

Neuromodulation of multisensory perception: A tDCS study of the sound-induced flash illusion

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ABSTRACT

This study explores whether brain polarization could be effective in modulating multisensory audiovisual interactions in the human brain, as measured by the 'sound-induced flash illusion' (Shams et al., 2000). In different sessions, healthy participants performed the task while receiving anodal, cathodal, or sham tDCS (2 mA, 8 min) to the occipital, temporal, or posterior parietal cortices. We found that up- or down-regulating cortical excitability by tDCS can facilitate or reduce audiovisual illusions, depending on the current polarity, the targeted area, and the illusory percept. Specifically, the perceptual 'fission' of a single flash, due to multiple beeps, was increased after anodal tDCS of the temporal cortex, and decreased after anodal stimulation of the occipital cortex. A reversal of such effects was induced by cathodal tDCS. Conversely, the perceptual 'fusion' of multiple flashes due to a single beep was unaffected by tDCS.

This evidence adds novel clues on the cortical substrate of the generation of the sound-flash illusion, and opens new attractive possibilities for modulating multisensory perception in humans: tDCS appears to be an effective tool to modulate the conscious visual experience associated with multisensory interactions, by noninvasively shifting cortical excitability within occipital or temporal areas.

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1. Introduction

Perception has traditionally been viewed as a modular function with the different sensory modalities operating largely as separate and independent processes (Boring, 1942). However, an overwhelming set of new findings has overturned this view (Calvert, Spence, & Stein, 2004). Senses work in concert, so that their information can be used synergistically (Stein, 1998). As shown in various perceptual tasks, multisensory interactions represent the rule rather than the exception (Calvert et al., 2004). The neural mechanisms underlying multisensory perception include modulations, activations, and connectivity at the level of high-order areas of multisensory convergence, as well as at the earliest stages of perceptual processing, in areas traditionally viewed as 'sensory-specific' (Macaluso, 2006; Schroeder & Foxe, 2005; Stein & Stanford, 2008).

Cross-modal illusions are the flip side of sensory coherence, and they illustrate some of the consequences of disrupting the normal relationships among different sensory cues (Stein, 1998). One of the most powerful examples of multisensory perception

is the 'sound-induced flash illusion' (Shams, Kamitani, & Shimojo, 2000). When a single flash is presented along with two or more beeps, observers often report seeing two or more flashes, the so-called 'fission' illusion. A corresponding 'fusion' illusion has also been described, where a single beep causes the fusion of a double flash stimulus (Andersen, Tiippana, & Sams, 2004; Innes-Brown & Crewther, 2009; Shams & Kim, 2010). These pervasive multisensory phenomena highlight how sensory-specific perceptual judgments concerning one sense (i.e., vision) can be dramatically affected by relations with other senses (i.e., audition). Using this audiovisual illusion, here we explore the possibility of modulating multisensory perception by polarizing with transcranial direct current stimulation (tDCS) putatively relevant cortical regions, which are likely to mediate audiovisual interactions.

tDCS is a technique of non-invasive brain stimulation, which has been applied to the human head since the distant past (see Priori, 2003; Zago, Ferrucci, Fregni, & Priori, 2008 for historical reviews); a reappraisal of this technique with claims of behavioural effects and clinical benefits took place more recently, at the turn of this century (Nitsche et al., 2003; Zaghi, Acar, Hultgren, Boggio, & Fregni, 2010). Indeed, tDCS has been rediscovered as an attractive tool for cognitive neuroscience, as it is a non-invasive, safe method, that may effectively modulate information processing in the brain (Wassermann & Grafman, 2005). During tDCS, low-amplitude direct currents penetrate the skull to enter the brain. Although there is substantial shunting of current at the scalp, suffi-

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cient current penetrates the brain to modify the transmembrane neuronal potential and, thus, influences the level of excitability, and modulates the neuronal firing rate (Nitsche et al., 2003; Zaghi et al., 2010). tDCS does not induce action potentials. Rather, tDCS is believed to exert its effects by polarizing brain tissue in a polarity-dependent fashion, with anodal stimulation generally increasing excitability, and cathodal stimulation generally reducing excitability (Nitsche et al., 2003). When delivered to specific cortical areas, tDCS can alter physiological, perceptual, and higher-order cognitive processes. Given these features, this technique is receiving a growing interest for its potential to facilitate skill acquisition, learning, and neural plasticity in the human brain (Bolognini, Pascual-Leone, & Fregni, 2009; Fregni & Pascual-Leone, 2007; Priori, 2003; Wassermann & Grafman, 2005).

So far, the efficacy of tDCS for modulating modality-specific sensory processing in the primary somatosensory (Antal et al., 2008; Boggio, Zaghi, Lopes, & Fregni, 2008; Celnik, Hummel, Harris-Love, Wolk, & Cohen, 2007; Ragert, Vandermeeren, Camus, & Cohen, 2008; Rogalewski, Breitenstein, Nitsche, Paulus, & Knecht, 2004), and visual (Antal, Kincses, Nitsche, Bartfai, & Paulus, 2004; Antal & Paulus, 2008; Antal, Nitsche, & Paulus, 2006) cortices has been demonstrated. However, the effects of brain polarization on multisensory processing remain largely unexplored.

Evidence from brain imaging studies in humans indicates that interactions between polysensory and visual cortical areas may represent the key neural substrate for the generation of the 'sound-induced flash illusion'. First, fMRI studies show a modulation of the evoked activity in the primary occipital cortex (V1), along with an activation of the right superior temporal sulcus (STS), on both 'fission' illusion trials (i.e., 1 Flash + 2 Beeps), and 'fusion' illusion trials (i.e., 2 Flash + 1 Beep), as compared to physically identical trials where no illusion is reported by participants (Watkins, Shams, Josephs, & Rees, 2007; Watkins, Shams, Tanaka, Haynes, & Rees, 2006). Similarly, MEG and ERPs studies show a modulation of activity in occipital, temporal, and parietal scalp locations, when participants experience both illusory effects (Bhattacharya, Shams, & Shimojo, 2002; Mishra, Martinez, & Hillyard, 2008; Shams, Iwaki, Chawla, & Bhattacharya, 2005).

On the basis of this evidence, we sought to determine the functional contribution of the temporal, occipital, and parietal cortices to the generation of the sound-induced flash illusion, by exploring the possibility of altering (increasing or reducing) audiovisual interactions by tDCS. To this aim, we ran two experiments in order to explore the specificity of the brain polarization effects on multisensory perception with respect to the stimulated region (i.e., temporal, occipital, parietal), the type of the evoked multisensory percept (i.e., 'fission' vs. 'fusion' illusion), and the stimulation parameters (i.e., current polarity: Experiment 1, anodal tDCS; Experiment 2: cathodal tDCS).

2. Experiment 1. ANODAL tDCS

2.1. Materials and methods

2.1.1. Participants

Twelve neurologically unimpaired participants (mean age \pm SD, 24 ± 6 ; 10 females) took part in Experiment 1. All participants were right-handed on a standard questionnaire (Oldfield, 1971), and had normal or corrected-to-normal vision and normal hearing. Participants were naïve both to the experimental procedure and to the purpose of the study. Participants gave their informed consent prior to be enrolled in the study, which was carried out according to the guidelines of the ethical committees of the University of Milano-Bicocca and of the Italian Auxological Institute (Milan, Italy), and the Declaration of Helsinki (BMJ 1991; 302: 1194). Participants

were suitable to participate in the experiment, since their history showed no medical disorders, no substance abuse or dependence, no use of central nervous system-effective medication, and, particularly, no psychiatric and neurological disorders, including brain surgery, tumour, or intracranial metal implantation (Poreisz, Boros, Antal, & Paulus, 2007).

2.1.2. Stimuli and procedure

Stimuli and procedure were adapted from the original study of Shams and collaborators (Shams et al., 2000). In a dimly illuminated room, participants sat ~ 57 cm in front of a CRT computer monitor (Samsung SyncMaster 1200NF: resolution 1024×768 , refresh rate 75 Hz), with their eyes aligned with the centre of the screen, and their head supported by a chinrest. Two speakers were located beside the screen, aligned with the flashes.

Each trial began with the appearance of a white fixation cross, displayed at the centre of a black screen (luminance: 0.02 cd/m^2). At the eccentricity of 5° of visual field, a white disk subtending 2° was flashed one to four times. Only flash trials were presented: single flash trials (1F), accompanied with 0–4 beeps (B) (i.e., 1F0B, 1F1B, 1F2B, 1F3B, 1F4B: 'fission' illusion); multiple flash trials (from 2F to 4F), accompanied with 0 or 1 beep (2F0B, 3F0B, 4F0B, 2F1B, 3F1B, 4F1B: 'fusion' illusion). Hence, the total number of conditions was 11. The temporal profile of the stimuli is illustrated in Fig. 1. Each flash (luminance: 118 cd/m^2) and beep (at 80 dB SPL) had durations equivalent to one screen refresh (13 ms). The first beep was followed by the first flash after 26 ms. The interval (stimulus onset asynchrony, SOA) was 65 ms (5 refreshes) between two flashes, and 52 ms (4 refreshes) between two beeps.

The participants' task was to judge the number of flashes seen on the screen. Each condition was repeated 8 times, for a total of 88 trials, in a random fixed order. The total duration of the task was about 5 min. At the beginning of each session, 10 practice trials were administered, and not included in the subsequent analysis.

The task was given to participants in 5 different sessions: a baseline session (no tDCS stimulation), and 4 tDCS sessions, in which the task was given during the tDCS stimulation of one of the target areas (temporal, occipital, parietal, or sham tDCS). The experimental procedure is illustrated in Fig. 1. The order of the 5 sessions was randomized across participants. The tDCS sessions were separated by at least 50 min, in order to avoid carry-over effects, and to guarantee a sufficient washout of the effects of the previous run (Boggio, Zaghi, & Fregni, 2009; Fregni et al., 2005; Ragert et al., 2008; Sparing, Dafotakis, Meister, Thirugnanasambandam, & Fink, 2008).

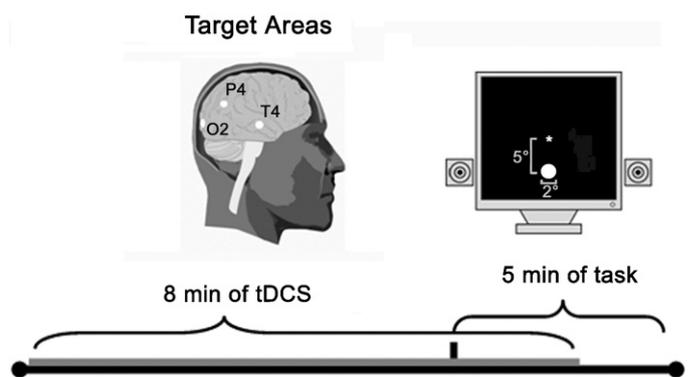


Fig. 1. Overview of study design. Each participant took part in five separate sessions, randomized across participants: baseline (No tDCS), sham tDCS, temporal, occipital, and parietal tDCS. Top left: picture of the targeted brain areas in white; locations refer to the standard 10–20 EEG system (O2 = right occipital cortex, V1; P4 = right posterior parietal cortex, PPC; T4 = right superior temporal gyrus, STG). tDCS stimulation started 5 min before the experimental task, lasting for a total of 8 min. The experimental task lasted for about 5 min. tDCS was anodal in Experiment 1, cathodal in Experiment 2.

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