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Anodal transcranial direct current stimulation of MPFC enhances humor processing

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ABSTRACT

The purpose of this study was to investigate whether the comprehension of a specific type of humorous situation requires the involvement of brain regions associated to mentalization or Theory of Mind processing and if the electrical stimulation of these areas would facilitate the comprehension of humor. To this aim, we analyzed the effects of tDCS stimulation on the MPFC and rTPJ during the presentation of humorous and non-humorous comic strips. In particular, the stimulus set included strips containing humorous scenes that required ToM abilities in order to be comprehended (*Humorous ToM*), non-ToM humorous strips (*Humorous non-ToM*), non-humorous strips which were semantically coherent but not funny (*Congruent*), and non-humorous strips which were semantically incoherent (*Incongruent*). Results suggest that the MPFC appears to be involved in both humor processing and in the incongruity resolution process: MPFC stimulation improved the ability to identify a non-humorous incongruent element and to recognize the humorous element of the scene. On the other hand, RTPJ activity doesn't seem to be specifically involved in humorous processing network and appears to be more related to the ability to understand the cognitive element of a social context.

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Humor; semantic processing; theory of mind; medial prefrontal cortex; temporo-parietal junction; transcranial direct current stimulation

Introduction

Humor is the ability to find something funny and be pleased by the joyful sensation. This capacity is based on a specific neural circuitry involving cognitive areas (for the comprehension of context and humoristic cues) and affective regions (for the pleasant emotional sensations), in addition to SMA for the laughing motor execution. Martin (2007) distinguished four components of the humor process: a social context, a cognitive-perceptual process (comprehension), an emotional response (appreciation), and the vocal-behavioral expression of laughter.

Recent studies showed that humor processing can be divided into three sub-stages including incongruity detection, incongruity resolution, and elaboration (Chan et al., 2013; Feng, Chan, & Chen, 2014). In addition, Ku, Feng, Chan, Wu, and Chen (2017) revealed that different degrees of surprise, comprehensibility, and amusement to jokes influenced the three sub-stages in humor processing.

In this study we investigated whether the processing of a specific type of humorous situation requires the involvement of brain regions associated to mentalization or Theory of Mind (ToM) processing and if the electrical stimulation of these areas would facilitate the comprehension and appreciation of humorous scenes. ToM is defined as our everyday ability to attribute mental states to ourselves and others in order to predict and explain behavior (Happè et al., 1996). Brain regions supporting ToM and mentalizations abilities are mostly cortical midline structures including the medial prefrontal cortex (MPFC), the anterior cingulate cortex and medial posterior parietal cortices including posterior cingulate and precuneus (Amodio & Frith, 2006, Mitchell et al., 2005), and temporal parietal junction (TPJ; Saxe, 2009; Young et al., 2010).

Neuroimaging works have investigated humor processing in adults. In an fMRI study, Goel and Dolan (2001) presented auditory semantic and phonological jokes to a group of adults who had to evaluate whether the auditory information was funny or not; in a similar work, Mobbs, Greicius, Abdel-Azim, Menon, and Reiss (2003) performed an event-related fMRI study (efMRI) in which they analyzed the activation of regions associated with funny visual cartoons. Their results found the activation of the left temporo-occipital junction, IFG, and

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temporal pole (Goel & Dolan, 2001; Mobbs et al., 2003). According to the authors, these regions fit well with Suls' incongruity-resolution theory (1972), according to which the comprehension of a joke involves two stages: in the first stage, the perceiver finds the expectations about the information disconfirmed by the ending of the joke (punchline); in the second stage, the perceiver engages in a form of problem solving to find a cognitive rule which makes the punchline follow from the main part of the joke and reconciles the incongruous parts (Attardo, 1997; Suls, 1972). Thus, the authors claimed that the temporo-occipital junction detects incongruity (first stage) (Goel & Dolan, 2001; Iwase et al., 2002), while more anterior regions, including Broca's area and the temporal pole, ascertain linguistic coherence (second stage). In addition, they revealed that humor processing involves a subcortical network, including the nucleus accumbens, which plays a key role in reward mechanisms (Schultz, 2002) and in medial ventral prefrontal cortex, a region involved in "'higher order'" reward processing (Mobbs et al., 2003).

In another fMRI study, Neely, Walter, Black, and Reiss (2012) examined humor processing in typically developing children by using scenes of slapstick humor. The results revealed that the funny videos activated the bilateral temporo-occipital-parietal junction, suggesting that this region might reflect incongruity resolution and the semantic processing of jokes (Goel & Dolan, 2001; Mobbs et al., 2003; Samson et al., 2009).

Moreover, other findings (Bartolo, Benuzzi, Nocetti, Baraldi, & Nichelli, 2006; Gallagher, 2000; Kohn, Kellermann, Gur, Schneider, & Habel, 2011) suggested that the activation of a specific brain network in response to humorous cartoons, including the medial prefrontal cortex, right inferior frontal gyrus, left superior temporal gyrus, left middle temporal gyrus and left cerebellum, could be associated both with ToM and mentalizing abilities and incongruity resolution (Bartolo et al., 2006; Brunet, Sarfati, Hardy-Baylé, & Decety, 2000). In particular, according to Bartolo et al. (2006) a humorous story can be fully understood when the perceiver engages in a subsequent process of attributing intention in resolving incongruity in humor. Therefore, according to the authors, the brain network associated to ToM skills might be recruited when resolving incongruous content and therefore may represent an important step in the comprehension of humor.

However, in this study the authors did not directly compare the brain activation in response to humor cartoons that involve ToM abilities and to non-humorous semantic incongruities. This comparison would provide insights into the cognitive mechanisms involved in humor ToM and semantic incongruities processing. In fact, it is not clear whether the brain network associated to the ToM-humor processing is selectively active during the process of information that require ToM abilities or if it is more generally involved in the resolution of a semantic incongruity.

Other works have contrasted the brain response during ToM and non-ToM humor processing (Samson, Zysset, & Huber, 2008; Watson, Matthews, & Allman, 2007). For example, Samson et al. (2008) conducted an fMRI study in which they contrasted different types of nonverbal humorous cartoons and non-humorous images containing a semantic incongruity. They found that non-humorous pictures containing incongruity and semantic cartoons were associated with activation in the left temporo-parietal junction, inferior frontal gyrus and ventromedial prefrontal cortex. On the other hand, visual puns processing was associated to the activation in the extrastriate cortex and ToM cartoons were associated with more activation in so-called mentalizing areas, including bilateral temporal-parietal junction, anterior medial prefrontal cortex and the precuneus.

Overall, the results of these previous investigations suggested that ToM and non-ToM humor processing might differentially stimulate MPFC (Samson et al., 2008; Watson et al., 2007) and that the processing of ToM humor involves the recruitment of areas that are typically associated to ToM processing but that are also active over the resolution of semantic incongruities (Bartolo et al., 2006). Therefore, the data from the previous studies did not offer direct evidence of the involvement of ToM-selective areas during the processing of specific types of humorous scenes.

Given the results of the previous works, in the present study we aimed to shed some light on the brain mechanisms that might be responsible for the processing of humorous scenes involving mentalization. In particular, in light of the previous neuroimaging evidences (Bartolo et al., 2006; Samson et al., 2008; Watson et al., 2007; Gallagher, 2000), we hypothesized that transcranial direct stimulation (tDCS) application to MPFC and rTPJ would improve humor perception during the observation of humorous scenes that involve ToM skills. In fact, since both the MPFC and the rTPJ are part of the so-called mentalizing areas (Amodio & Frith, 2006; Brunet et al., 2000; Fletcher et al., 1995; Gallagher et al., 2000; Samson, Apperly, Chiavarino, & Humphreys, 2004; Saxe & Powell, 2006; Saxe & Wexler, 2005; Scholz, Triantafyllou, Whitfield-Gabrieli, Brown, & Saxe, 2009), we hypothesized that anodal electrical stimulation of these regions could affect the subjects' comprehension and appreciation of ToM humor (see Baptista, Manfredi, & Boggio, 2018). In other words, if the processing of a specific type of humor requires ToM abilities, the stimulation of brain regions involved in ToM network would facilitate the processing of this type of humor.

To this aim, the current study analyzes the effects of tDCS stimulation on the MPFC and rTPJ during a task in which participants were instructed to categorize various comic strips as "humorous" or "not humorous". In addition, as a control area, we also stimulated the occipital cortex.

Therefore, several humorous and non-humorous comic strips were presented to healthy volunteers. In particular, the stimulus set included strips containing humorous scenes that required ToM abilities in order to be comprehended (*Humorous ToM*), non-ToM humorous strips (*Humorous non-ToM*), non-humorous strips which were semantically coherent but not funny (*Congruent*), and non-humorous strips which were semantically incoherent (*Incongruent*).

We expected to observe a significant modulation of the ability to categorize the different comic strips as humorous or not following the application of tDCS. In particular, over the MPFC and the rTPJ stimulation conditions, we expected to observe a significant improvement of the ability to categorize the comic strips as humorous or not, only when they involved ToM abilities (Humorous ToM strips).

In addition, previous evidences that investigated humor processing showed several brain regions overlap between the mentalizing system and the one involved in the incongruities resolutions (Bartolo et al., 2006; Brunet et al., 2000). Therefore, we wanted to clarify if the processing of a specific type of humor that requires ToM abilities involves a brain network that is specifically involved in ToM processing or that is required in the resolution of non-humorous semantic incongruities (Samson et al., 2008; Watson et al., 2007). Consequently, if humor was based on the ability to find an incongruity or in the sudden violation of expectancy, it would probably share some mental processes with those required to perceive a not humoristic (semantic) incongruity. In this vein, processing of funny ToM cartoon and non-humoristic incongruent cartoon would share similar brain mechanisms and the stimulation of the MPFC and rTPJ would possibly also improve the ability to recognize a non-humorous semantic incongruity (*Incongruent condition*).

Methods

Participants

Forty healthy volunteers (age range: 18–25 years, SD = 3.2; 20 women and 20 men) were recruited from Mackenzie Presbyterian University to participate in this study. Participants were native Portuguese speakers with normal or corrected-to-normal vision. We excluded participants with prior or current psychiatric disorders.

They were assessed with the Brazilian versions of the Beck Anxiety Inventory (BAI) and Beck Depression Inventory (BDI; Gorenstein & Andrade, 1996), and the Brazilian Empathy Inventory (EI; De Oliveira Falcone et al., 2008). The EI is a 40-item self-report questionnaire designed to evaluate both cognitive and affective empathy. We assessed the empathy scores in order to have a measure of participants' ToM abilities. The EI includes four-item subscales: Perspective Taking, Interpersonal Flexibility, Altruism and Affective Sensibility. Responses are made on a 5-point Likert scale ranging from 0 ("*it does not describe me well*") to 4 ("*it describes me very well*").

Four participants of the initial sample were excluded from the data analysis due to their high scores on the depression scale (greater than 8 points; see Gorenstein & Andrade, 1996). Thus, the final sample contained 36 subjects. The mean empathy score of the participants was 150 (score range = 124–179; SD = 13.47).

All participants were right-handed according to the Edinburgh Handedness Inventory (Oldfield, 1971). The study adhered to the Declaration of Helsinki guidelines and was approved by the institutional ethics committee at Mackenzie Presbyterian University, Brazil, and registered with the Brazilian National Ethics Committee. Each participant received course credit for participating and provided written informed consent prior to the experiment. All participants had previous knowledge of *Monica's Gang*, however after each session, they reported that they were not familiar with the strips presented during the experiment.

Stimuli

The data set included 248 three-panel long narrative sequences using panels from the *Monica's Gang*™ comics by Mauricio de Sousa. All panels were gray scale and had a coherent narrative structure (see Cohn & Paczynski, 2013).

Four different types of strips were considered (Figure 1): i) the *Humorous Non-ToM* strips (a) had the third panel (punchline) containing a comic element that did not require ToM abilities to understand; ii) the *Humorous ToM* strips (b) had the last panel containing a comic element that required ToM abilities to comprehend; iii) the *Congruent* strips (c) had the last panel which didn't contain any humorous elements, and the content of which was coherent with the previous panels; iv) the *Incongruent* strips (d) had the last panel which didn't contain any humorous elements, the content of which was incoherent with the previous panels (Figure 1).

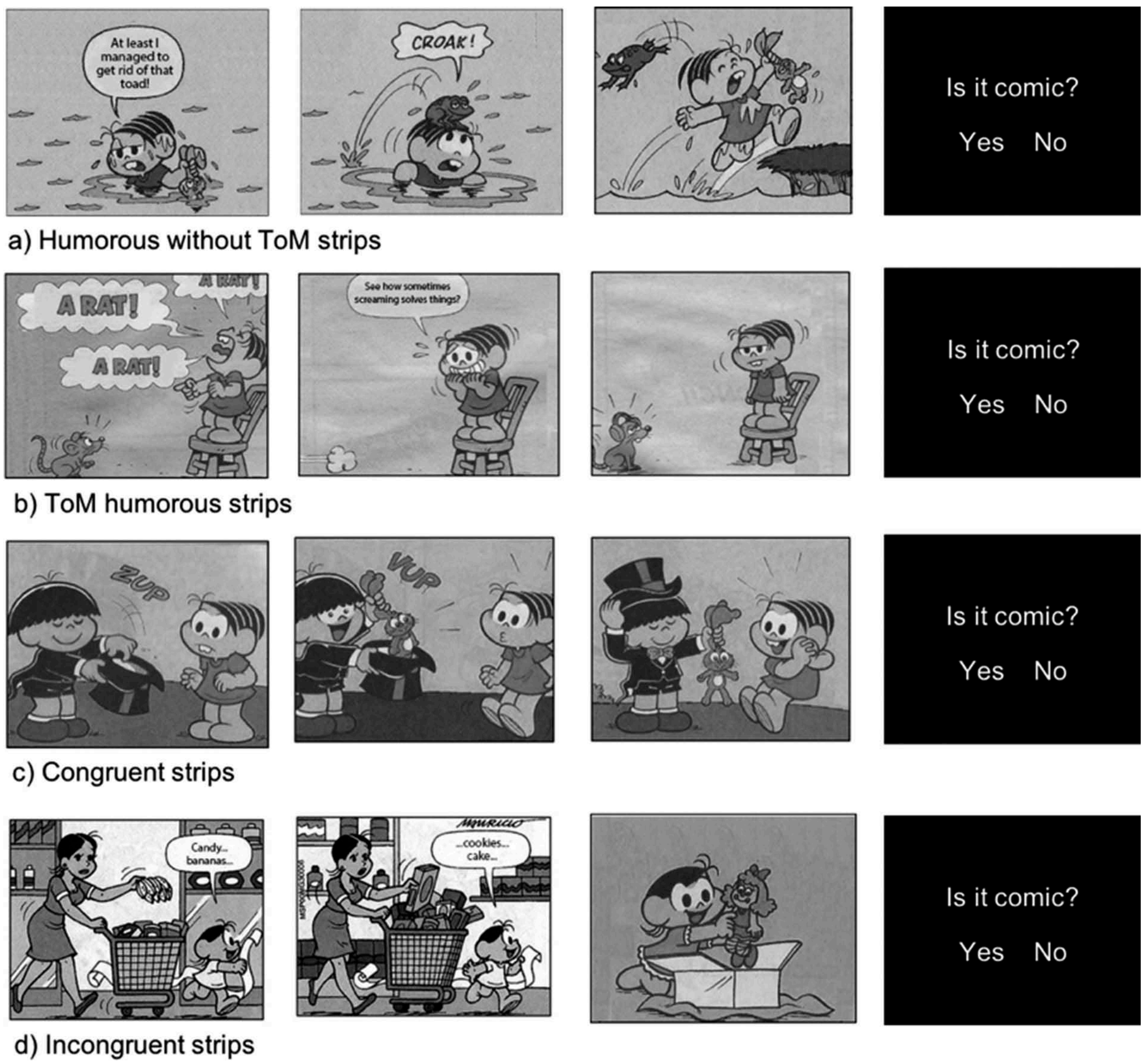

Figure 1. Examples of visual sequences of the four stimulus categories used as experimental stimuli.

In order to be validated, each strip was previously presented to a group of 15 judges (6 males, 9 females) of similar age (mean age = 22.8, SE = 2.6) and educational level as the experimental subjects. The examiners had to evaluate the strips for their humorous content and difficulty level (how easy their meaning was to understand). In addition, they decided whether the strip required ToM abilities to understand. The experimenter provided the participant with a definition of ToM (i.e. "Theory of mind is the ability to attribute mental states beliefs, intents, desires, emotions, knowledge, etc. – to oneself, and to others, and to understand that others have beliefs, desires, intentions, and perspectives that are different from one's own." Premack & Woodruff, 1978) and then verified that the concept was well understood through a pre-test.

After this preliminary phase, judges were asked to rate narrative sequences for their humorous content in a self-paced mode, by means of a 4-point scale [3 = "*very humorous*"; 2 = "*quite humorous*"; 1 = "*a little humorous*"; 0 = "*not at all humorous*"], and for their difficulty by means of a 4-point scale [3 = "*very difficult*"; 2 = "*difficult*"; 1 = "*a little difficult*"; 0 = "*not at all difficult*"], indicating how immediate or difficult their understanding of the strip was. In addition, the participants were asked to determine whether the sequence required ToM skills or not to understand by pressing a "*yes*" or a "*no*" key on the computer keyboard [1 = "*yes*"; 0 = "*no*"].

To provide a clear distinction between stimuli, strips scoring above 1.5 on the humor scale were categorized as Humorous (both Humorous ToM and Humorous non-ToM), whereas strips scoring below 1.0 were categorized as Non-Humorous (either Congruent or Incongruent) (see Manfredi, Adorni, & Proverbio, 2014; Manfredi et al., *under review* for a similar procedure). In the Incongruent category, the content of the last panel was not semantically related to the previous panels, thus the incongruent strips were evaluated as difficult to comprehend (see Figure 1). Therefore, strips scoring above 1.5 on the difficulty scale were placed in the Incongruent category. In addition, strips that were categorized both as humorous and requiring ToM skills were placed in the Humorous ToM category.

A repeated-measures ANOVA carried out on the humor scores attributed to the 4 groups of stimuli categories ($F_{3,\ 42} = 59.17$, $p < 0.01$) revealed significant differences in humor levels between category types (Mean *Humorous Non-ToM* = 1.6, SE = 0.14; Mean *Humorous ToM* = 2.0, SE = 0.12; Mean *Congruent* = 0.82, SE = 0.12; Mean *Incongruent* = 0.74, SE = 0.13). In particular, humorous ToM strips were evaluated as significantly more humorous than the other categories. In addition, humorous non-ToM strips were rated as significantly more humorous than the Congruent and Incongruent categories ($p < 0.01$). No significant differences in humor level were found between the Congruent and Incongruent categories.

In addition, a repeated-measures ANOVA analysis ($F_{3,\ 42} = 33.32$, $p < 0.01$) revealed that incongruent strips were rated as significantly more difficult to be comprehended than the other categories (Mean *Humorous Non-ToM* = 0.5, SE = 0.11; Mean *Humorous ToM* = 0.60, SE = 0.11; Mean *Congruent* = 0.72, SE = 0.11; Mean *Incongruent* = 1.64, SE = 0.16).

Finally, a repeated-measures ANOVA applied to the ToM values attributed to the sequences by the participants ($F_{3,\ 42} = 8.16$, $p < 0.01$) revealed that the Humorous ToM strips values were significantly higher than the other categories (Humorous non-ToM = 0.38, SE = 0.04; Humorous ToM = 0.60, SE = 0.05; Congruent = 0.35, SE = 0.04; Incongruent = 0.45, SE = 0.04).

At the end of this process, 248 strips were selected as stimuli (62 for each category). The presence of each character was balanced across categories. Strips were also balanced for number of characters involved. The stimulus size was 12 cm × 14.5 cm.

Transcranial direct current stimulation (tDCS)

Direct electrical current was applied by conductive rubber electrodes (16 cm^2) inserted in saline-soaked sponges and delivered by a battery-driven stimulator. We stimulated three distinct brain regions: Medial Prefrontal Cortex (MPFC), right Temporoparietal Junction (rTPJ), and Medial Occipital Cortex. In order to stimulate the MPFC, the anodal electrode was positioned centered on the scalp at one-third of the distance between the nasion and the inion on the midline (see Mattavelli, Cattaneo, & Papagno, 2011; Riva, Manfrinati, Sacchi, Pisoni, & Lauro, 2019; Baptista et al., 2018 for similar procedure); to stimulate the rTPJ, the anodal electrode was positioned centered over CP6 according to the International 10–20 system for electroencephalogram electrode placement (Jasper, 1958); finally, to stimulate the mid-occipital region (control area) the anodal electrode was placed over Oz. In all the conditions, the cathode was placed over the right deltoid muscle (Baptista et al., 2018). The regions under CP6 and Oz are Brodmann's areas BA40 and BA18 (Talairach & Tournoux, 1988), located mainly within the right parietal cortex and medial occipital cortex respectively (Koessler et al., 2009). For sham stimulation, the position of the electrodes was the same as during MPFC stimulation, however, the tDCS device was turned off after 20 s of current delivery (Figure 2).

During active stimulation conditions, a constant current of 1.5 mA intensity was applied for 5 minutes before the task began and over the performance of the task (6 minutes). Therefore, the total time of stimulation was 11 minutes. To prevent adaptation effects from the first stimulation, the second tDCS session was conducted after an interval of at least 48 h.

Task and procedure

The study was performed as a double-blind, randomized, and placebo-controlled study. All participants underwent MPFC, rTPJ, occipital and sham tDCS in separate sessions. The order of stimulation session was randomized between subjects.

During each stimulation session, only 62 comic strips (~15 for each category) were presented. Therefore, each stimulus was presented only once to the participants.

The order of the list presentation was counterbalanced across participants and type of stimulation.

The task was programmed using the E-prime 2.0 software package. The participants viewed the stimuli on a high-resolution VGA computer screen located at a distance of 50 cm from them (see Manfredi et al., 2017). Each strip was presented panel by panel at the center of the computer screen. During the presentation of the third panel, participants had to evaluate if the strip presented was humorous or not by pressing response keys for yes or no with their index fingers. The first two panels were presented for 2500 ms and the last one for either a maximum duration of 5000 ms or until the participant responded. The location of the response keys (left or right) was counterbalanced across participants.

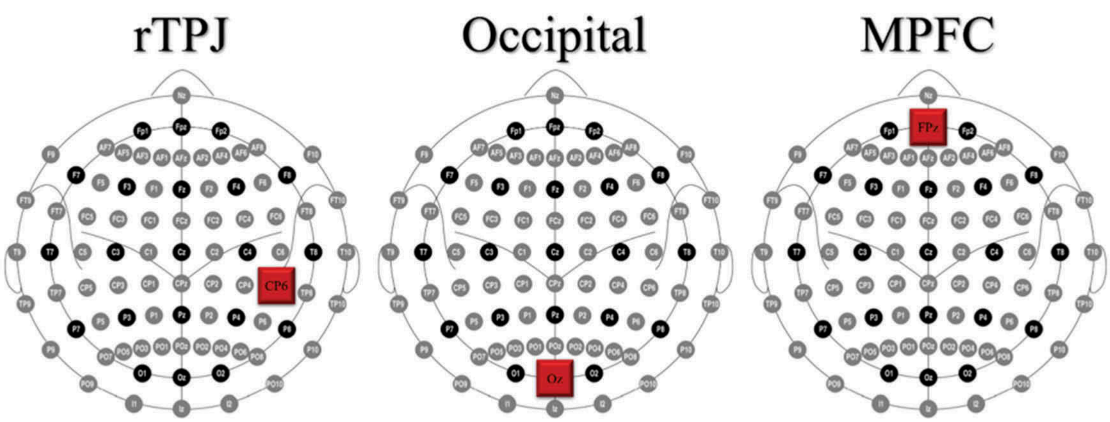

Figure 2. tDCS montages for all active conditions.

Stimuli were randomly displayed in two different blocks of 30 trials that lasted approximately 3 minutes per block. The task lasts approximately 6 minutes.

Statistical analysis

We analyzed the effects of stimulation on the task by performing repeated-measures ANOVAs on mean humor rates and reaction times. The ANOVAs included two within-subject factors: Condition (Humor non-ToM, Humor ToM, Congruent, and Incongruent) and tDCS stimulation (MPFC, rTPJ, occipital and sham).

Multiple comparisons of means were performed by means of the Fisher post-hoc test. Since the assumption of normality was not met even after excluding the outliers, a log $_{10}$ transformation was performed. Although the analyses were performed on the transformed data, we reported the raw descriptive statistics to aid interpretation.

Results

All subjects reported that they could not feel the difference between the active and sham conditions. Regarding the response times, the ANOVA did not reveal any significant effects. Differently, the ANOVA on the humor rates revealed a significant main effect of Condition ($F_{3,\ 27} = 26.33$; $p = 0.00$; $\eta_p = 0.75$; $\beta = 1.00$), showing that both the humorous strips (Humorous ToM strips: 84%; SE = 1.61; Humorous non-ToM strips: 68%; SE = 2.93) were evaluated as significantly more humorous than the other strips (Congruent: 19%; SE = 2.77; Incongruent: 14%; SE = 2.16; $p = 0.00$). However, the Humorous ToM strips were considered significantly more humorous that the Humorous non-ToM strips ($p = 0.04$).

In addition, the analysis revealed a significant interaction between Condition and tDCS stimulation ($F_{9,\ 81} = 2.87$, $p = 0.00$; $\eta_p = 0.24$; $\beta = 0.95$). In particular, in the sham condition the post-hoc comparisons showed that the humor conditions were rated as significantly more humorous compared to the other ones ($p = 0.00$). However, the Humorous ToM strips (82%; SE = 2.20) were rated as more humorous than the Humorous non-ToM strips (68%; SE = 3.75; p = 0.00). No significant differences were found between Congruent (17%; SE = 3.10) and Incongruent strips (14%; SE = 2.34) in the sham condition ($p = 0.07$). Similar results were observed over the occipital and the rTPJ stimulations (see Figure 3): humor conditions were rated as significantly more humorous as compared to the other ones ($p = 0.00$). Again, as observed for the sham condition, the Humorous ToM strips (Occipital: 81%; SE = 2.72; rTPJ: 82%; SE = 2.62) were rated as more humorous than the Humorous non-ToM strips (Occipital: 66%; SE = 3.82; rTPJ: 68%; SE = 3.14; p = 0.00), and no significant differences were found between the Congruent (Occipital: 20%; SE = 3.46; rTPJ: 17%; SE = 2.95) and Incongruent strips (Occipital: 16%; SE = 3.66; rTPJ: 18%; SE = 2.64) in the sham condition ($p = 0.60$).

Regarding the MPFC stimulation, similarly to the other stimulations, the post-hoc comparisons revealed that the humorous strips were considered more humorous than the Congruent and Incongruent strips ($p = 0.00$) and that Humorous ToM strips (88%; SE 1.85) were considered more humorous than the Humorous non-ToM ones (69%; SE = 2.96). In addition, the Incongruent strips (10%; SE = 2.36) were considered significantly less humorous than the Congruent ones (20%; SE = 3.42; $p = 0.00$).

Moreover, the post-hoc comparisons revealed that the Humorous ToM strips were considered significantly more humorous over the MPFC stimulation (88%; SE 1.85) as compared to the others (Sham: 82%; SE = 2.20; Occipital: 81%; SE = 2.72; rTPJ: 82%; SE = 2.62). The

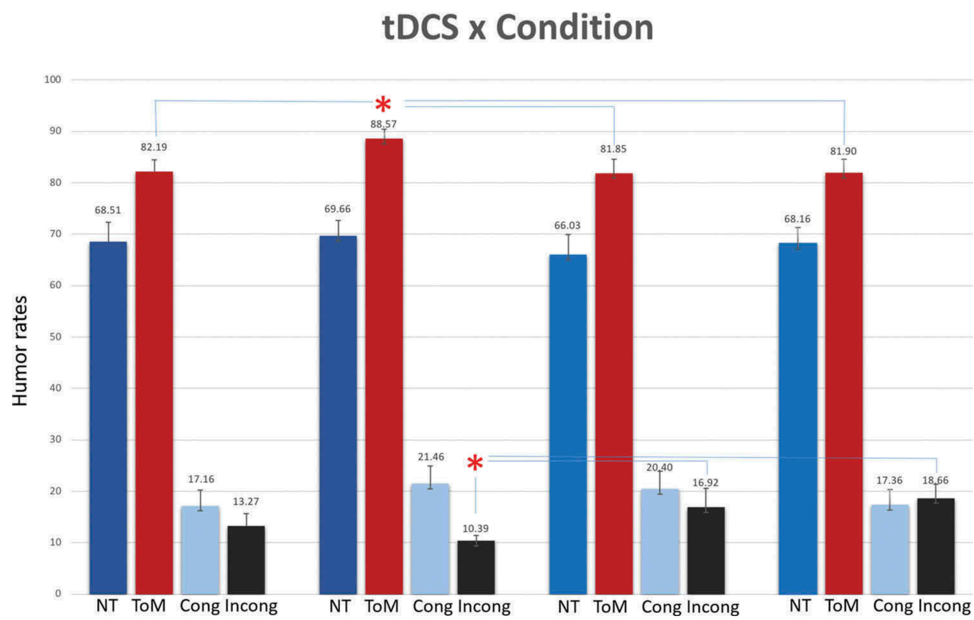

Figure 3. Humor rates for the Humor non-ToM, humor ToM, congruent and incongruent strips in each tDCS stimulation condition (sham, MPFC, occipital and rTPJ). The error bars represent the standard deviation.

results did not show any significant differences in the humor rates for the Humorous non-Tom strips (Sham: 68%; SE = 3.75; MPFC: 69%; SE = 2.96; Occipital: 66%; SE = 3.82; rTPJ: 68%; SE = 3.14; $p = 0.6$; $p = 0.3$; $p = 0.9$) and Congruent strips (Sham: 17%; SE = 3.10; MPFC: 21%; SE = 3.42; Occipital: 20%; SE = 3.46; rTPJ: 17%; SE = 2.99; $p = 0.1$; $p = 0.2$; $p = 0.9$) in each of the tDCS Stimulation conditions.

Finally, the results showed that the Incongruent strips were considered significantly less humorous in the MPFC stimulation (10%; SE = 2.36) as compared to the occipital (16%; SE = 3.66; $p = 0.02$) and rTPJ conditions (18%; SE = 2.64; $p = 0.00$), but not compared to the sham condition (13%; SE = 2.34; $p = 0.3$).

However, no significant differences were found in the humor rates for the Incongruent strips in the sham stimulation as compared to the occipital ($p = 0.1$) and the rTPJ stimulations ($p = 0.06$).

Finally, we did not find significant differences between tDCS conditions ($F_{3, 27} = 0.38$, $p = 0.77$; $\eta_p = 0.04$; $\beta = 0.11$).

Discussion

In this study, we applied tDCS stimulation to three different brain regions (MPFC, rTPJ, occipital cortex) to modulate humor perception during the observation of different types of comic strips. In particular, since the MPFC and rTPJ are thought to support the ToM neural network (Amodio & Frith, 2006; Brunet et al., 2000; Fletcher et al., 1995; Gallagher et al., 2000; Samson et al., 2004; Saxe & Powell, 2006; Saxe & Wexler, 2005; Scholz et al., 2009) we investigated whether the electrical stimulation of these brain regions would improve/affect the processing of a specific type of humorous situations that require ToM skills to be understood and appreciated.

In addition, since previous evidences that investigated humor processing showed several brain regions overlap between the so-called mentalizing system and the brain network involved in the incongruities resolutions, we verified whether the processing of ToM-humorous scenes requires brain mechanisms that are also involved in the resolution of non-humorous semantic incongruities. If similar brain mechanisms were involved in humor and incongruities processing, the stimulation of the MPFC and/or rTPJ would also improve the ability to recognize a (non-humorous) semantic incongruity.

It is worth to mention that the statistical results did not show significant differences between tDCS conditions and revealed a small observer power. This result would suggest that the lack of significance could be attributable to the sample size.

However, the statistical analysis showed differences between the mean humor rates observed in the different tDCS conditions in response to the four categories of comic strips. Overall, for all stimulation conditions, the humorous strips were considered more humorous than both the Congruent and Incongruent strips but Humorous ToM strips were considered more humorous than the Humorous non-ToM ones. No differences were observed between the responses to Congruent and Incongruent strips in all tDCS conditions except for the MPFC stimulation condition.

In addition, our data suggest a functional dissociation between the MPFC and the rTPJ: the MPFC activity could be involved in the ability to recognize the ToM humorous element of a complex scene while the rTPJ activity might be more related to the cognitive ability to understand a social situation. Below, we elaborate further on these findings.

Sham condition

In the sham condition, the results showed that humoristic strip were rated as significantly more humorous compared to the other ones. Interestingly, the Humorous ToM strips were rated as more hunmorous than the Humorous non-ToM strips, possibly reflecting effort required in understanding intentions of the characters. This result was in line with the findings of the pretest described above which revealed that Humorous ToM strips were indeed evaluated as significantly more humorous than the other categories. A recent ERP study by our group (Manfredi et al., *under review*) revealed a greater Late Positive (LP) response to Humorous ToM strips compared to non-ToM strips in frontal areas and a positive correlation between LP amplitude values to Humorous ToM strips and humor ratings. We argued that the greater LP response to ToM humorous strips in our study could reflect the combined activation of neural mechanisms involved in the experience of amusement and in the effort expended in attributing intentions to the characters in humorous strips, requiring ToM abilities. Interestingly, Bartolo et al. (2006) performed an fMRI study in which they observed greater bold signals in the right inferior frontal gyrus, left superior temporal gyrus, left middle temporal gyrus and left cerebellum in response to humorous cartoons and claimed that the degree of amusement generated by humoristic cartoons was a function of the effort expended in attributing intentions to the characters in humorous strips. Therefore, they claimed that the cognitive effort required by the comprehension of context and expectancy violation (generating humorous response) was directly correlated to the feelings of amusement. Overall, these previous findings suggest that the greater the involvement of cognitive resources to understand a humorous situation (such as ToM skills), the more the elicited feeling of amusement. Therefore, it is possible that in our study the Humorous ToM strips were judged as more humorous than the non-ToM strips also in virtue of the greater cognitive effort to be comprehended.

MPFC vs rTPJ conditions

The results of our investigation showed no improvements in the humor rates for Incongruent strips neither over the MPFC nor the rTPJ stimulation when compared to the sham condition. In addition, we found that the rTPJ stimulation failed in improving the humor rates to ToM humorous strips while the MPFC stimulation did improve the humor rates in response to this humorous category. On the other hand, we observed that the stimulation of rTPJ impaired the humor rates in response to Incongruent stimuli, suggesting that the stimulation of this brain region might have led to a misinterpretation of the Incongruent strips that were judged as more humorous.

However, over the MPFC stimulation, we observed that Incongruent strips were considered significantly less humorous than the Congruent ones. Previous studies revealed that the MPFC is part of a network that is active during the incongruity-detection processes (Samson et al., 2009). For example, Samson and colleagues performed an fMRI study in which they analyzed the brain responses associated to incongruity-resolution and nonsense cartoons processing. The results of their investigation revealed that a brain network, including the MPFC, showed more activation during processing of incongruity-resolution than of nonsense cartoons. In light of these evidences, the stimulation of this brain region in our study might have enhanced the ability to recognize the incongruities presented in the Incongruent strips and thus the ability to categorize them as “not humorous”.

Post-hoc comparisons across the tDCS conditions

The post-hoc comparisons performed across the tDCS conditions revealed no humor rates improvement in response to the four types of strips during the occipital stimulation (i.e. the control area) as compared to the sham condition, suggesting that this area is not specifically engaged in humor processing. Contrariwise, the post-hoc analysis revealed that the MPFC stimulation significantly improved the humor rates specifically for ToM-humor relative to the sham condition. However, no improvement was observed in the humor rates for ToM-humor over the rTPJ stimulation.

Moreover, we tested the possibility that the stimulation of these areas would improve also the humor rates to Incongruent strips as compared with the sham condition. In fact, one of the aims of this study was to verify if the type of humor that requires ToM abilities and the detection of a semantic incongruity are associated to similar brain mechanisms. Our results revealed a worsening of the performance to the Incongruent strips during the rTPJ stimulation (as compared to the sham condition) and an humor rates improvement in response to the Incongruent strips over the MPFC stimulation when compared to the occipital and rTPJ stimulations (no differences were observed compared to the sham condition). In light of these results, we could hypothesize that the MPFC is also involved in incongruity-detection processes. However, since the humor rates to the Incongruent strips did not show any improvement in the MPFC condition when compared to the sham condition, it is possible that this type of strip was already at peak efficiency. Future investigations can help to clarify the role of this region in the comprehension of incongruent elements depicted in complex social scenes.

As mentioned before, several neuroimaging studies have revealed that both the MPFC and rTPJ are strongly activated in response to the ToM processing (Amodio & Frith, 2006; Brunet et al., 2000; Fletcher et al., 1995; Gallagher et al., 2000; Samson et al., 2004; Saxe & Powell, 2006; Saxe & Wexler, 2005; Scholz et al., 2009). However, new findings revealed functional dissociations between these two regions (Saxe & Young, 2014). For example, the rTPJ seems to be more active in true and false beliefs processing, while the MPFC would be more active for descriptions of status and personality and physically traits (Jenkins & Mitchell, 2009). In addition, evidences showed that lesions to the MPFC might lead to a difficulty in thinking about other people's emotions (Shamay-Tsoory, Tomer, Berger, & Aharon-Peretz, 2003), but the ability to think about other people's thoughts seems to be preserved (Bird, Castelli, Malik, Frith, & Husain, 2004). Therefore, the MPFC might have a critical role in understanding belief about emotions and recognition of *faux pas* (Shamay-Tsoory, Tomer, Berger, & Aharon-Peretz, 2005).

On the other hand, the rTPJ activity might be associated to a process of constructing a coherent model of the other person's mind (Young, Dodell-Feder, et al., 2010). In 2010, Young and colleagues performed an fMRI study to test whether the rTPJ is specifically involved in the processing of any unexpected stimulus or more specifically involved in ToM processing. In this study, participants read stories describing mental or physical states, which were unexpected or expected. The analysis showed higher response in the rTPJ, LTPJ, and precuneus, for mental versus physical stories, but no difference for unexpected and expected stories.

Differently, another fMRI study (Saxe & Wexler, 2005) revealed that the rTPJ response was more active for contextually unexpected beliefs and desires. However, in this study participants were provided with information about the characters of a story that they used to build a theory about the relationship between the mental state and the protagonist. In light of these evidences, it seems that contextually unexpected mental states may require more effort in building a theory which may be associated to a stronger involvement of the rTPJ (Young, Dodell-Feder, et al., 2010).

Given these previous evidences, the specific improvement in humor rates observed in response to ToM-humorous strips during the MPFC stimulation, would suggest that the stimulation of this region could have improved the ability to recognize and integrate the affective element (i.e. humorous element) depicted in the scene. In fact, since this region is associated to other people's emotions processing (Shamay-Tsoory et al., 2003), it is possible that its stimulation leads to a better recognition of belief about emotions and therefore to a better comprehension and appreciation of the humorous content.

On the other hand, the humor rates to ToM-humorous strips did not show any improvement over the rTPJ stimulation when compared to the sham condition, suggesting that that this area could be more involved in the processing of the cognitive component of a complex social scene and less involved in the processing of the affective element (i.e. humorous element). In addition, during the rTPJ stimulation, a slight decline in the performance of the Incongruent strips was observed. In line with previous evidences (Saxe & Wexler, 2005), we can speculate that the stimulation of this brain region might have increased the cognitive effort in constructing a coherent model of the unexpected characters' beliefs and mental states depicted in the Incongruent strips, leading to a misinterpretation of the nature of the scene.

Moreover, as we expected, the stimulations of the MPFC and rTPJ did not show any improvement in the humor rates to the Humorous non-Tom condition when compared to the sham condition. In fact, previous evidences revealed that this type of non-ToM humorous stimuli (i.e. slapstick humor) involves the recruitment of other areas such as the superior temporal sulcus, the superior temporal gyrus, the middle occipital gyrus, and the precuneus (Manfredi et al., 2017; Samson et al., 2008; Watson et al., 2007) and involves cognitive mechanisms that are different from those involved in ToM humorous stimuli. For example, this type of humor is often labeled as aggressive or disparaging humor in the literature (Ferguson & Ford, 2008; Ford & Ferguson, 2004; Zillman, 1983). Therefore, we cannot exclude that these differences could also have affected the ratings and processing assessed in the present study. In light of these considerations, we believe that further studies will be necessary to better differentiate the cognitive mechanisms involved in the two types of humor.

One important limitation of this study is that the task employed didn't allow to identify the three different stages underlying humor comprehension and appreciation that previous studies have pointed out (Bartolo et al., 2006; Chan et al., 2013; Feng et al., 2014; Ku et al., 2017). In fact, the different processing stages involved in the humor processing are confounded in our task. Therefore, we are aware that future studies will have to use tasks that will better allow to differentiate the three stages of humor processing.

Finally, another limitation of the study is the short duration of tDCS stimulation (i.e. 11 minutes) that could have caused the lack of significant differences in response times between tDCS conditions.

Conclusions

In summary, our study suggests that the MPFC appears to be involved in both the complex network implicated in humor processing and in the incongruity resolution process. Indeed, our data suggest that MPFC stimulation improved the ability to identify a non-humorous incongruent element and to recognize the humorous element of the scene. In particular, this region might have a role in the ability to efficiently recognize and integrate specific humorous element in a complex scene. On the other hand, the rTPJ activity doesn't seem to be specifically involved in humorous processing network and appears to be more related to the ability to understand the cognitive element of a social situation.

Disclosure statement

No potential conflict of interest was reported by the authors.

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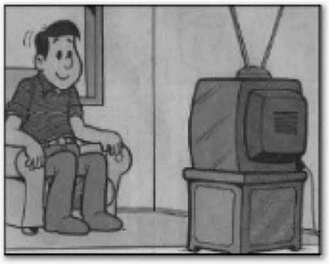
Appendix A. Examples of comic strips

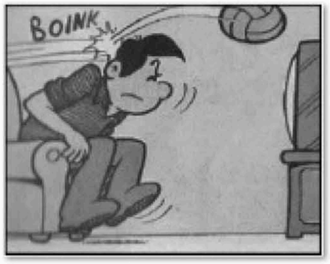
- 5 congruent comic strips

C.3a

C.3b

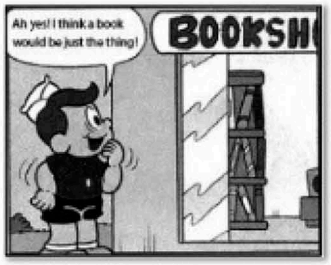

C.3c


C.12a



C.12b


C.12c



C.38a

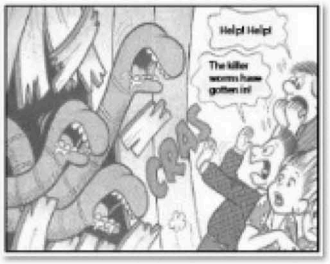
C.38b


C.38c

C.49a

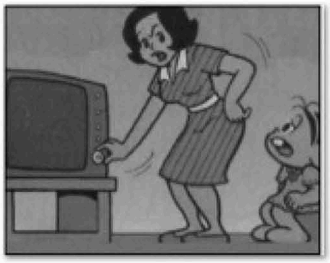
C.49b


C.49c



C.25a

C.25b


C.25c

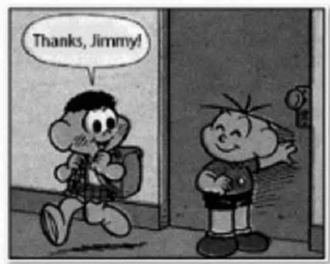
- 5 incongruent comic strips

CI.8a

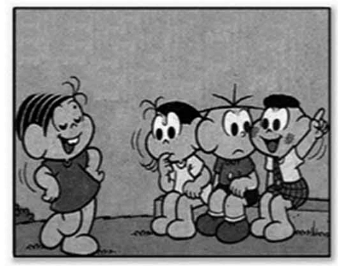
CI.8b


CI.8c

CI.27a



CI.27b


CI.27c


CI.71a


CI.71b


CI.71c

CI.18a

CI.18b


CI.18c


CI.61a

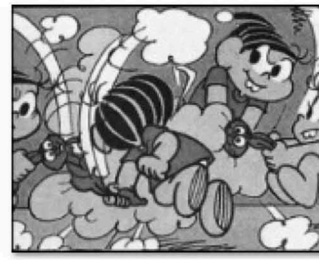
CI.61b


CI.61c

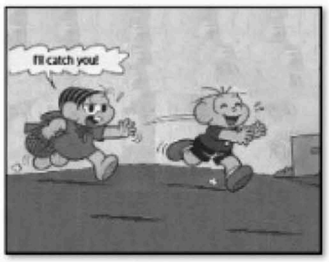
- 5 non-ToM humorous comic strips

NT.8a

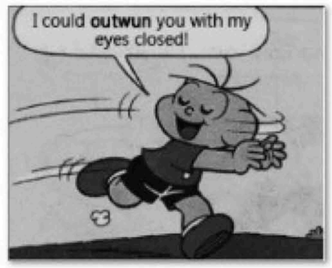
NT.8b



NT.8c



NT.19a



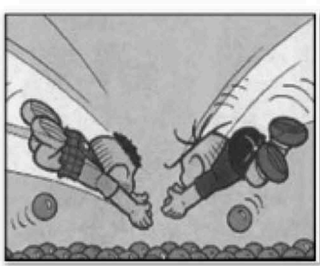
NT.19b

NT.19c

NT.72a

NT.72b

NT.72c



NT.16a

NT.16b

NT.16c

NT.26a

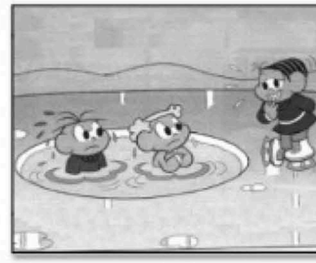
NT.26b

NT.26c

- 5 ToM humorous comic strips

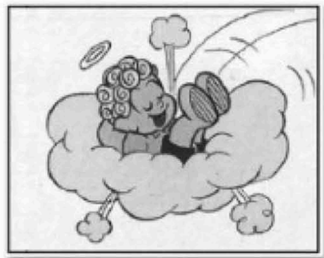
T.7a

T.7b

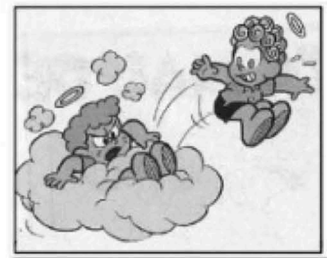


T.7c

T.13a

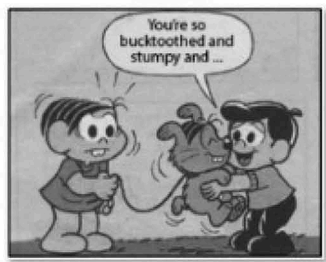


T.13b



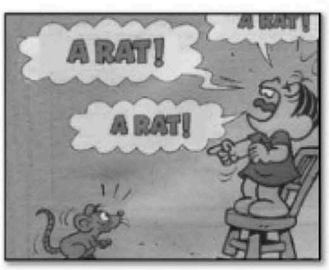
T.13c

T.27a



T.27b

T.27c



T.45a

T.45b

T.45c

T.42a

T.42b

T.42c