

The role of the right parietal lobe in the perception of causality: a tDCS study

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Abstract Inferring causality is a fundamental feature of human cognition that allows us to predict outcomes in everyday events. Here, we use direct current stimulation (tDCS) to investigate the role of the right parietal lobe in the perception of causal events. Based on the results of a previous fMRI investigation, we hypothesized that the right parietal lobe plays a specific role in the processing of spatial attributes that contribute to judgments of causality. In line with our hypothesis, we found polarization-dependent modulation of causal judgments and corresponding reaction times (RTs) for trials with increasing violation of spatial contiguity in launching events. This effect was further modulated by temporal violations, as the effect of tDCS on the use of spatial information for causality judgements was strongest for trials with high temporal violations. Thus, especially for ambiguous trials with regard to temporal patterns, cathodal stimulation led to more liberal causality judgments for trials with high angles in movement trajectory. Furthermore, we found faster RTs after anodal stimulation of the right parietal lobe. These findings suggest a reduced influence of spatial attributes on the perception of causality after cathode stimulation of the right parietal lobe and an increased processing efficiency after anodal stimuli of the same region. These data demonstrate polarization-dependent tDCS modulation of spatial

processing mechanisms within the right parietal lobe that contribute to the perception of causality.

Keywords Perception of causality · Spatial continuity · Temporal contiguity · Parietal lobe · Event structure

Introduction

Inferring causality is a fundamental feature of human cognition. This ability allows us to theorize about and prepare for the consequences of events. Philosophers and psychologists have long thought about how we know whether one event causes another (Hume 1740/1960, 1748/1977; Michotte 1946/1963). Neuroscience now has new tools and methods that can be used to investigate the underlying brain processes involved in forming impressions of causality.

Relatively few studies have examined the neural basis for causality perception. The typical paradigms follow the kinds of experiments designed by Michotte (1946/1963), in which one ball collides with another and is perceived as causing the second to move. These events are referred to as “launching events.” Most functional magnetic resonance imaging (fMRI) studies have focused on differences in activation produced by causal events as compared to non-causal ones (Blakemore et al. 2001; Fugelsang et al. 2005). Whereas the first study reported that perceiving causal relationships produce greater activation of bilateral occipital (V5/MT/MST), superior temporal regions and the left intraparietal sulcus (Blakemore et al. 2001), the other found activation in the right middle frontal gyrus and the right inferior parietal lobule for causal relative to non-causal events (Fugelsang et al. 2005). Fugelsang et al. (2005) further distinguished between the shared and

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distinct regions of activation for the contributions of spatial and temporal contiguity to causal perception. Areas of the right prefrontal cortex were active for both processes. There is further evidence suggesting that, perceptual causality can be distinguished from inferential causality. Inferential causality activates the medial frontal cortex (Fonlupt 2003) and seems to be especially dependent on the left hemisphere as demonstrated in callosotomy (split-brain) patients (Roser et al. 2005).

In a recent fMRI study, we investigated the neural basis of causality perception, taking a different approach than adopted by previous studies. Rather than compare the extremes of events judged as causal and non-causal, we examined how individual differences in attending to spatial and temporal characteristics predict causality judgments (Straube and Chatterjee 2010). We did this by using stimuli in which a spatial variable (angular trajectory) or a temporal variable (delay) varied parametrically. It has been shown that several parameters contribute to the perception of causality (see Michotte 1946/1963). Spatial continuity and temporal contiguity have received most attention in behavioral and cognitive neuroscience studies (see Scholl and Tremoulet 2000; Blakemore et al. 2001; Fugelsang et al. 2005; Roser et al. 2005; Schlottmann et al. 2006). However, in previous research, most spatial violations were defined as physical gaps between stimuli (the objects never make contact) (e.g., Fugelsang et al. 2005; Roser et al. 2005; Schlottmann et al. 2006). The advantage of inducing spatial violations by variation of movement direction is that contact between the objects occurs in every event. In this fMRI study, we found bilateral occipito-parietal and frontal brain activation in response to ball movements, which is consistent with previous literature on movement perception (Billino et al. 2009), the perception of launching events (Blakemore et al. 2001) and the extraction of specific movement parameters in event perception (Zacks et al. 2006; Grosbras et al. 2011). However, we did not find consistent patterns of brain activation that distinguished between events judged as causal and those judged as non-causal. We proposed that it is unlikely that a universal “causal network” is engaged by perceptual causality. However, we did find that individual differences in judging causality have distinct neural signatures. Participants differed in their sensitivity to spatial and temporal characteristics of events when perceiving causal relationships (Straube and Chatterjee 2010). Sensitivity to spatial information when perceiving causality was correlated with activation of the right parietal lobe, an area often implicated in spatial perception (Shulman et al. 1999, 2010; Keehner et al. 2006). Attention to path trajectories engages the dorsal fronto-parietal networks (Wu et al. 2008; Battelli et al. 2009) and is likely responsible for violation detection in spatial continuity tasks. In contrast, sensitivity to time

information was correlated with increased activation within the left basal ganglia when judging causality. The basal ganglia have been implicated in the perception of time delays in the sub- and supra-second range (Lewis and Miall 2003; Meck et al. 2008). Our results revealed that individual differences in perceptions of causality are associated with different neural signatures depending on whether individuals are sensitive to time or to space. We proposed that time and space are fundamental elements that contribute to our perception of causality.

Motivated by these fMRI findings, we now ask the following question: if temporal and spatial characteristics each individually contribute to the perception of causality, can we manipulate the underlying brain processes with available stimulation techniques, such as direct current stimulation (tDCS), and influence the perception of causality?

Transcranial direct current stimulation (tDCS) can be used to induce increased or decreased cortical excitability by polarizing the underlying brain tissue (Stagg and Nitsche 2011). During tDCS, weak, polarizing, direct currents are delivered to the cortex via two electrodes placed on the scalp. Both cognitive facilitation and inhibition as from tDCS have been reported. Most studies show the enhancement of functions during or after anodal stimulation (Marshall et al. 2004; Fregni et al. 2005; Boggio et al. 2006a, 2009a; Sparing et al. 2008). By contrast, inhibition or the disruption of processes is predominantly observed during or after cathodal stimulation (Ferrucci et al. 2008; Knoch et al. 2008) of the target brain region. For example, tDCS of the motor cortex can induce long-lasting changes in cortical excitability (Nitsche et al. 2005, 2007; Boggio et al. 2007; Boros et al. 2008). The nature of these effects depends strongly on the polarity of the current. Motor cortex excitability increases with anode placement over the motor cortex and the cathodal electrode over the contralateral orbit. However, excitability decreases when the electrodes are placed in the opposite positions. Unlike transcranial magnetic stimulation (TMS), tDCS does not directly induce neuronal depolarization. tDCS is thought to influence the resting membrane potential through the modulation of sodium and calcium-dependent channels and NMDA-receptor activity, thereby promoting LTP/LTD-like mechanisms (Liebetanz et al. 2002; Nitsche et al. 2004a, b, c). tDCS in healthy subjects can also enhance complex motor functions (Antal et al. 2004b; Hummel et al. 2010; Kwon and Jang 2011), auditory memory (Vines et al. 2006), working memory (Fregni et al. 2005; Boggio et al. 2006b; Andrews et al. 2011), memory consolidation during sleep (Marshall et al. 2004, 2011; Reis et al. 2008a, b), learning (Kincses et al. 2004), language (Iyer et al. 2005; Sparing et al. 2008; Fertonani et al. 2010) and planning (Dockery et al. 2009) and therefore provide a

variety of implications for neurorehabilitation (Vallar and Bolognini 2011). Relevant to our investigation, recent studies also reported visuospatial processing modulation by applying tDCS over the posterior parietal lobe (Ko et al. 2008; Sparing et al. 2009; Bolognini et al. 2010a; Giglia et al. 2011).

In this study, we investigated whether modulating the activity of the right parietal cortex can influence judgments of causality. Based on our findings from the fMRI study, we assumed that the right parietal lobe is specifically involved in processing the spatial contributions to the perception of causality, whereas the basal ganglia processes the temporal contributions to perceptual causality. Thus, we predicted that stimulation of the right parietal lobe by tDCS would affect the spatial contributions to perceptual causality. In line with previous literature regarding anode-related enhancement (Ko et al. 2008; Bolognini et al. 2010a, b) and cathode-related disruption of visuospatial processes (Giglia et al. 2011), we expected that anodal stimulation of the right parietal lobe would enhance and cathodal stimulation would decrease an individual's sensitivity to violations of the spatial contiguity of movement of the stimuli (angles in movement direction) in a causality judgment task. Thus, we predicted more conservative causal judgments (CJs) as the result of anodal stimulation and more liberal causal judgments as the result of cathodal stimulation for trials with violations of spatial contiguity. Correspondingly, we predicted faster reaction times (RTs) as the result of anodal stimulation and slower reaction times as the result of cathodal stimulation for trials with violations of spatial contiguity based on the following logic. Anodal stimulation is thought to lower the threshold at which a neuron fires by affecting its resting membrane potential. If these particular neurons are relevant to the process under consideration, we would expect quicker neural engagement and consequently faster RTs. Analogously, we predicted slower RTs after cathode stimulation due to less efficient processing of stimulus information.

Methods and materials

Participants

Fourteen healthy participants took part in the study (7 male, 7 female, mean age 25 years, SD = 5.7 years, range 20–42 years). All participants were right handed, native or fluent English speakers (one subject learned English by the age of 6). All participants had normal or corrected-to-normal vision. One additional female participant was excluded after the first stimulation session because of an enhanced skin reaction in response to stimulation. All participants gave written informed consent prior to participation in the study.

The University of Pennsylvania's Internal Review Board approved the study.

Experimental design

The experiment was conducted in a three session within-subject design, applying counterbalanced anodal, cathodal and sham stimulation. Counterbalancing was performed on a predefined schedule to avoid systematic order effects: 5 subjects received anodal stimulation at the first session, 5 at second and 4 at the third session; 4 received sham stimulation at the first session, 5 at the second and 5 at the third; and 5 received cathodal stimulation at the first, 4 at the second and 5 at the third session. All sessions were at least 24 h apart from each other to prevent carry-over effects. In each stimulation session (anodal, cathodal and sham), participants were required to perform two blocks of trials, one before tDCS (baseline) and another immediately after tDCS (test trial; see Fig. 1). Before the first block of trials, participants were given detailed instructions and completed six practice trials. The instruction included the information, "please respond as quickly as possible after each video," and that we are interested only in their perception and that there are no right or wrong answers. At the end of the instruction, trial participants were asked if there are further questions or if they would like to repeat the practice trial for clarification. No subject asked for a repetition or clarification.

The stimuli were animated video clips of a blue ball colliding with a red ball (a launching event). The direction of movement of the red ball varied (seven angles: 0°, 7.5°, 15°, 22.5°, 30°, 45°, 60° with respect to the direction of movement of the blue ball), and the duration before the initial movement of the red ball also varied (seven time delays: 0, 33, 67, 100, 133, 200, 267 ms) after contact with the blue ball. All possible combinations of angles and time delays resulted in 49 different trial types (see Fig. 1). Each of these 49 trial types were flipped horizontally, so that the balls were presented moving both left to right and right to left, resulting in a set of 98 events. In each condition (cathodal baseline [CB], cathodal stimulation [CS], sham baseline [SB], sham stimulation [SS], anodal baseline [AB] and anodal stimulation [AS]), all 98 videos were presented in random order and participants were instructed to judge the causal relationship between the balls (Did the blue ball cause the red ball to move? Yes or no). Each video was followed by a fixation cross with a variable duration of 1,000 to 3,000 ms (average: 2,000 ms).

Due to the high number of trial types and low number of stimuli repetitions, this approach is not suitable to make any claims about a specific trial type. However, this approach gives us the opportunity to investigate stimulation effects in relation to a parametric variation of stimulus

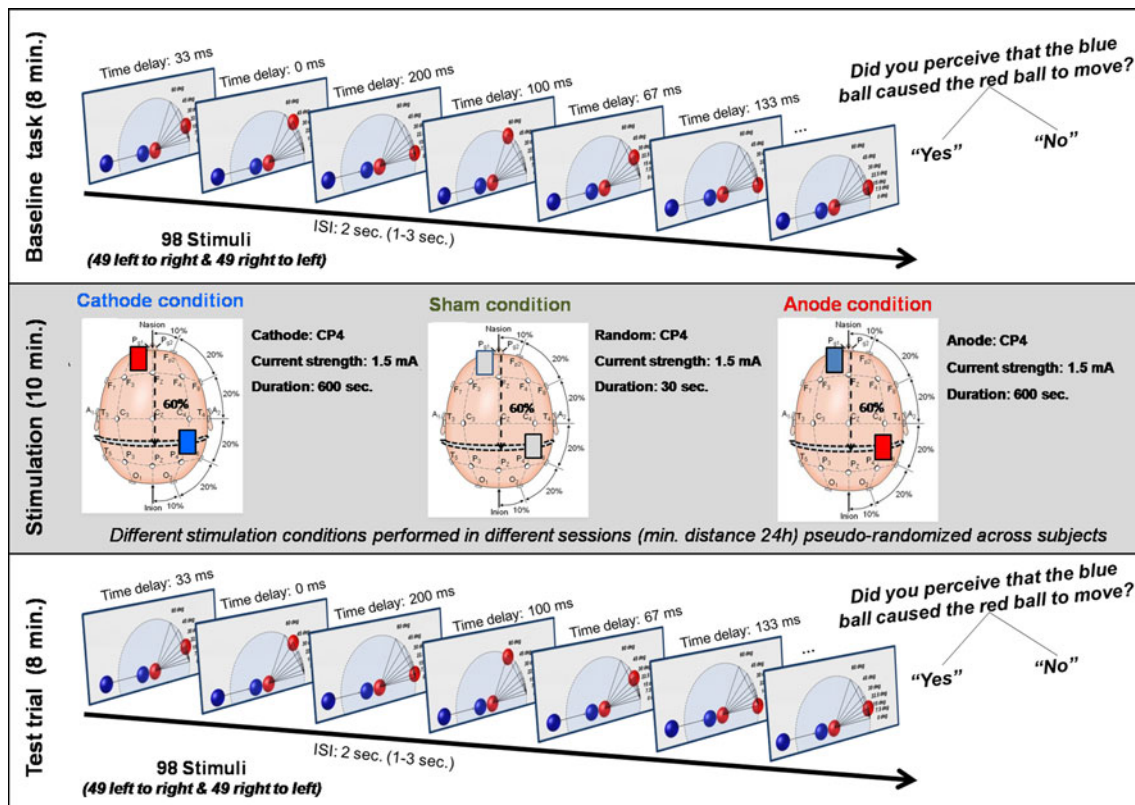


Fig. 1 Illustration of the task and procedure of the three session within-subject design. Each subject performed three sessions that differed only in the tDCS condition. Each session starts with a baseline task (*top*). Electrodes were then fixed to the head with elastic bands. In each of the three sessions, a different stimulation (anode, cathode or sham) was applied in a pseudo-randomized order (*middle*). After the 10-min stimulation period, the electrodes were removed from the head, and the participant completed the causality test trials

(*bottom*). The *top* and *bottom* of figure illustrate the parametric violations of spatial continuity (7 angles) and temporal contiguity (7 time delays, written). All combinations of angle and time delay were presented to the subjects twice (once in which the balls moved *left to right* and once in which they moved *right to left*) in a pseudo-randomized order. For each trial, the participants were instructed to judge the causal relationship between the balls (Did the *blue* ball cause the *red* ball to move? Yes or no)

parameters. Importantly, this design allowed us to link these data more directly to our fMRI findings, since the identical experimental paradigm was used. Although we cannot make any claims about a single stimulus type, we can make claims about perceptual changes regarding a whole stimulus set. Thus, here we focus on the influence of stimulation on a stimulus set of specific parametric characteristics. We decided to use the applied approach because of the following two reasons: (1) in our previous fMRI study, this approach has been shown to be effective in separating the sensitivity to spatial and temporal information for judgments of causality and (2) this approach gives enough room to detect changes in the one or other direction on the level of the whole stimulus set (causality judgments about 50% across all trials; see (Straube and Chatterjee 2010)). The advantage of this approach is that effects of repetition such as habituation or perseveration are minimal. The presentation of a given trial in a repeating manner is likely to produce repetitive response behavior, which might be difficult to influence by stimulation.

Stimulus construction

The stimuli were constructed using *Strata-3D* software. Each stimulus was two seconds long. The balls were shaded to give the impression of three-dimensional objects and not flat disks. The first ball (colored blue) began to move 400 ms after video onset and stopped moving 600 ms after animation onset (1,000 ms after video onset). The blue ball always rolled along a horizontal plane and stopped once it came into contact with the second ball (colored red). The red ball varied in the direction and the time at which it began to move (see Fig. 1). Since speed and length of trajectory were the same for both balls in all conditions, the time without motion at the end of each video clip varied in accordance with the time delay between 133 (267 ms delay) and 400 ms (no delay). All stimuli were rendered and converted to the Windows Media File format (WMV2/PAL; frame rate = 60 frames per second, resolution = 720 × 576 pixels). The final visual appearance of the stimuli on the screen of a laptop with an observer to screen distance of approximately 40 cm was as follows: object

size (diameter) approximately 1.4° visual angle and movement trajectories approximately 5.7° visual angle.

Transcranial direct current stimulation

tDCS was delivered by a battery-driven, constant current stimulator (Magstim eldith DC Stimulator, The Magstim Company Ltd Spring Gardens, Whitland Carmarthenshire SA34 0HR, Wales UK) through a pair of saline-soaked sponge electrodes (5×7 cm) placed on the surface of the scalp. A constant current of 1.5 mA intensity (current density 0.04 mA/cm^2) was applied for 10 min (plus 10 s fade in/fade out) complying with current safety guidelines (Nitsche et al. 2003; Iyer et al. 2005). The stimulation protocol was defined primarily based on evidence from prior studies with regard to duration (Monti et al. 2008; Sparing et al. 2009) and current strength (e.g., 1 mA: Sparing et al. 2009; 2 mA: Monti et al. 2008; Sparing et al. 2008) to maximize the likelihood to obtain stimulation-induced effects in the causality judgment task.

The anode or cathode electrode (depending on condition) over the target region was located over CP4, thus, between P4 and C4 of the international 10–20 system for EEG electrode placement (see Fig. 1 for illustration).

This region corresponds to the brain areas that were activated when the spatial trajectory contributed to the judgment of causality in our previous fMRI study (Straube and Chatterjee 2010). Furthermore, this location lies near the posterior parietal cortex (PPC; e.g., Hilgetag et al. 2001; Dambeck et al. 2006).

The “reference” electrode was placed contralaterally above the orbit, consistent with standard placement practices in studies of primary motor cortex (e.g., Nitsche and Paulus 2000; Nitsche et al. 2005). The placement of the reference electrode is relevant for the effect of stimulation. We choose to place the reference electrode over the contralateral orbitofrontal cortex because of the following two reasons: 1. This placement of the reference electrode was often applied successfully before (e.g., Nitsche and Paulus 2000; Nitsche et al. 2005; Dockery et al. 2009) and 2. We did not find any differential activation within the frontal cortex in our fMRI study. Thus, we assumed that this reference region would be independent of the task and stimulus processing.

Three different stimulation sessions were conducted: (A) anodal; (B) cathodal and (C) control sham stimulation (see Fig. 1, middle). tDCS sham was performed with the same current strength as the active stimulation, but the stimulator was turned off after 30 s and the current increase and decrease were performed as a sinus curve (sinus mode [hw]). This ensured that subjects felt the initial itching sensation at the beginning of tDCS and therefore remained blind to the stimulation condition (Gandiga et al. 2006). The stimulation sessions were separated by at least 24 h and counterbalanced

across subjects in order to control for learning and carry-over effects as well as guarantee a sufficient washout of the effects of the previous run (Vines et al. 2006).

Data analyses

Causal judgments and reaction times were analyzed to test the hypotheses of tDCS-related changes in the use of spatial information (“Angle”) in the causal judgment task. To reduce the complexity of the design, the factor “Time,” which is not of interest here, was included only as dichotomous variable in the following analyses: *small delays* [0–100 ms] and *large delays* [133–267]. The generalized estimating equations (GEE) approach was used to account for correlation among repeated measures over time using an AR (1) working correlation structure and robust (sandwich) covariance estimators for the regression coefficients. Predictors included in each model in addition to the intercept were the main effects: “Baseline-Stimulation” (before vs. after tDCS), “Stimulation” (cathode, sham and anode), “Angle” (0° , 7.5° , 15° , 22.5° , 30° , 45° , 60°) and “Time” (*low* [0–100 ms], *high delays* [133–267]) as well as the corresponding factorial interaction terms (“Baseline-Stimulation \times Stimulation,” “Baseline-Stimulation \times Angle,” “Baseline-Stimulation \times Time,” “Stimulation \times Angle,” “Stimulation \times Time,” “Angle \times Time,” “Baseline-Stimulation \times Stimulation \times Angle,” “Baseline-Stimulation \times Stimulation \times Time,” “Baseline-Stimulation \times Angle \times Time,” “Stimulation \times Angle \times Time,” “Baseline-Stimulation \times Stimulation \times Angle \times Time”). The logit link function and binomial variance function specified for dichotomous variables were used for the analyses of causality responses (causal = 1; non-causal = 0). For the analyses of reaction times, the identity link function and normal variance function for continuous variables were used. Within this approach, our interest was focused on the effects of “Angle” with regard to the “Baseline-Stimulation contrast” and the “Stimulation-Condition,” and the main coefficients of interest in the analyses were therefore the two-way and three-way interactions with “Angle.” Because “Angle” and “Time” were both manipulated within the same stimuli, the interaction of both factors was also calculated. To maintain the family-wise error rate associated with testing multiple outcomes, we used the sequential Bonferroni adjustment for the analyses. All statistical analyses were performed using SPSS 15 for Windows software package.

Results

Causal judgments

Within the GEE-model, we found significant main effects of the factors “Angle” (0° – 60°) and “Time” (*low* vs. *high*)

on the proportion of causal judgments (see Table 1). Despite the trend for the main effect of “Stimulation” ($P = .094$), the interaction of the factors “Baseline-Stimulation (before/after tDCS)” and “Stimulation (cathode, sham and anode)” did not reached significance (see Table 1).

By contrast, we found a significant three-way interactions of “Baseline-Stimulation (before/after tDCS),” “Stimulation (cathode, sham and anode)” and “Angle” (0° – 60°), indicating a tDCS-related change in causal judgment with regard to the spatial characteristics of the stimuli (Angle). The corresponding three-way interaction with time was not significant. However, the factor “Time” seems to be additionally important for the stimulation effect on “Angle” as indicated by an significant four-way interaction: “Baseline-Stimulation” \times “Stimulation” \times “Angle” \times “Time” (see Table 1). Figure 3 illustrates the estimated marginal means of the corresponding analyses. The four-way interaction seems to be a result of increased causal judgments after cathode stimulation of the parietal lobe for trials with high angles and high time delays. The opposite effect can be observed for anodal stimulation of the parietal lobe (more causal judgments for low angles and high time delays; see Fig. 3). As predicted, tDCS

stimulation of the parietal lobe seems to affect causal judgments with regard to spatial characteristics in a causal judgment task.

Reaction times

Within the GEE-model, we found significant main effects of the factors “Baseline-Stimulation” (before/after tDCS) and “Time” (low vs. high) on the reaction times in the causal judgment task (see Table 1). The main effects of “Angle” and “Stimulation” did not reach significance (see Table 1).

However, there was a trend for the interaction of “Baseline-Stimulation (before/after tDCS)” and “Stimulation (cathode, sham and anode),” which was mainly driven by a significant reduction of reaction times after anodal stimulation ($P < .05$; see Fig. 2).

Again, we found a significant three-way interactions of “Baseline-Stimulation (before/after tDCS),” “Stimulation (cathode, sham and anode)” and “Angle” (0° – 60°), indicating a tDCS-related change in reaction times with regard to the spatial characteristics of the stimuli (Angle). The corresponding three-way interaction with the factor

Table 1 Tests of model effects for the “generalized estimation equation” (GEE) analyses for causal judgments (top) and reaction times (bottom)

Source	Wald chi-square	df	Sig.
Tests of model effects: causal judgments			
(Intercept)	5.420	1	.020
Baseline-Stimulation (<i>before and after tDCS</i>)	1.523	1	.217
Stimulation (<i>cathode, sham and anode</i>)	4.736	2	.094
Angle (0° , 7.5° , 15° , 22.5° , 30° , 45° , 60°)	28.905	6	<.001
Time (<i>low delays</i> [0–100 ms], <i>high delays</i> [133–267])	78.456	1	<.001
Baseline-Stimulation \times Stimulation	.686	2	.710
Baseline-Stimulation \times Stimulation \times Angle	158.779	12	<.001
Baseline-Stimulation \times Stimulation \times Time	.177	2	.915
Baseline-Stimulation \times Stimulation \times Angle \times Time	114.668	12	<.001
Tests of model effects: reaction times			
(Intercept)	917.766	1	<.001
Baseline-Stimulation (<i>before and after tDCS</i>)	8.855	1	.003
Stimulation (<i>cathode, sham and anode</i>)	1.947	2	.378
Angle (0° , 7.5° , 15° , 22.5° , 30° , 45° , 60°)	4.126	6	.660
Time (<i>low delays</i> [0–100 ms], <i>high delays</i> [133–267])	11.286	1	.001
Baseline-Stimulation \times Stimulation	5.105	2	.078
Baseline-Stimulation \times Stimulation \times Angle	56.238	12	<.001
Baseline-Stimulation \times Stimulation \times Time	5.659	2	.059
Baseline-Stimulation \times Stimulation \times Angle \times Time	323.546	12	<.001

Dependent Variable: Response (top) and RT (bottom)

Model: (Intercept), Baseline-Stimulation, Stimulation, Angle, Time, Baseline-Stimulation \times Stimulation, Baseline-Stimulation \times Angle, Baseline-Stimulation \times Time, Stimulation \times Angle, Stimulation \times Time, Angle \times Time, Baseline-Stimulation \times Stimulation \times Angle, Baseline-Stimulation \times Stimulation \times Time, Baseline-Stimulation \times Angle \times Time, Stimulation \times Angle \times Time, Baseline-Stimulation \times Stimulation \times Angle \times Time

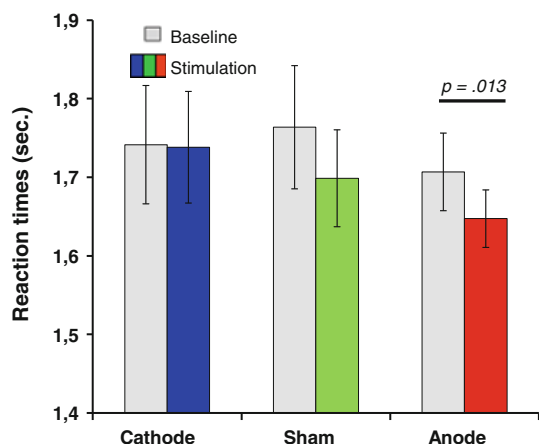


Fig. 2 Reaction times across conditions. Figure shows the estimated marginal means of the reaction times (measured from stimulus onset) for all conditions. Error bars represent the standard error of the mean. There was a trend for an interaction between the factors “Baseline-Stimulation” (before and after tDCS) and “Stimulation” (cathode, sham and anode) in the tests of model effects (see Table 1). Furthermore, the overall Wald chi-square test for this interaction was significant (Wald chi-square = 18.007, $df = 5$, $P = .003$). Post hoc analysis revealed significant reduction in response time only after anodal stimulation (anodal baseline > anodal stimulation: $P = .013$; sham baseline > sham stimulation: $P = .11$; cathode baseline > cathode stimulation: $P > .20$; sequential Bonferroni corrected)

“Time” resulted just in a trend ($P = .059$). However, the factor “Time” seems to be additionally important for the stimulation effect on “Angle” as indicated by a significant four-way interaction: “Baseline-Stimulation” \times “Stimulation” \times “Angle” \times “Time” (see Table 1). Figure 3 illustrates the estimated marginal means of the corresponding analyses. The four-way interaction seems to be a result of reduced reaction times after anode stimulation of the parietal lobe. The differences between anode and cathode stimulation were highest for trials with high angles (see Fig. 3). As predicted, tDCS stimulation of the parietal lobe seems to affect reaction times with regard to spatial characteristics in a causal judgment task.

Discussion

Inferring cause-and-effect relationships is central to our understanding of the physical world. For decades, philosophers and scientists have tried to understand how we know that one action causes another, even in simple events such as one billiard ball colliding with and causing another to move (Hume 1740/1960, 1748/1977). In this study, we investigated the role of the right parietal lobe in the perception of causality. Specifically, we hypothesized that the right parietal cortex instantiates a sensitivity to spatial variables in perceiving causal sequences. Modulating neural activity in this region would modulate the perception

of causality, specifically spatial contributions to this perception.

In line with our hypotheses, we found a significant effect of stimulation on causal judgments and reaction times in relation to spatial stimulus characteristics (three-way interaction of Baseline-Stimulation \times Stimulation \times Angle). Thus, for trials with large angle variations, subjects seem to judge a greater number of trials to be causal after cathodal stimulation than after anodal stimulation. Correspondingly, subjects were slower to respond after cathodal stimulation (see Fig. 3).

These data provide the first evidence that the perception of causality can be influenced by the application of transcranial direct stimulation to the right parietal lobe. They converge with the findings of our previous fMRI study to suggest the right parietal lobe is involved in the processing of spatial attributes in the perception of causality (Straube and Chatterjee 2010). In recent years, there have been many reports of the effects of tDCS on performance on cognitive tasks, such as sensory processing (Ragert et al. 2008), memory (e.g., Fregni et al. 2005; Boggio et al. 2006b, 2009b; Vines et al. 2006; Andrews et al. 2011; Diaz et al. 2011), learning (e.g., Kincses et al. 2004; Stagg et al. 2011), executive functions (e.g., Fecteau et al. 2007; Dockery et al. 2009; Boggio et al. 2010a, b; Hsu et al. 2011), language (e.g., Iyer et al. 2005; Sparing et al. 2008) and visual perception (e.g., Antal et al. 2004a, b, 2006; Lang et al. 2007; Antal and Paulus 2008). Added to this list, our results show that tDCS applied over the right parietal lobe can lead to polarization-dependent changes in the perception of causality. In line with previous findings about “inhibitory” (i.e., low-frequency) or “facilitatory” (i.e., high-frequency) rTMS (e.g., Hilgetag et al. 2001; Kim et al. 2005; Battelli et al. 2009; Kang et al. 2011), anode/cathode tDCS in humans (Ko et al. 2008; Sparing et al. 2009; Bolognini et al. 2010a, b), as well as cathodal tDCS in cats (Schweid et al. 2008) on visuospatial attention processes within the parietal lobe, our observation of increased causal perceptions for trials with high angles after cathodal stimulation is most likely due to a reduced sensitivity to violations of movement trajectory. A real distinction between pure perceptual and high level function is difficult to draw with the present data. However, in line with our fMRI study, our results suggest that spatial and temporal stimulus characteristics contribute to the perception of causality. Here, we could show that stimulation of the parietal lobe changes the perception of causality specifically with regard to spatial violations of continuity. This domain-specific effect suggests modulation of a specific perceptual contribution to the awareness of causality.

Previous studies about the effect of tDCS applied over the parietal cortex could demonstrate improvement of visual exploratory and attentional skills (Bolognini et al. 2010a) or enhancement of multisensory spatial orienting by anodal

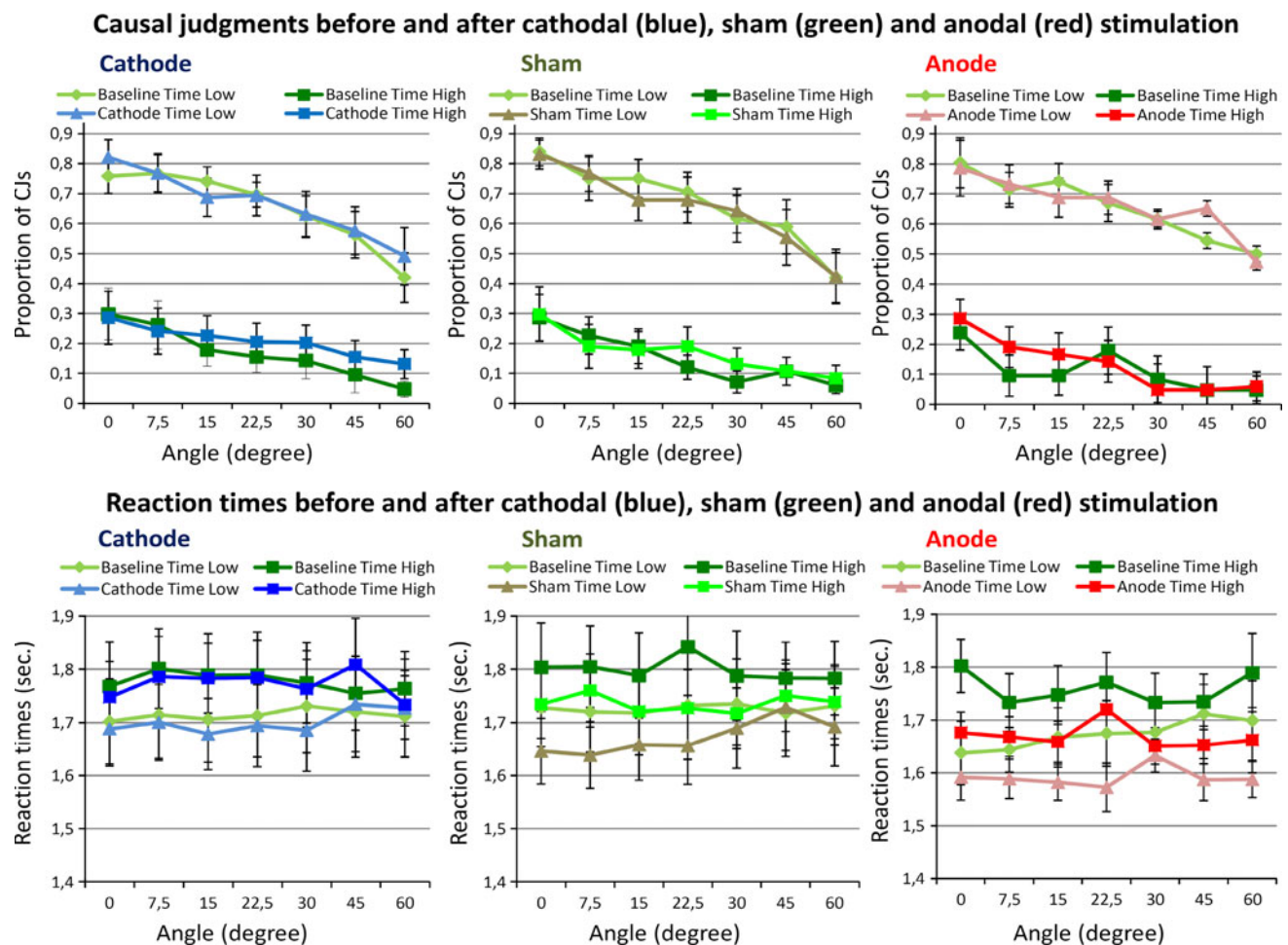


Fig. 3 Causal judgments and reaction times in relation to spatial characteristics. Figure illustrates the estimated marginal means for causal judgments (*top*) and reaction times (*bottom*) in relation to variation of spatial continuity (*angle*) in the movement pathway. Temporal delays were split up in trials with low temporal violation

(time low; 0–100 ms) and trials with high temporal violation (time high; 133–267 ms). The effect of stimulation with regard to angle variation was strongest for trials with high temporal violations (see Table 1; significant interaction of angle and time). Error bars represent the standard error

stimulation of the parietal cortex (Bolognini et al. 2010b). These studies are consistent with our finding of faster reaction times after anodal stimulation, but suggest a specific role of attention processes in the behavioral facilitation effects. The relevance of attention processes for working memory tasks has also been used as an explanation for the finding that cathodal stimulation of the right parietal lobe leads to decline in working memory performance (Berryhill et al. 2010). However, in our task, subjects were instructed to judge their perception of causality for each trial without saying anything about space and time. Interestingly, we found an effect of tDCS on the use of spatial information (angle) in their causality judgments. Thus, stimulus-triggered attention processes can just partly explain our finding, since they are relative specific for spatial violations of contingencies.

Despite the predicted effect for polarization-dependent modulation of causal judgments and corresponding reaction times for trials with increasing violation of spatial

contiguity, this effect was further modulated by temporal violations. The effect of tDCS on the use of spatial information for causality judgements was strongest for trials with high temporal violations. This result might be due to the fact that on these trials, temporal violations were clear, and therefore, space became the main variable of relevance. As such, space may have become easier to influence by tDCS in this context. Despite this interaction of angle and time manipulation, the effect of stimulation on time irrespective of angle (Baseline-Stimulation \times Stimulation \times Time) was not significant, supporting our interpretation that the perception of the spatial manipulation is primarily affected through tDCS.

A specific limitation of the study is the placement of the reference electrode. Despite our fMRI data did not suggest a specific role of the left orbitofrontal cortex in the causality judgment task, we cannot exclude that stimulation of this region has an effect on the perception of causality or

related judgment processes. Further investigations are necessary to disentangle prefrontal and parietal contribution to perceptual causality. Another limitation refers to the fact that we did not observe any general effect of stimulation on proportion of causal judgments and reaction times (Baseline-Stimulation \times Stimulation-Condition). Only the post hoc comparison (anode: Baseline > Stimulation) for reaction times reached the significance threshold and therefore has to be considered with caution. The lack of general effects may reflect the overall small effect of tDCS of the neural processes relevant in the causality task. However, the specificity of stimulation on trials with high angle manipulations (reflected in the significant three-way and four-way interactions) is in line with our hypothesis and the previous findings of the fMRI study (Straube and Chatterjee 2010).

In this study, we demonstrated that the manipulation of brain regions involved in the processing of basic stimulus parameters can influence the perception of causality. In line with our fMRI study, this supports the view that the perception of causality is built upon sensitivity to elemental spatial and temporal attributes. The specific modulation of spatial parameters is consistent with this view and conflicts with the hypothesis that humans have universal neural correlates for the perception of causality (Blakemore et al. 2001). The current study demonstrated that tDCS can influence the perception of causal relationships. Future investigations should explore how these findings can be translated to the understanding of higher-order causal relationships in the world (like fire and heat; Satpute et al. 2005) or applied to therapeutic treatments for patients with symptom-specific over- or underestimation of causal relationships (e.g., Tschacher and Kupper 2006).

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