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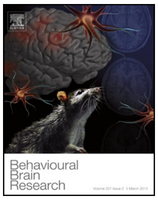

Research report

The role of primary auditory and visual cortices in temporal processing: A tDCS approach

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HIGHLIGHTS

- The first study using tDCS to test the possibility of modality-specific timers.
- No effect of stimulation on perceived duration when tDCS was applied over A1.
- Under-estimation of perceived duration and higher variability when tDCS was applied over V1.
- Effect of cathodic stimulation over V1 in visual modality.

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ABSTRACT

Aim: Many studies showed that visual stimuli are frequently experienced as shorter than equivalent auditory stimuli. These findings suggest that timing is distributed across many brain areas and that "different clocks" might be involved in temporal processing. The aim of this study is to investigate, with the application of tDCS over V1 and A1, the specific role of primary sensory cortices (either visual or auditory) in temporal processing.
Method: Forty-eight University students were included in the study. Twenty-four participants were stimulated over A1 and 24 participants were stimulated over V1. Participants performed time bisection tasks, in the visual and the auditory modalities, involving standard durations lasting 300 ms (short) and 900 ms (long).
Results: When tDCS was delivered over A1, no effect of stimulation was observed on perceived duration but we observed higher temporal variability under anodic stimulation compared to sham and higher variability in the visual compared to the auditory modality. When tDCS was delivered over V1, an under-estimation of perceived duration and higher variability was observed in the visual compared to the auditory modality.
Conclusion: Our results showed more variability of visual temporal processing under tDCS stimulation. These results suggest a modality independent role of A1 in temporal processing and a modality specific role of V1 in the processing of temporal intervals in the visual modality.

1. Introduction

The understanding of the mechanisms underlying the temporal representation of duration in milliseconds/seconds range remains a complex issue. A critical issue in the field of time perception is whether or not explicit judgments about time are processed by a central internal clock mechanism or by some timing mechanisms within sensory modes.

The predominant model for event timing involves a centralized internal clock (Scalar Expectancy Theory (SET); [19] and timing behaviors are based on the output of an internal clock, which is composed by an internal pacemaker emitting pulses. The pulses are accumulated in a counter, and this accumulation is the basis of the representation of time: time is perceived as longer when more pulses are accumulated. Depending on the task to be performed, this accumulation will likely have to be compared with the representation of past temporal events in long term memory. The model assumes that timing is centralized, that is, the brain uses the same circuit, for example, to determine the duration of an auditory tone and the duration of a visual flash. Indeed, SET involves

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perceptual, memory, and decision mechanisms, and recent studies even indicate that the brain circuitry responsible for these mechanisms would be partly the same for time interval categorization and spatial categorization, at least for some duration or distance ranges; moreover, these mechanisms are shared by human and non-human primates [37,38].

The alternate view is that timing is distributed across many brain areas capable of temporal processing and that the area or areas involved depend on the task, modality, and lengths of the temporal intervals. Many studies have pointed out that visual stimuli are frequently experienced as shorter than equivalent duration auditory stimuli, and that interval discrimination is much easier in the auditory than in the visual modality [21,27,33,39,46,48]; for reviews, see [22]. Furthermore, when empty time intervals are marked by two brief stimuli delivered from different sensory modalities (for instance an auditory-visual or visual-auditory sequence), duration discrimination is much more difficult than when intervals are marked by stimuli delivered within a modality [26,25]. This fact may indicate that if timing cannot occur within the cerebral area of a given sensory modality, performance is impaired. Although many non-temporal effects on time perception may be explained within the perspective of SET, the different performance levels across sensory modalities suggest that timing may be distributed across different brain areas experienced for temporal processing; in other words, there would be “different clocks” involved in temporal processing [29,35].

Brain stimulation techniques have been extensively used to modulate cortical activity and investigate sensory processing, and more recently the specific brain areas and networks involved in temporal processing. Bueti et al. [8] showed that the disruption of area MT/V5 by transcranial magnetic stimulation (TMS) impaired time estimation of visual stimuli, but not of auditory stimuli. Furthermore, it was demonstrated that TMS over an auditory area deteriorates time estimation without affecting pitch perception [9,31], using TMS (theta-burst stimulation) over V1 and A1, found that disruption of A1 impaired temporal processing of both auditory and visual stimuli whereas, when TMS was applied over V1, temporal processing was compromised (higher Weber ratio) only in the visual condition. These asymmetric contributions of A1 and V1 in time perception was interpreted as a superiority of the auditory cortex in temporal processing.

Another technique useful for studying temporal processing is the transcranial direct current stimulation (tDCS). tDCS is a non-invasive brain stimulation technique able to induce a temporary modulation of the cortical excitability (depolarization or hyperpolarization), through a weak electrical current (usually between 1 and 2 mA) delivered over the scalp [41]. The tDCS effects depend on several factors, first of all the polarity. Current is delivered through two electrodes of different polarities: generally, cathodal stimulation leads to a hyperpolarization and, consequently, to inhibition, while anodal stimulation causes the resting membrane potential to become more positive and, therefore, it results into facilitation. This distinction is confirmed especially by studies on motor function [4,51], but is not generalizable to all cognitive functions, since the timing of stimulation, the excitability status of the cortical area and the type of task, among others, can influence the outcome [30].

Many advantages make the tDCS a very interesting technique, useful in the study of time perception and in the study of sensory perceptual processing [12]. First of all, using tDCS it is possible to manipulate the cortical excitability and to test the “inhibitory”-like effect induced by the cathodic stimulation and “facilitatory”-like effect induced by the anodic stimulation [3,12,41]. Moreover, tDCS includes a sham condition in which participants are set with the same montage as in the anodic and cathodic condition but they do not receive any stimulation. Other advantages include the reduced cost, simplicity of use, and the possibility of having easily a control condition (sham) perceptually very similar to the active stimulation. For the investigation of time perception, tDCS seems to be also suitable because, unlike the TMS, there is no noise caused by the instrument. In fact, a number of studies have previously reported that the presentation of a rapid series of auditory clicks alone are capable of leading to the subjective lengthening of perceived duration, possibly by increasing arousal, thereby increasing the speed of the pacemaker [11,54,53].

The aim of this study is to investigate the role of primary sensory cortices (either visual or auditory) in the processing of short time intervals. To this end, we applied tDCS over V1 and A1 for investigating the specific role of these brain areas when participants are engaged in a time bisection task. The time bisection task has already been extensively used and requires classifying into two categories (short and long) variable temporal intervals. The shortest and the longest anchor intervals are first presented several times and are then followed by all temporal intervals (including the standards) that have to be categorized as being closer to one of the two anchor durations [20,24]. The task will involve either visual or auditory stimuli, and tDCS will modulate the excitability/inhibition of underlying brain cortices. We expected an increased excitability, producing a facilitatory-like effect, with anodic stimulation, and reduced excitability, producing an inhibitory-like effect, with cathodic stimulation.

2. Method

2.1. Participants

Forty-eight University students were included in the study. Twenty-four participants were stimulated over A1: 12 of which performed a visual time bisection task (mean age = 24.50; *SD* = 1.88) and 12 performed an auditory time bisection task (mean age = 23.20; *SD* = 1.70); 24 participants were stimulated over V1: 12 performed the visual time bisection task (mean age = 23.90; *SD* = 1.43) and 12 performed the auditory time bisection task (mean age = 26.42; *SD* = 5.25). Assessment of handeness was evaluated with the Edinburgh handeness Inventory: [44] all participants were right handed. The study was approved by the ethics committee of Department of General Psychology of Padova (Italy) and conducted according to the Declaration of Helsinki (59th WMA General Assembly, Seoul, 2008). All participants gave their informed written consent before participating in the study. Exclusion criteria included a history of neurological or psychiatric illness, pregnancy, and use of drugs or alcohol 24 h prior the experimental session. Participants were informed about the objective of the study only after completing the third experimental session.

2.2. Materials

2.2.1. tDCS stimulation

A direct current of 1.5 mA intensity was delivered by a battery-driven, constant-current stimulator (Brainstim) through two saline-soaked surface sponge electrodes. Previous studies have shown that this intensity of stimulation is safe in healthy volunteers [42,47,6]. The stimulating electrode (anode or cathode area = 25 cm^2) was then positioned over the right A1 or right V1, and the reference electrode (area = 35 cm^2) was placed on the skin overlying the ipsilateral shoulder region. The stimulating electrode was placed over A1 or V1 according to the international 10/20 system for EEG electrode placement [45] and following [31] study. The position of the auditory cortex was localized according to Brodmann areas 41 and 42 and we targeted the right auditory cortex because previous studies reported selectively right-sided dominance during timing tasks [15,14,28]. The stimulation electrode was placed over the temporal cortices T8 in the international 10/20 system [45,49]. The position of the visual cortex was localized according to Brodmann areas 17 and the position of Oz in the international 10/20 system [45]. We decided to use an extra-cephalic montage for the reference electrode. The choice of an extra-cephalic montage was to avoid any confounding effect in the brain that could derive from the positioning of the reference electrode [42] and the same montage was successfully used in a previous study on time perception [52]. As for the sham stimulation, it consisted of the first 30 s of real stimulation in order to give participants the sensation of electrical stimulation. Even in this case the electrode was placed over V1 or A1 regions. None of the participants reported experiencing pain caused by the stimulation, and all participants included in the study completed all experimental sessions.

2.2.2. *Time bisection task*

The experimental session started with the learning phase in which participants were required to memorise the two standard durations: 300 ms (short standard) and 900 ms (long standard). Both standard durations were presented 10 times. After the training phase, participants were required to judge different temporal intervals (300, 400, 500, 600, 700, 800, 900 ms) and decide if the comparison interval was more similar to the short standard or to the long standard. Participants were required to press the key labelled "B" ("B" refers to the Italian word "Breve" = short) if the duration presented was closer to the short standard, or to press the key labelled with "L" ("L" refers to the Italian word "Lungo" = long) if the duration presented was closer to the long standard. The visual stimulus was a grey circle (filled intervals) presented on a white background, while the auditory stimulus was a white noise ramped on and off with two 10-ms raised cosine ramps (filled intervals). Each comparison duration was presented 8 times for a total of 56 trials in each block; participants performed 4 blocks for a total of 224 trials. The participants were asked to respond with their left and right index finger and response keys were counterbalanced between participants. After the response, there was a 1000-ms inter-trial interval.

2.3. *Sensation experienced questionnaire*

We included a questionnaire about the sensations experienced during the different types of stimulations (anodal, cathodal and sham; [17]. The questionnaire includes 8 possible sensations commonly experiences during tDCS stimulation (and participants were asked to rate each intensity in a Likert scale from "0 = not experienced" to "4 = intense sensation"). The questionnaire was introduced to evaluate whether unspecific stimulation effects related to different experimental conditions could account for differences in behavioural performance.

2.4. *Procedure*

Participants were tested in three different sessions, anodal, cathodal and sham performed in three different days; between sessions there were at least 48 h to avoid long lasting effects of the stimulation [42,43]. Participants were randomly assigned to one of the two experimental conditions, depending on the stimulated area: A1 or V1. Half of the participants stimulated on A1 or V1 performed the time bisection task with visual stimuli and half with auditory stimuli. At each experimental session, participants first performed the time bisection task and then the sensation experienced questionnaire to control for possible inconveniences induced by the stimulation. Instruction and training were conducted off-stimulation and the stimulation started after the training phase. This procedure was adopted to avoid any effect of stimulation during the training phase.

2.5. *Data analyses*

For each participant in each experimental condition, a 7-point psychometric function was traced, plotting the seven comparison intervals on the *x*-axis and the probability of responding "long" on the y-axis. The cumulative normal function was fitted to the resulting curves. More specifically, we used a non-linear least squares analysis, with a Levenberg-Marquardt algorithm. To further explore the effect of stimulation on brain area and modality we calculated two indexes, one that defines perceived duration and one for sensitivity. The first was the Point of Subjective Equality (PSE), that is, the stimulus duration at which the participants responded "short" or "long" with equal frequency. An observed shift of the PSE can be interpreted as an indicator of differences in time processing, with smaller PSE values meaning longer perceived durations. The second dependent variable was the Weber ratio (WR), which is based on one standard deviation (SD) on the psychometric function and is an index of time sensitivity. The WR is the SD divided by 600 ms, which is the midpoint duration used in the experiment [23].

Data were analysed in terms of PSE and WR as dependent variables, using a mixed-model ANOVA separately for A1 and V1 with *modality* (auditory, visual) as between-subject factor and *stimulation* (anodic, cathodic, sham) as within-subject factor. To further validate our findings and the effect of stimulation on time perception we calculated the elevation of the WR after anodic and cathodic stimulation compared to the sham (see Kanai et al. [31] for similar procedure). These data were submitted to a mixed-model ANOVA separately for A1 and V1 with *modality* (auditory, visual) as between-subject factor and *stimulation* (anodic, cathodic) as within-subject factor.

Data from the sensation experienced questionnaire were analysed adding the number of times participants reported a specific sensation at the end of each experimental session. We calculated a total index of sensation for anodic, cathodic and sham sessions. Data were included into a mixed-model ANOVA separately for A1 and V1 with *modality* (auditory, visual) as between-subject factor and *stimulation* (anodic, cathodic, sham) as within-subject factor.

The significant analyses were followed by post-hoc analyses with Bonferroni's correction to reduce the Type I error rate, and the effect size was estimated with the partial eta squared index ($\eta^2{}_p$).

3. Results

Fig. 1 reports the mean proportion of "long" responses as a function of stimulation, modality and temporal intervals for both stimulation conditions, over A1 (Fig. 1a) and over V1 (Fig. 1b). For each individual psychometric function in each experimental condition, the goodness-of-fit was highly satisfactory, with R^2 values above 0.98.

3.1. *tDCS over A1*

Analyses of PSE showed no significant main effects or interaction (all $ps \geq 0.471$, $\eta^2{}_p \leq 0.034$). Analyses of WR showed main effects of *modality* [$F(1,22) = 7.55$, $p = 0.012$, $\eta^2{}_p = 0.256$] and *stimulation* [$F(2,44) = 3.97$, $p = 0.026$, $\eta^2{}_p = 0.153$] indicating that participants had higher WR in the visual (.20) compared to auditory (.15) modality and that participants had higher WR under anodic stimulations compared to sham (anodic = 0.20; cathodic = 0.17; sham = 0.15). The interaction *modality* × *stimulation* ($p = 0.082$, $\eta^2{}_p = 0.107$) was not significant (Fig. 2a). The analyses on the elevation of the WR after stimulation revealed a main effect of *modality* [$F(1,22) = 4.49$,

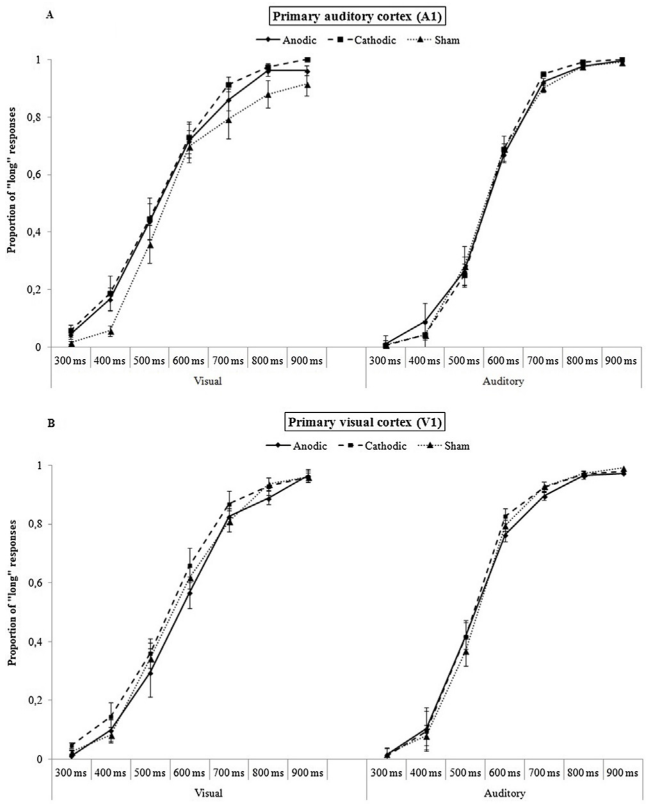

Fig. 1. Aand B. Mean proportion of "long" responses for each area (A1 and V1) stimulated as a function of modality, stimulation and temporal intervals. Error bars indicate standard errors.

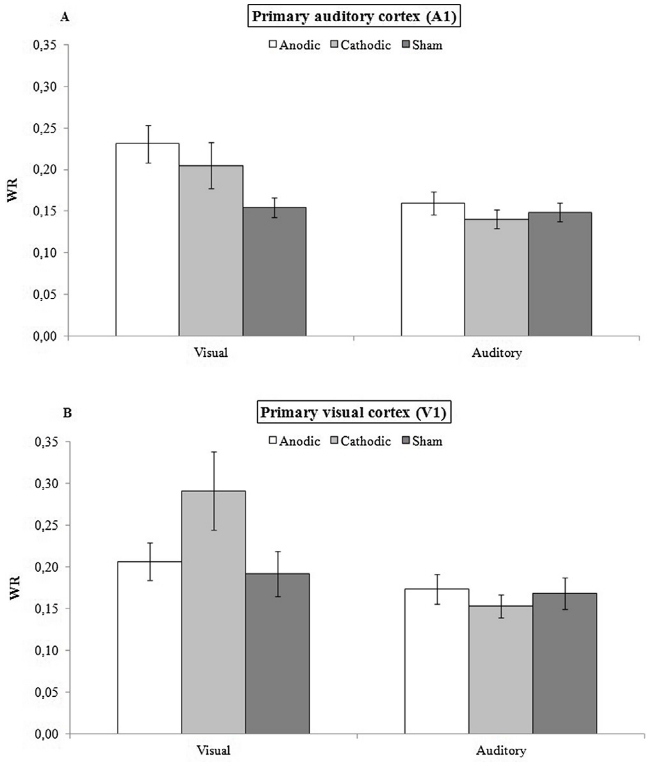

Fig. 2. A and B. Men Weber ratio for each area (A1 and V1) stimulated as a function of modality and stimulation. Error bars indicate standard errors.

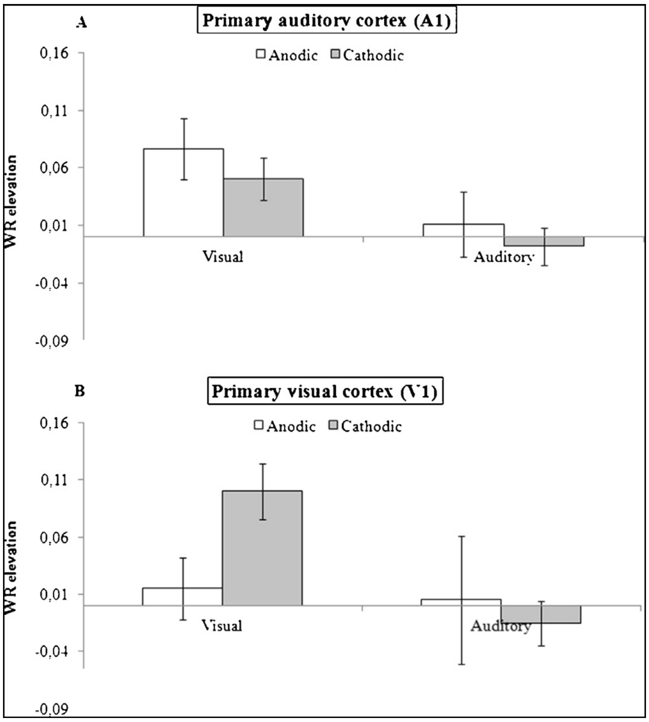

Fig. 3. A and B. Mean elevation of the Weber ratio for each area (A1 and V1) stimulated as a function of modality and stimulation. Error bars indicate standard errors.

$p = 0.046$, $\eta^2_p = 0.170$], indicating that participants were worse in the visual compared to the auditory time bisection task. Neither the main effect of *stimulation* ($p = 0.124$, $\eta^2_p = 0.104$) nor the interaction was significant ($p = 0.820$, $\eta^2_p = 0.002$) (Fig. 3a).

3.2. tDCS over V1

Analyses of PSE showed a main effect of *modality* [$F(1,22) = 6.70$, $p = 0.017$, $\eta^2_p = 0.233$] indicating a left shift of the psychometric function indicating longer perceived duration in auditory compared to visual task (auditory = 526.01, visual = 579.27). Neither main effect of *stimulation* ($p = 0.923$, $\eta^2_p = 0.004$) nor interaction ($p = 0.926$, $\eta^2_p = 0.004$) was found. Analyses of WR showed a main effect of *modality* [$F(1,22) = 6.02$, $p = 0.023$, $\eta^2_p = 0.215$], indicating that participants were more variable in the visual compared to the auditory modality (visual = 0.23, auditory = 0.17). A significant interaction *modality* × *stimulation* [$F(2,44) = 3.73$, $p = 0.032$, $\eta^2_p = 0.145$] was also found (Fig. 2b). Post hoc analyses showed that, within the visual time bisection task, significant differences were observed between cathodic and the two other conditions, anodic stimulation and sham (all $ps \leq 0.034$, $\eta^2_p \geq 0.275$); no differences between stimulations were found in the auditory time bisection task ($p = 0.777$, $\eta^2_p = 0.024$).

The analyses on the elevation of the WR after stimulation revealed a significant interaction *modality* × *stimulation* [$F(1,22) = 6.40$, $p = 0.019$, $\eta^2_p = 0.225$] (Fig. 3b), indicating that participants in the visual time bisection task were more variable under cathodic compared to anodic stimulation ($p = 0.009$, $\eta^2_p = 0.274$) and that participants in the auditory time bisection task were equally affected by the stimulations ($p = 0.495$, $\eta^2_p = 0.021$).

3.3. Sensation experienced questionnaire

Table 1 reports the mean score assigned after each experimental session separately by area of stimulation (A1, V1) and modality (visual, auditory). The analyses were conducted on the total

Table 1
Mean intensity and standard deviation of the sensations reported by the participants after the tDCS stimulations.

			Total sensation index
Brain area	Modality		M (*SD*)
Primary auditory cortex (A1)	Visual	Anodic	3.17 (1.72)
		Cathodic	2.67 (2.06)
		Sham	1.17 (1.60)
	Acoustic	Anodic	5.83 (3.31)
		Cathodic	2.83 (2.04)
		Sham	1.50 (1.52)
Primary visual cortex (V1)	Visual	Anodic	2.83 (2.32)
		Cathodic	2.83 (2,23)
		Sham	2.50 (1.64)
	Acoustic	Anodic	4.67 (5.78)
		Cathodic	2.17 (2.48)
		Sham	1.67 (1.63)

intensity of sensation reported (total sensation index in Table 1). When tDCS was applied over A1, a main effect of *stimulation* [$F(1,22) = 13.97$, $p < 0.001$, $\eta^2_p = 0.583$] was found indicating that participants felt bad sensation under anodic stimulation compared to cathodic and sham. No effect of modality or interaction was found (all $ps \geq 0.091$, $\eta^2_p \leq 0.213$). When tDCS was applied over V1 no main or interaction effects were found (all $ps \geq 0.262$, $\eta^2_p \leq 0.125$).

3.4. Correlation between time perception and sensation experienced questionnaire

Correlational analyses were conducted separately on A1 and V1 between indices of WR and results at the sensation experienced questionnaire to investigate if the sensation experienced during the stimulation may have influenced time perception. No significant correlations were found between the indices (all $ps \geq 0.264$).

4. Discussion

It is becoming increasingly clear that many different brain regions contribute to our perception of time and recent imaging studies have shown that several brain areas are involved for processing time [2,7,10,24,40]. The present study was conducted to evaluate the potential contribution of A1 and V1 in the processing of time intervals. To this end, we modulated the excitability status of the underlying cortical tissue, applying tDCS stimulation during a visual or an auditory time bisection task.

Results showed that, when tDCS was delivered over A1, no effect of stimulation was observed when data were analyzed in term of PSE, indicating no effect of stimulation or modality of the time bisection task on perceived duration. The stimulation over A1 had an impact on the WR: compared to the auditory time bisection task, there was higher variability in the visual time bisection task. When we analyzed the elevation of WR after stimulation, no differences between stimulations were observed, indicating that both anodic and cathodic stimulation affected temporal performance [16,18]. When, tDCS was delivered over V1, we observed a right shift of the PSE on the psychometric function in the visual modality. This shift indicates more short responses when the time bisection task was performed in visual compared to auditory modality. Moreover, when participants performed the task under cathodic stimulation, a higher WR (higher temporal variability) was observed in the visual compared to the auditory time bisection task. This result was confirmed by the analyses of the WR elevation: in the visual modality, the WR was higher in the cathodic than in the anodic condition.

Our results suggest that cathodic stimulation applied over V1 affects time perception only in the visual bisection task; participants' temporal performance in the auditory modality was not modulated by the stimulation over V1 (either anodic or cathodic). When tDCS was applied over A1, higher WR was observed under anodic stimulation, but the elevation of the WR indicated that both stimulation (anodic and cathodic) equally affected time perception in the visual modality. These results confirm and extend previous findings investigating the different involvement of visual and auditory cortices on time perception [8,31]. In fact, Bueti et al. [8] suggested that MT/V5 has a role in visual temporal processing and that the right parietal cortex has a role in temporal processing in both visual and auditory modalities. Kanai et al. [31] extended Bueti et al. findings showing that theta-burst TMS over the V1 compromises temporal processing of visual stimuli without affecting temporal processing of auditory stimuli. When theta-burst TMS was delivered over A1, time perception was compromised in both visual and auditory temporal processing.

Regarding the specific effect of stimulation on time perception, our results are only partially consistent with the idea of anodic stimulation will result in facilitation and the cathodic stimulation in inhibition of the underlying cortical areas [41]. We expected an increased excitability, producing a facilitatory-like effect, with anodic stimulation, and reduced excitability, producing an inhibitory-like effect, with cathodic stimulation. However, we observed an increased variability after both anodic and cathodic stimulation when tDCS was applied over A1 independently of the modality used, but when we targeted V1, a specific effect of cathodic stimulation was observed in visual bisection task. Although several studies revealed an effect of tDCS over cognitive functioning, there is no systematic correspondence between the anodal-excitation and cathodal-inhibition effects [16,18,32,30,36,50] since several important factors such as the timing of stimulation, the excitability status of the underlying cortical tissue, the site of application, and the type of task, all have a critical role in determining the outcome of this stimulation procedure [12]. Thus, a possible explanation to why we obtain different effects with cathodal/anodal tDCS may be due to the combination of characteristics of the underlying brain areas and electrode positioning [1,5]. The tDCS effects appear to be site-specific but not site limited: [12] the current spreads away from the stimulating electrodes and might have functional effects in areas that are not being targeted at first. Therefore the role of the reference electrode is crucial with regard to tDCS focality. We have opted for the extra-cephalic montage over the right shoulder, so we reduced site effects of the stimulation under other brain areas and limited the confounding factors [12,52].

For explaining the differential tDCS effects over A1 vs. over V1, it is important to consider two more issues. First, there are differences in the potential effects of tDCS over A1 and V1. The tDCS applied over A1 does not necessarily affect the excitability of the area since A1 is deep in the sulcus. However, V1 is directly affected by the same stimulation. This is a limitation of the tDCS technique and future studies should further address this issue. Secondly, note that tDCS might affect in different ways the different cell groups within the stimulated area [12]. Some studies investigating the properties of visual areas in the brain showed that different cell groups within the visual cortex were distinctively affected by the same tDCS stimulation polarity on a number of occasions [13]. Similarly, other studies showed such differential effects of tDCS in the auditory cortex [34,55]. In fact, Costa et al. [12] stated that "researchers are advised to be aware of the fact that different cell groups in one area might not be affected in the same way by tDCS" (p. 1833).

To control for the possible effect of sensation induced by the stimulation on temporal performance we included a sensation questionnaire [17]. Participants reported having felt more the stimulation when it was located in A1 compared to V1. However, the subjective feeling of stimulation did not covaried with time perception; therefore we can conclude that the results regarding the different tDCS effects on temporal processing were due to the specific effect of the stimulation on the underlying brain areas rather than by the subjective experience of the stimulation.

The present study is along the same line of research as the one of [31]. Indeed, it is one of rare studies addressing, with brain stimulation, the modality issue in the study of time perception. However, a few critical differences should be pointed out. First, although both studies used brain stimulation techniques, Kanai et al. used TMS while we used tDCS. tDCS has the advantage to allow the manipulation of cortical excitability; more specifically, it is possible to induce "inhibitory"-like and "facilitatory"-like effects, and to reduce the noise caused by the TMS instrument. Secondly, we included the sensation questionnaire, which provides interesting information regarding the effect of tDCS stimulation. Overall, as we previously stated, our results provide additional support, with a different technic, to the idea that visual and auditory cortices would have different roles in the processing of brief time intervals. However, it is important to note that tDCS has some limitation compared to TMS, in particular in the spatial resolution. Moreover, we acknowledge other potential limitations of our study. Kanai et al. [31] utilized MRI images to determine the position of A1 over which TMS was applied, but such method was not adopted in the current study. In the present study we located A1 using the international 10/20 system [45,49]. Considering the location of A1deep in sulcus different techniques might be used (i.e. tACS) to further explore the involvement of this area in temporal processing.

In sum, our results showed more variability of visual temporal processing under tDCS stimulation. These results suggest a modality independent role of A1 in temporal processing and a modality specific role of V1 in processing temporal intervals in visual modality. These results should be replicated but bring some support to the idea that time is distributed across different brain areas and that the recruitment of the different areas depends on the modality solicited.

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