*ong adapter*). Subsequent trials were classified into two conditions. During *opposite direction trials* a top-up adapter (both gratings moving inwards for 4s) was followed by a test stimulus moving outward for 0.5 s. During *adapted direction trials* the adapter was followed by a test stimulus moving inward for 0.5 s. The sequence of trials (i.e., after the initial 30 s *long adaptation)* alternated between three opposite direction trials and three adapted direction trials. We define these 6 trials as one block. Each block was presented 7 times in one run. Each subject participated in four experimental runs in the same session; two with tACS (tACS-on), two without tACS (tACS-off).

In the tACS-on conditions, the current was applied whenever the adapter (both *long adapter* and the *top-up adapter*) stimulus was on the screen (i.e., only during the induction of adaptation). Because the visual stimuli were presented in both hemifields, both left and right hMT+ adapted. We placed the stimulation electrodes such that left hMT+ received larger tACS stimulation than right hMT+. Hence, in this paradigm, we predicted that adaptation should be less in left hMT+ (the stimulated hemisphere) than in right hMT+.



**Figure 1.** Experimental paradigm. Subjects fixated on the central dot throughout. A) Adaptation was induced with outward drifting gratings, these were presented first for 30 s at the start of a block, and then for 4 s in each trial. The adapted responses were measured with gratings moving in the same (adapted direction) or opposite direction. A set of three opposite-direction trials was alternated with sets of three adapted direction trials (always with the same adapter), and this set of 6 trials was repeated 7 times in one block. B) Schematic of the predicted neural and BOLD time course.

## fMRI

### Data Acquisition

We conducted all imaging at the Rutgers University Brain Imaging Center (RUBIC) using a 3T MRI (Tim Trio, Siemens) scanner, and a 32-channel head coil with ample padding around the head to minimize head movement. We used a T1-weighted MPRAGE sequence to collect 1 mm3 resolution anatomical images from each subject. For functional scans, we used a T2\*-weighted echo planar imaging sequence (repetition time = 2 s, echo time = 25 ms, flip angle = 90°, matrix = 64 x 64). The 35 slices (in plane resolution = 3 x 3 mm; slice thickness = 3 mm) covered the entire brain and were oriented approximately parallel to the anterior commissure and posterior commissure (ACPC) line.

## Data Analysis

### **ROI Analysis**

#### Data Preprocessing

We analyzed the fMRI data with BrainVoyager (version 2.6; Brain Innovation, Maastricht, Netherlands) and MATLAB (MathWorks). We discarded the first nine volumes of each functional scan. We then preprocessed the functional data. This included a linear trend removal, slice scan time adjustment, 3-D motion correction with alignment to the first volume within an MRI session, and temporal filtering using a high-pass fast Fourier transform filter with a 0.0078 Hz cut-off. The functional images were superimposed on the high-resolution anatomical images and incorporated into the 3D data sets through trilinear interpolation. The complete data set was transformed into Talairach space. We defined area hMT+ by a sphere (10 mm radius) around its canonical Talairach coordinates: (40,-60, 0) for the right hemisphere and (-40,-60, 0) for the left hemisphere.

#### BOLD adaptation

Based on the known properties of MT neurons in the macaque {kar}, and previous studies in humans {huk,tootell} we predicted that for our choice of stimuli, adaptation would primarily reduce the neural response in the adapted-direction trials compared to the opposite-direction trials. Due to the slow response dynamics of the BOLD signal, this results in a prediction that the BOLD signal would be higher than average in the opposite direction trials, and lower than average in the adapted-direction trials. Formally, we computed a predictor by convolving the predicted neural effects with a two-gamma hemodynamic response function (HRF, onset = 0 s, response to undershoot ratio = 6, time to response peak = 5 s, time to undershoot peak = 15 s, response and undershoot dispersion = 1). See Figure XXXb. The strength of direction-selective adaptation for each voxel was quantified as the Pearson correlation between this predictor and the BOLD time course of the voxel. In voxels with a positive correlation adaptation reduced the response, in voxels with a negative correlation adaptation increased the response.

### **Functional Connectivity Analysis**

#### Data Preprocessing

All connectivity preprocessing and analyses were performed using MATLAB and AFNI (version 2011-12-21) {Cox 1996}. The first nine volumes of each scan were discarded. EPI images were slice-time corrected, aligned to the subject’s skull-stripped MPRAGE in native space, motion-corrected, and transformed to Talairach space. A linear regression was subsequently performed to remove nuisance parameters from the time series. This included the six motion parameters, and ventricle and white matter time series along with their derivative time series. In addition, to remove any potential spatial co-activation confounds with functional connectivity (FC) analyses, we also regressed out BOLD signals related to stimulus presentation (adapter on/off, test on/off and tACS on/off), all convolved with the same canonical HRF as in the above analysis involving BOLD activity during adaptation (Parameters: XXXX). The residual time series was then spatially smoothed within a one-voxel dilated gray matter mask at 6mm FWHM.

#### ROI-based functional connectivity analysis

To perform ROI-based FC analyses, we extracted the average time series from 264 pre-defined functional regions each affiliated with one of 12 functional networks (Power et al., 2011). We also included the two hMT+ regions (stimulated and non-stimulated hemisphere) in our ROI set. To match the spherical size of the ROIs used in the Power atlas (5mm radius), we defined the area hMT+ by a 5mm radius sphere around the canonical coordinates at (40, -60, 0) for the right hemisphere and (-40, -60, 0) for the left hemisphere. We excluded region 257 in the Power atlas given that its voxels overlapped with the right hMT+ sphere, resulting in a 265 ROI set. For each ROI, we split up the time series according to stimulation condition (tACS OFF and tACS ON) and adaptation condition (opposite and same). We then computed the Pearson correlation from each of the hMT+ to all other regions across the entire brain to obtain FC measures for each of the conditions, resulting in four connectivity vectors for each hMT+ (adapt/non-adapt X stimulation ON/OFF). All correlation values were Fisher z-transformed prior to statistical analyses. We ran a 4-way mixed effects model with 3 fixed-effects (stimulation condition, adaptation condition, hMT+ hemisphere), and subjects as a random-effects factor. As a first test, we computed the weighted degree centrality for each of the hMT+, a graph-theoretic measure that computes the average FC of a region across the entire, and modeled a 3-way interaction between the 3 fixed effects (Rubinov and Sporns, 2010). Next, to obtain more specificity with regards to which functional networks were driving this whole brain FC effect, we computed the average FC from each of the hMT+ to each functional network across the different conditions, running the same ANOVA on the network average FC values. Lastly, to obtain region-to-region specificity, we tested the same 3-way interaction on FC values from every region to each hMT+. For the network and region-level statistical tests, p-values were corrected for multiple comparisons with false discovery rate (FDR).

# Results

We have argued based on behavioral and electrophysiological data that tACS at 10 Hz attenuates sensory adaptation. Here we tested this hypothesis by measuring the influence of tACS (±0.5mA, 10 Hz) on adaptation of the BOLD response in hMT+.

## tACS reduces adaptation in hMT+

We used the method of Huk et al. {huk} to measure the strength of adaptation in hMT+ (see Methods). In brief, we compared the BOLD response to inward and outward drifting gratings, after the prolonged exposure to outward drifting gratings. Under these conditions one expects primarily a reduced response to the outward drifting (i.e. adaptation in one direction reduces the subsequent response to motion in the same direction). Our data confirm this; the bilateral stimulus led to significant adaptation in both hemispheres. This replicates Huk et al’s study.

Here we were primarily interested in the extent to which tACS affects this measure of adaptation. We placed tACS stimulation electrodes to target hMT+ in the left hemisphere, stimulated at 10 Hz whenever the bilateral adapting stimulus (the outward moving grating) was on the screen, and then compared the adaptation in the stimulated left hMT+ and unstimulated right hMT+. Figure 1b shows the strength of adaptation from one example subject in the tACS ON trials. The red clusters show the voxels that adapted significantly. Clearly, there are many more significantly adapted voxels in the unstimulated right hemisphere than the tACS stimulated left hemisphere.

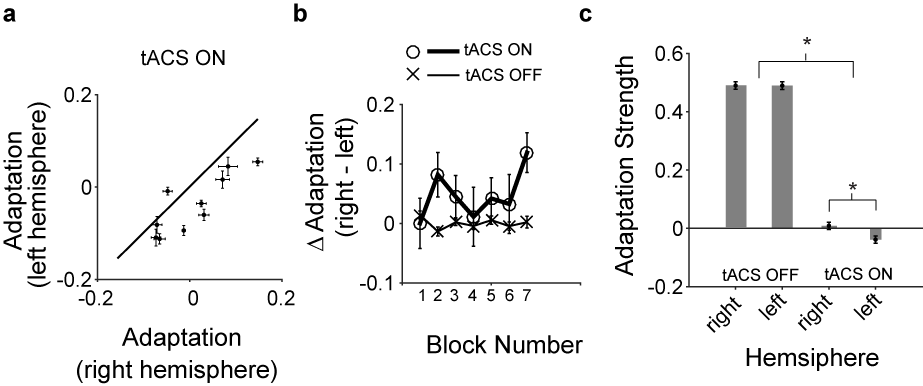
**Figure 1.** Results froman individual subject. Color maps show the amount of BOLD adaptation as quantified by the correlation between the BOLD signal and the adaptation predictor (see Methods). Images are in neurological convention. The white cross hairs in the coronal and the sagittal slices are at the Talairach coordinates x = 40, y= -72, z = -7. hMT+ in the unstimulated (right) hemisphere shows significant adaptation, but adaptation was non-significant in the stimulated (left) hemisphere.

To quantify this observation, we calculated the average BOLD adaptation in the stimulated and unstimulated hMT+ ROIs for each subject (see Methods) and performed a three-way repeated measures ANOVA with factors of block (1-7), hemisphere (stimulated/unstimulated) and tACS (ON/OFF). The main effect of tACS was significant (F(2,1) > 1000; p<0.001) and so was the interaction between tACS and hemisphere. (F(2,1) = 5; p<0.05). The man effect of block was not significant (F = XXX;p>XXX). In other words, adaptation was consistently reduced more in the hMT+ above which the stimulation electrode was placed. Figure 2a shows a direct comparison of adaptation in the stimulated and non-stimulated hemisphere; this conforms that adaptation was reduced in the stimulated compared to the unstimulated hemisphere (Wilcoxon sign rank test; p<0.05).

Next we asked whether this attenuation

In Figure 2b we investigated whether the influence of tACS

shows the comparison of the difference in adaptation between the two hemisphere per block, with (solid bold curve) and without (solid thin curve) tACS.



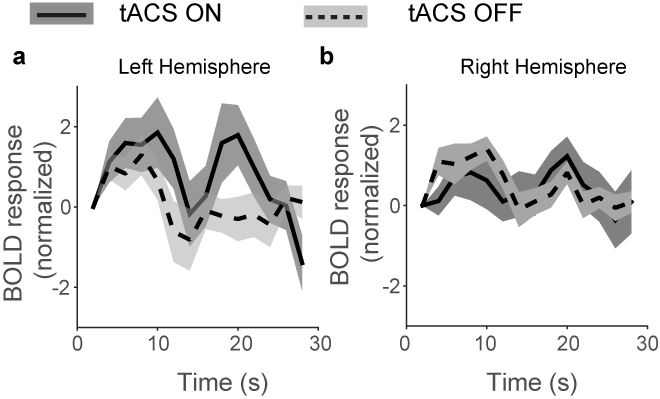
**Figure 2.** tACS attenuates BOLD adaptation in a hemisphere specific way.

## tACS interferes with the induction of adaptation

Because MT neurons typically adapt more when they respond more, tACS could reduce adaptation by reducing neural activity in the adaptation phase. If this were the case, one would expect a decreased BOLD signal during stimulation.

To test this hypothesis, we compared the BOLD response in hMT+ during the *long adapter* stimulus in the trials when tACS was on, with those in which tACS was off. We performed a two way repeated measures ANOVA with hemisphere (stimulated/unstimulated) and tACS (ON/OFF) as the factors. There was a main effect of tACS (increase in BOLD response; F(2,1) = 7.8, p = 0.02) …main effect of hemisphere… interaction.

This shows that contrary to the prediction of the hypothesis that tACS reduces neural activity, BOLD responses during tACS were in fact higher. This result is consistent with the hypothesis that tACS does not affect neural activity directly, but indirectly by interfering with the induction of adaptation {kar}. Because adaptation typically leads to reduced neural activity, attenuating adaptation will lead to an effective increase in neural activity, consistent with the increase in BOLD response during stimulation shown here.



**Figure 3.** Effects of tACS on BOLD signal during long adaptation.

## Functional Connectivity

Although we had no prior hypothesis concerning the influence of tACS stimulation on functional connectivity, the data set allowed us to perform exploratory analyses that may provide some insight into more general brain changes associated with tACS. To first quantify the general effect of FC changes during stimulation and adaptation on the stimulated left hMT+, we computed the weighted degree centrality, a graph theoretic measure which computes the average FC changes of a region to the entire brain (Rubinov and Sporns, 2010). As a control, we also computed the weighted degree centrality of the non-stimulated right hMT+ to ensure our analyses were not confounded by time, since the tACS OFF condition always preceded the tACS ON condition. Additionally, we also computed weighted degree centrality for each of the hMT+ separately for the adapted and non-adapted trials. Together, we constructed a 4-way mixed effects model, with three fixed effects (tACS ON versus OFF, left versus right hMT+, and adapt versus non-adapt trials) and subjects as a random-effect. We computed a 3-way interaction of stimulation, hemisphere, and run, and found a significant effect (F(1,9) = 11.52; p = 0.008) (**Fig. ??**). This result supports the idea that stimulation was spatially specific to the stimulated hMT+, and that the effect of stimulation was not confounded by time or adaptation condition. These results demonstrate that in addition to modulating BOLD activity, stimulation can affect and modulate spatially specific FC across the brain.

To explore the possibility that this effect is driven by a specific set of regions (e.g., a functional network), we computed the average FC from each hMT+ to each of the 12 functional networks defined by the Power et al. (2011) atlas. For each of these networks, we then computed the same 3-way interaction as above. We found a significant 3-way interaction effect with the average FC values to the dorsal attention network (DAN) (F(1,9) = 16.03; p = 0.04 FDR-corrected; Fig ??), providing evidence to support the hypothesis that stimulation might influence (and increase) top-down visual attention, given the DAN’s putative role in top-down attention (Corbetta and Shulman, 2002; Fox et al., 2006). A possible interpretation for this finding is that stimulation increases the saliency of the visual signals emanating from the stimulated hMT+ due to attenuated adaptation, thereby increasing coherence and connectivity with top-down attentional modulation signals in the DAN.

Lastly, to consider the prospect that individual regions might increase FC during stimulation with the stimulated hMT+, we searched for the same significant 3-way interaction across all functional regions. No regions were statistically significant after multiple corrections. However, with a liberal threshold of p < 0.01, we found six regions that showed a 3-way interaction effect (Figure ??). Of the six regions, three belonged to the visual network (left middle occipital gyrus, left lingual gyrus, left cuneus), one in the DAN (right superior parietal lobule), default mode network (right supramarginal gyrus), and the somatosensory hand network (right post central gyrus). Given that these results are not statistically significant in a rigorous sense, we do not interpret these region-wise findings any further.

# Discussion

We investigated how tACS affected BOLD signal changes in area hMT+ in human subjects. We found that tACS reduced fMRI BOLD adaptation. We also observed that the application of tACS increases functional connectivity between the stimulated and non-stimulated hemispheres.

This increment was due to a specific increase in functional connectivity during the *opposite direction trials.*

We first address some of the confounding factors and limitations in the interpretation of our data. Then we speculate on the neural mechanisms that might be responsible for the tACS-effects we reported, and conclude with a brief discussion of the implications of our findings for the future use and interpretation of tACS-effects.

## Confounding factors

### Phosphenes

Application of tACS produces phosphenes via retinal stimulation (Schutter and Hortensius, 2010; Kar and Krekelberg, 2012; Laakso and Hirata, 2013). The phosphene can act as a distractor and therefore reduce attention during the motion adaptation task. The difference in adaptation between the left (stimulated) and right (non-stimulated) hemisphere control for this confound. We observe that attenuation of fMRI adaptation is larger for the left compared to the right hemisphere. This confirms that the effect is tACS-driven-cortically-induced and not a side effect of perceiving phosphenes.

### Artifacts introduced by tACS in the scanner

Transcranially applied electric fields in the MRI scanner has been previously reported to produce changes maximally in the EPI signal on the scalp and the CSF (Antal et al., 2012). Our experimental control design takes these observations into account. An increased or decreased BOLD response due to the artifacts, do not change the interpretation of our data. tACS was applied simultaneously during the adapter stimulus both for the *adapted direction trials* and the *opposite direction trials*. Hence the changes in adaptation as reported in this study cannot be biased by or attributed to tACS-induced imaging artifacts.

### Interhemispheric interactions

A possible crosstalk between area hMT+ of the two hemispheres through the corpus callosum and its functional significance has been previously proposed {Genc 2011}. Our stimulus was present in both the visual hemifield. Hence both the left and right hMT+ were simultaneously driven by the visual stimulus. We speculate that a reduction in adaptation in the left hMT+ produced by the direct influence of tACS might drive the effects on the right hMT+. The increase in functional connectivity during the *opposite direction trials* hint further towards this speculation. In our previous study (Kar and Krekelberg, 2014), we did not use a bilateral stimulus presentation. Given that the ipsilateral control experiment (Kar and Krekelberg, 2014) did not have any effect on motion adaptation, we speculate that the presence of a visual stimulus in both hemifield is necessary to elicit any significant inter-hemispheric effect.

## tACS mechanism

We have previously shown two distinct behavioral effects of 10 Hz tACS, applied over the parietal cortex, during presentation of a visual motion stimulus. First, it improved motion direction discrimination sensitivity. This led us to speculate that tACS might prevent the loss of sensitivity due to motion adaptation by attenuation adaptation, and thereby improving sensitivity. Indeed, further experiments showed that tACS reduced the adaptation induced motion aftereffect. Here we have investigated the neurophysiological changes that underlie the attenuation of adaptation. Our results (Figure 3a) suggest that tACS disrupts adaptation and likely increases the firing rate of the cells during adaptation. Hence, we have demonstrated that the behavioral effect is consistent with the tACS-induced changes in BOLD responses during motion direction selective fMRI adaptation. Taken together, this strongly suggests that tACS interferes and likely disrupts the induction of sensory adaptation in the brain. In addition, this is not due to a tACS-induced reduction in the activity of the area, rather an increase in population activity upon tACS. However, these results don’t allow us to derive at a unique prediction as to how tACS might reduce adaptation at a cellular or network level. First, the electric field induced by tACS is not limited to the area directly underneath the electrode (Datta et al., 2008; Kar and Krekelberg, 2012). Therefore it is difficult to predict whether the behavioral effects of tACS originate at any specific brain region. However, given that tACS specifically attenuated motion adaptation, both behaviorally and in terms of BOLD responses, we propose a cellular mechanism of tACS. Contrast adaptation in the cat visual cortex has been previously attributed to the recruitment of an intrinsic membrane hyperpolarization (Sanchez-Vives et al., 2000b). This adaptation-induced hyperpolarization of the membrane potential was mainly attributed to sodium and calcium dependent potassium currents (Sanchez-Vives et al., 2000a). We speculate that the membrane voltage fluctuations produced by tACS directly interacts with the dynamics of the Na+ and Ca2+ activated K+ channels, thereby reducing the after effect of adaptation. This hypothesis can be explicitly tested in vitro Specific genes termed slick and slack genes have been identified that encode for these sodium activated potassium channels (KNa) (Sanchez-Vives et al., 2000). Recently mouse visual cortical cells have been shown to exhibit adaptive properties like that of the macaques and cats (Stroud et al., 2012). Future studies can utilize slick and slack knockout mice to test how the lack of these genes modify the efficacy of tACS. . A previous study has reported that even small (<2mV) membrane voltage fluctuations reduce spike frequency adaptation in rat hippocampal CA1 neurons (Fernandez et al., 2011) by specifically interfering with Na+ channel de-inactivation. This can also be a possible candidate to account for the tACS induced effect.

## Conclusion

Our results show that tACS when applied during prolonged visual stimulation reduces the effects of adaptation. It also increases the overall activity in the area during the adaptation phase. This provides a mechanistic explanation for the action of tACS. We speculate that the cognitive enhancements reported {cite} using tACS might be a direct consequence of this increased overall responsivity of an area. However, the enhancement for one functionality might come at a cost of other cognitive functions {Luculano 2013}. Hence, a more detailed cellular level description of tACS mechanism is necessary.

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