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TRANSCRANIAL DIRECT CURRENT STIMULATION (tDCS) TRACES THE PREDOMINANCE OF THE LEFT AUDITORY CORTEX FOR PROCESSING OF RAPIDLY CHANGING ACOUSTIC INFORMATION

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Abstract—In the present study we investigated the effects of anodal transcranial direct current stimulation over the auditory cortex (AC) on the perception of rapidly changing acoustic cues. For this purpose, in 15 native German speakers the left or right AC was separately stimulated while participants performed a between-channel gap detection task. Results show that stimulation of the left but not right AC deteriorated the auditory perception of rapidly changing acoustic information. Our data indicate a left hemispheric dominance for the processing of rapid temporal cues in auditory non-speech sounds. Moreover, we demonstrate the ability of non-invasive brain stimulation to change human temporal information processing in the auditory domain. © 2013 IBRO. Published by Elsevier Ltd. All rights reserved.

Key words: tDCS, auditory cortex, auditory temporal resolution, hemispheric lateralization, gap detection.

INTRODUCTION

The two cerebral hemispheres of the human brain have traditionally been described in terms of their functional specialization with the auditory cortex (AC) of the left hemisphere being pre-dominant for the perception and production of speech, and the AC of the right hemisphere dedicated to the processing of prosodic and emotional content of speech (Galaburda et al., 1978; Ross, 1981; Weintraub et al., 1981). However, research in the past decades clearly suggests that the functional asymmetries of the left and right auditory system can be described along a low-level acoustic processing dimension (Zatorre and Belin, 2001; Tallal and Gaab, 2006; Zatorre and Gandour, 2008).

In this regard, recent neurobiological frameworks of auditory cognition propose a ''division of labor'' between the left and the right auditory-related cortices, encompassing a relative trade-off in spectral and temporal processing of complex acoustic signals such as speech and music, with left auditory cortical areas being highly tuned for temporal resolution and right auditory cortical areas being more amenable to spectral resolution (Zatorre and Belin, 2001; Meyer, 2008). According to the ''asymmetric sampling in time'' (AST) hypothesis, asymmetries in the auditory system may be accounted for by hemispheric differences in sampling time: the left auditory areas preferentially extract information from short and the right auditory areas from long temporal integration windows (Poeppel, 2003; Luo and Poeppel, 2012). Moreover, the authors have argued that these time windows also correspond to different spectral resolution constants (25-ms time window corresponds to 40-Hz spectral resolution; 200-ms time window corresponds to 5-Hz spectral resolution), which leads generally to a ''division of labor'' as mentioned by Zatorre and Belin (2001). In contrast to this proposal the more flexible AST model suggests that the spectro-temporal asymmetry is attributed to differences in neuronal integration windows on the left and right auditory-related cortex. However, to this date, the asymmetry of the auditory domain for temporal acoustic features is still controversially discussed (Scott and McGettigan, 2013). While a majority of hemodynamic (Zaehle et al., 2004; Meyer et al., 2005), electrophysiological (Sandmann et al., 2007; Zaehle et al., 2007; Okamoto et al., 2009) behavioral (Schwartz and Tallal, 1980; Sulakhe et al., 2003), as well as animal studies (Wetzel et al., 2008; Rybalko et al., 2010) have shown lateralized auditory processing of temporo-spectral sounds, also several contradicting results have been reported showing no (Uther et al., 2003) or reversed auditory hemispheric lateralization (Reiterer et al., 2005; De Sanctis et al., 2009).

In the majority of these studies, the conclusions are drawn on correlational inferences, e.g. statistical relationship between a set of variables that, in principle, do not allow a direct causal inference. In contrast, the possibility to directly modulate circumscribed brain areas by non-invasive electrical stimulation offers a research tool for investigating such causal relations (Fox, 2011). Transcranial direct current stimulation (tDCS) can influence cortical activity via weak direct current to the head. The current flows between an active and a reference electrode. While a part of this current is shunted through the scalp, the rest is delivered to the brain tissue (Miranda et al., 2006; Neuling et al., 2012),

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Abbreviations: AC, auditory cortex; ANOVA, analysis of variance; AST, asymmetric sampling in time; GDT, gap detection task; tDCS, transcranial direct current stimulation.

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thereby inducing diminutions or enhancements of cortical excitability (Nitsche et al., 2008). The direction of the tDCS-induced effect depends on the current polarity. Anodal tDCS typically has an excitatory effect while cathodal tDCS decreases the cortical excitability in the region under the electrode (Nitsche and Paulus, 2000; Nitsche et al., 2003). Neuromodulatory changes induced by tDCS have been successfully demonstrated in the motor (Priori et al., 1998; Nitsche and Paulus, 2000; Sehm et al., 2013b), visual (Antal et al., 2003; Accornero et al., 2007; Peters et al., 2013), and somatosensory system (Dieckhofer et al., 2006; Antal et al., 2008; Sehm et al., 2013a) as well as in the cognitive domain (Heimrath et al., 2012; Santiesteban et al., 2012; Floel, 2014). In the auditory system it has been shown that tDCS can alter primary AC reactivity (Zaehle et al., 2011) as well as temporo-spectral perception (Ladeira et al., 2011; Tang and Hammond, 2013). In particular, using silent gaps in white noise clicks, anodal but not cathodal tDCS improved gap detection performance (Ladeira et al., 2011). Electrophysiologically, anodal stimulation over temporal cortex specifically enhances the P50 component of auditory evoked potentials, with no effect of cathodal tDCS.

In the present study, we investigated the effects of anodal tDCS over the AC of both hemispheres on the perception of rapidly changing acoustic cues. Here, by systematically modulating the neuronal activity of either the left or right AC, we studied hemispheric lateralization for the processing of rapidly changing acoustic cues in non-speech sounds. According to the neurophysiological frameworks mentioned above we hypothesize that the modulation of the left, but not the right AC reactivity by means of tDCS will alter participant's temporal resolution abilities.

EXPERIMENTAL PROCEDURES

Participants

Fifteen native German speakers (mean age 24.4; range 20–29; 7 male) participated in this study. After explanations about risk of the research, the subjects gave written informed consent to the study. All subjects were right-handed and had no history of neurological, psychological or hearing impairment. All procedures in the study were approved by the ethics committee of the University of Magdeburg.

Stimuli

To study individual temporal processing abilities, we utilized a between-channel gap detection task (Phillips et al., 1997; Zaehle et al., 2004). Generally, a gap detection task (GDT) is the most common method used to measure auditory temporal resolution. Two different GDT approaches exist, a traditional paradigm with temporal operation executed in a discontinuity detection within one perceptual or neural channel caused by one stimulus frequency (within-channel paradigm). On the contrary, there is a paradigm presenting stimuli with a gap between markers (leading and trailing element) with different frequency content, which requires different perceptual channels (between-channel paradigm). Performing a between-channel GDT imperatively requires a relative timing of the offset of activity evoked by the leading element and the onset of activity mediating the trailing element (Phillips et al., 1997, 1998). The auditory stimuli were generated with a sampling depth of 16 bits and a sampling rate of 44.1 kHz using the SoundForge 4.5. Software (Sonic Foundry Inc., www.sonicfoundry.com). The leading element was wideband noise burst with a length of 7 ms. The trailing element was a band-passed noise centered on 1000 Hz and a width of 500 Hz with a length of 300 ms. Fig. 1A illustrates spectrogram and waveform of a Gap stimulus.

We determined the individual gap detection threshold as an adaptive measurement of temporal resolution abilities by using an up/down staircase procedure. The listener was presented with two streams of sounds, one of which had a brief silent period ('gap') at its temporal midpoint. The listener's task was to identify this signal and the shortest detectable gap ('gap threshold') is determined. The first detectable stimulus was presented with the initial gap of 100 ms and were than adjusted stepwise by an up/down staircase: if the gap was identified correctly, the gap in the next trail was decreased; if the gap was identified incorrectly, the gap in the next trial was increased. The trails were terminated following 10 reversals and the gap detection threshold was computed by the arithmetic mean of the last four reversals (Treutwein, 1995). All sessions were performed in an acoustically and electromagnetic shielded room. GDT was applied by a Notebook (Samsung RC730, with Intel (R) Core i7 2.2 GHz processor) connected with headphones (Sennheiser, HD 65TV) and with a sound pressure level of 80 dB.

tDCS procedure

All participants received on three different days one session of either sham (S), anodal stimulation over the left (tDCS_left) or right (tDCS_right) AC in a randomized order. TDCS was applied by a battery driven constant current stimulator (ELDITH, NeuroConn GmbH, Ilmenau, Germany) using two rubber electrodes placed in 0.9% saline-soaked synthetic sponges. The 5 × 5-cm stimulation electrode was placed over T7/T8 according to the 10–20 system for EEG electrode placement, the 5 × 10-cm reference electrode was placed contralateral to the stimulation over C4/C3. The active electrode placement has been shown to modulate AC reactivity (Zaehle et al., 2011). The reference position was chosen to minimize tDCS effects in the contralateral auditory area. Fig. 1B illustrates electrode positioning and modeled current density for the left anodal stimulation. The direct current was applied with a strength of 1.5 mA with a 10-s fade in/out. After 10 min stimulation, the GDT started, while the stimulation continued. For sham condition the stimulation stopped after 15 s with a 5-s fade out. This procedure ensured