RESEARCH ARTICLE



Transcranial direct current stimulation (tDCS) of the inferior frontal cortex affects the "social scaling" of extrapersonal space depending on perspective-taking ability

Chiara Fini^{1,4} · Lara Bardi² · Alessandra Epifanio³ · Giorgia Committeri³ · Agnes Moors^{4,1} · Marcel Brass²

Received: 9 June 2016 / Accepted: 1 November 2016 / Published online: 17 November 2016 © Springer-Verlag Berlin Heidelberg 2016

Abstract When we have to judge the distance between another person and an object (social condition), we judge this distance as being smaller compared to judging the distance between two objects (nonsocial condition). It has been suggested that this compression is mediated by the attribution of a motor potential to the reference frame (other person vs. object). In order to explore the neural basis of this effect, we investigated whether the modulation of activity in the inferior frontal cortex (IFC) of the left hemisphere (recruited during visuospatial processes with a social component) changes the way we categorize space in a social compared with a nonsocial condition. We applied transcranial direct current stimulation to the left IFC, with different polarities (anodal, cathodal, and sham) while subjects performed an extrapersonal space categorization task. Interestingly, anodal stimulation of IFC induced an higher compression of space in the social compared to nonsocial condition. By contrast, cathodal stimulation induced the opposite effect. Furthermore, we found that this effect is modulated by interindividual differences in cognitive

Chiara Fini Chiara.Fini@ugent.be

- ¹ Department of Experimental-Clinical and Health Psychology, Ghent University, Henri-Dunantlaan 2, 9000 Ghent, Belgium
- ² Department of Experimental Psychology, Ghent University, Henri-Dunantlaan 2, 9000 Ghent, Belgium
- ³ Laboratory of Neuropsychology and Cognitive Neuroscience, Department of Neuroscience, Imaging and Clinical Sciences, and ITAB, University G. d'Annunzio, Chieti, Italy
- ⁴ Research Unit for Quantitative Psychology and Individual differences, Centre for Social and Cultural Psychology, University of Leuven, Oude Markt 13, 3000 Louvain, Belgium

perspective taking. Our data support the idea that IFC is recruited during the social categorization of space.

Keywords Distance · Body · Perspective taking · Anodal · Cathodal · Motor resonance

Introduction

Recent research has provided evidence for the idea that we perceive the space around us by taking into account our bodily resources and action opportunities (Proffitt et al. 2003, 2006; Coello and Delevoye-Turrell 2007; Schnall et al. 2010; Sugovic and Witt 2013). In the peripersonal space (i.e., reaching space), we perceive the target object as closer when holding a tool to reach an object compared to when no tools are available (Witt et al. 2005). Furthermore, when judging a distance in extrapersonal space (i.e., beyond the reaching space), we scale the distance according to the specific motor potential and intention we have (Proffitt et al. 2003; Witt et al. 2004; Proffitt 2006; Witt and Proffitt 2008). The distance can be scaled by the walking effort necessary to cover it, or by the throwing effort if we plan to throw a ball (Witt et al. 2004). These findings support the idea that potential anticipated behavior directly affects space perception [see Proffitt (2006)]. However, since we share the space with others, our space perception is also altered by the other's action opportunities and action intentions (Costantini et al. 2011; Cardellicchio et al. 2011; Fini et al. 2014). In reaching space, for example, observing someone else using a tool to reach a target causes a compression of the perceived target distance (Costantini et al. 2011; Bloesch et al. 2012). Furthermore, we have recently shown that in extrapersonal space, a target object is judged as closer when adopting a human as an external reference frame (Fini et al. 2014). We will refer to this effect as "compression of extrapersonal space" or "space compression." Moreover, the compression of extrapersonal space is greater if the space categorization is anticipated by the observation of a target-oriented walking/running movement (Fini et al. under review).

Such results suggest that our space perception is rooted in shared motor representations, coherent with the action afforded by the environment. The space would be judged as compressed in the social compared with the nonsocial condition, because filtered by an implied biological motion.

Starting from this evidence, an intriguing question concerns what are the underlying mechanisms of this social scaling of extrapersonal space perception.

The inferior frontal cortex is known to be involved in different processes; one of this is the matching of motor plans (Iacoboni et al. 1999; Rizzolatti et al. 2001) through the encoding and representation of goals and intentions from observed actions (e.g., the goal or intention to drink from the grasping of a cup) (Cattaneo et al. 2009; Rizzolatti and Sinigaglia 2010; Gallese and Sinigaglia 2011). Moreover, a recent study showed that transcranial direct current stimulation (tDCS) stimulation of the inferior frontal gyrus (IFG) significantly modulates motor resonance as indexed by psychophysiological measures of motor activation (Enticott et al. 2012). IFC plays also a role in the semantic processing (Mazoyer et al. 1993; Thompson-Schill et al. 1997, 1998; Wagner et al. 1997, 2001).

In a study using chronically implanted depth electrodes in the lateral inferior prefrontal cortex (LIPC), it has been found greater activity in that region related to semantic decision relative to a perceptual decision (Abdullaev and Bechtereva 1993). By considering all these evidences, we hypothesize that IFC could be involved in the categorization of a human as biological agent, and it might form the functional basis for the motor remapping of extrapersonal space when judging the distance between another person and an object (social condition). To investigate whether IFC plays a role during the social scaling of extrapersonal space, we applied tDCS to this area during a distance judgment when adopting a person (social condition) versus an object (nonsocial condition) as reference frame (RF). With tDCS, anodal stimulation enhances cerebral excitability, while cathodal stimulation diminishes it (Nitsche and Paulus 2000; Jang et al. 2009; Stagg et al. 2009). Although excitation and inhibition induced by tDCS do not necessarily correspond to behavioral improvements and impairments, anodal stimulation has been shown to increase performance in different tasks (e.g., Galea and Celnik 2009; Hsu et al. 2011).

Thus, by enhancing activity (anodal stimulation) in the IFC cortex, we expect increased compression of space in the social compared with nonsocial condition. Conversely, by inhibiting (cathodal stimulation) the IFC activity, we predict a reduced compression of space in social compared with nonsocial condition.

Moreover, when a person is in the scene and participants are asked to express a spatial judgment, an automatic visuospatial perspective taking toward the person in the scene is promoted (e.g., Tversky and Hard 2009) that correlates with cognitive perspective-taking ability (Erle and Topolinski 2015). Here, we tested whether cognitive perspectivetaking ability modulates the impact of the stimulation on the social space compression effect.

Methods

Participants

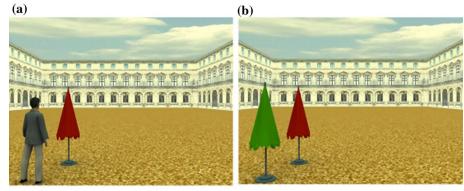
Twenty-seven healthy students recruited at Ghent University participated at this experiment (11 females, all but three right handed, mean age 22.25 ± 2.48 , range 18–30), all with normal or corrected-to-normal vision. Participants received financial compensation for their participation. The study was in accordance with the Declaration of Helsinki and approved by the local ethics committee.

Materials

Stimuli included a 3D scene created by means of 3D modeling software (3D Studio Max 4.2, Autodesk, Discreet). The scene was a 3D environment, representing a square arena defined by the two short lateral wings and the long central wing of a palace (Fig. 1). In the first set of stimuli (Fig. 1a), a human body (other RF) was located 45° to the right (left) of the central camera representing the participant's perspective, and a target red beach umbrella was located along a central vector aligned with the avatar at 25 different distances (from 1 to 25 m). The avatar and the umbrella were 177 and 192 cm tall, respectively, resembling their ecological relative proportion in a real scenario. The second set of stimuli (Fig. 1b) was identical to the first one, except for the presence of a green beach umbrella instead of the avatar (object RF). Note that, the avatar and the green umbrella had the same spatial extension in the anterior direction. We administered the stimuli using the method of limits. This is a method for measuring perceptive thresholds, in which the subject is presented with series of stimuli with progressively increasing or decreasing (in steps of a predetermined value) intensity (distance in our case), until he/she reports to feel a change.

Fig. 1 Stimuli in 3D scenario:

a the other RF, b the object RF



other RF

object RF

Procedure

Before starting the experiment, participants were asked to complete the interpersonal reactivity index (IRI) (Davis 1983). We focused on the subscale of cognitive perspective taking (PT) that measures the reported tendency to spontaneously adopt the psychological point of view of others in everyday life (i.e., the process of projecting oneself "into the shoes" of another person).

The experiment followed the same experimental procedure employed in previous works (Fini et al. 2014, 2015a, b) and consisted of ascending and descending series of trials. Each series started with a white fixation cross on a black background (1.5 cm \times 1.5 cm) for 2500 ms and consisted of a maximum of 25 trials, but was terminated when a perceptual switch occurred. Each trial lasted 2500 ms. Subjects were asked to judge whether the red beach umbrella was "Near" or "Far" from the two different RFs, by pressing two different buttons arranged horizontally on the computer keyboard and counterbalanced in the "Near"/"Far" judgment. In ascending series, the red umbrella was progressively moved away from the RF until the participants provided three consecutive "Far" judgments. In descending series, the red umbrella was progressively moved closer to the RF until the participants provided three consecutive "Near" judgments. Then, the following series started. A mean was calculated for each subject as the average distance at which the subject expressed a transition from "Far" to "Near" (descending series) and from "Near" to "Far" (ascending series). The single-subject Judgment Transition Thresholds (JTTs) were averaged together to obtain a final group mean referring to the different RFs. Higher JTT values show a categorization of space as "Near" at longer target distance compared to lower JTT values. In other words, the higher the JTT, the wider the space categorized as "Near." Thus, a wider "Near" space corresponds with a more compressed distance.

Each series was repeated 4 times for each RF. In total, each participant was submitted to 16 series: two RFs (other,

object) \times 8 series (four ascending, 4 descending). Stimuli were presented at full screen on a 17' computer display placed 57 cm from the subject. The presentation of the stimuli and the recording of the participant's responses were controlled by a customized script for Presentation version 14.9.08.11.

tDCS

A direct current of 1.5 mA intensity was delivered by a battery-driven, constant-current stimulator (Magstim, UK) through two electrodes placed in saline-soaked sponges. All participants indicated that they felt the stimulation. Previous studies have shown that this intensity of stimulation is safe in healthy volunteers (Iyer et al. 2005). The active electrode (anodal or cathodal) was placed over the left IFC (equivalent to electrode position FC5 in a 10–10 EEG nomenclature; Holland et al. 2011; Enticott et al. 2012). The active electrode (IFC) measured 5×7 cm and was placed with a horizontal orientation. With this electrode placement, stimulation covers both the inferior frontal gyrus (IFG) and the ventral premotor cortex (vPMC).

The reference electrode was placed over the supraorbital area of the right hemisphere. The reference electrode measured 10×10 cm. A large electrode was used for the reference in order to minimize the risk of stimulation effect in this area (Nitsche et al. 2007). Finally, for the Sham condition, anodal or cathodal pseudo-stimulation was applied for 30 s. The sham stimulation caused temporary itching sensation but delivered little actual current.

The tDCS stimulation lasted 20 min (with a 30 s rampup, ramp-down), and was started five minutes before the beginning of the task for two reasons. This delay was implemented to make the participant familiar with the sensation of being stimulated and to have the peak of stimulation during the task. All participants took part in three counterbalanced conditions: anodal, cathodal, and sham. The extrapersonal space categorization task was also administered immediately after the period of stimulation (post-tDCS) in order to capture any long-lasting effect of the tDCS stimulation.

Results

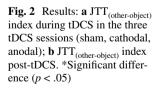
In accordance with Fini et al. (2015a), we first computed a score that captures the difference in JTT between the person and the object as RF. More specifically, we subtracted the Near space threshold for the object as RF from the Near space threshold for the person as RF ($JTT_{(other-object)}$). Positive values indicate a Near space extension (i.e., a stronger compression of space) with the human versus the object as RF. Negative values indicate the opposite [see Fini et al. (2015a)]. We hypothesized that this index should have decreased when cathodal stimulation was applied to the IFC. Conversely, this index should have increased when cortical excitability was enhanced via anodal tDCS.

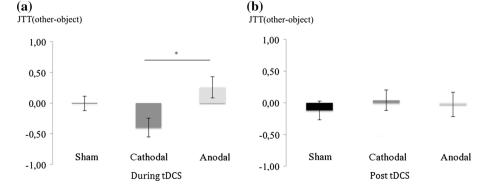
A repeated measures ANOVA with stimulation (anodal, cathodal, and sham) and task session (during tDCS, posttDCS) as within-subjects factor was conducted. The stimulation × task session interaction was significant $[F(2,52) = 3.5, p < .05, \eta = .12]$. Using Post Hoc Newman-Keuls tests, we found a significant difference between cathodal $\left[-.39 \ JTT_{(other-object)}\right]$ and anodal stimulation [.25 JTT_(other-object)] in the tDCS session (p < .04), but not in the post-tDCS session [cathodal: .04 JTT_(other-object); anodal: $-.02 \text{ JTT}_{(\text{other-object})}$; p = .94] (Fig. 2). The positive JTT_(other-object) index (.25) that we observed for anodal tDCS indicates that during the boosting of IFC activity, the "Near" space was wider when a human versus an object was the reference (social condition). Conversely, the negative JTT_(other-object) (-.39) index for cathodal tDCS indicates that during the inhibition of IFC activity, the "Near" space was wider when an object versus a human was the reference (nonsocial condition). These results are in line with the hypothesis that the social scaling of extrapersonal space recruits IFC. For a better understanding of the abovedescribed effects, we also looked at the Near space thresholds for the object and the other RF separately. With the other RF, anodal and cathodal stimulation equally affected extrapersonal space categorization by reducing the space judged as "Near" (sham other JTT = 9.8 m; cathodal other JTT = 9.53 m; anodal other JTT = 9.58 m), whereas with the object RF, only the anodal stimulation strongly reduced the threshold (sham object JTT = 9.81 m; anodal object JTT = 9.32 m), and a slight enlargement was observed with cathodal stimulation (cathodal object JTT = 9.93 m). This resulted into opposite effects of anodal and cathodal tDCS on the JTT_(other-object), as presented above within the repeated measures ANOVA.

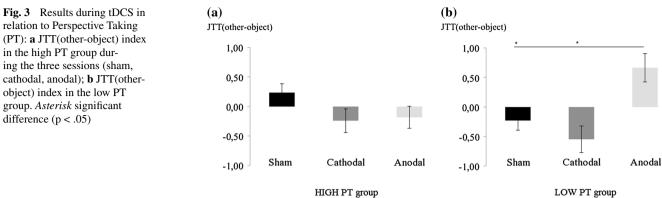
In order to investigate whether the perspective taking measured with IRI modulates the impact of the stimulation, the score of the perspective-taking (PT) subscale was entered as covariate in a repeated measures ANOVA with stimulation (cathodal, anodal, and sham) as within-subjects factor. The PT score significantly modulated the effect of the stimulation [F(2,24) = 3.7, p < .03, $\eta = .25$]. To additionally explore the relation between perspective taking and space compression expressed by the JTT_(other-object) index, the sample was split in two groups: The high PT group were those with a PT score above the median (PT <15); the low PT group were those with a PT score below the median (PT <15). Crucially, the sham in the low PT group [JTT_{other-object} = -0.23] was significantly different from the sham in the high PT group (JTT_{other-object} = 0.23) (p < .05).

This result indicates that perspective taking does not only affect the response to brain stimulation but determines the baseline effect.

A repeated measures ANOVA with stimulation (anodal, cathodal, and sham) as within-subjects factor and group (high PT group, low PT group) as between-subjects factor was performed. We obtained a main effect of the stimulation [F(2,50) = 5.75, p < .001, $\eta = .18$] and a significant interaction between group and stimulation [F(2,50) = 7.16, p < .001, $\eta = .22$]. The stimulation had an impact only in the low PT group, in which anodal tDCS significantly increased JTT_(other-object) (.66 JTT) as compared to sham [-.23 JTT_(other-object)] (p < .01) and cathodal tDCS (-.55 JTT_(other-object)) stimulation (p < .01).







Conversely, in the high PT group the stimulation had not an impact. The anodal tDCS [-.18 JTT_(other-object)] was not different from the sham [.23 JTT_(other-object)] (p = .12) and the cathodal tDCS $[-.24 \text{ JTT}_{(\text{other-object})}]$ (p = .29) (Fig. 3). Again, for descriptive purposes, we looked at the Near space thresholds for the object and the other RF separately. In the low PT group, cathodal and anodal stimulation impacted as in the general sample (sham object JTT = 10.78 m; anodal object JTT = 9.46 m; cathodal object JTT = 11.25 m; sham other JTT = 10.55 m; anodal other = 10.13 m; cathodal other JTT = 10.7 m). The only difference was that the cathodal stimulation did not reduce the other JTT compared with the sham. In the high PT group, the cathodal stimulation reduced both the object (8.76 m) and the other (8.28 m) JTT compared with the sham object (8.52 m) and other (8.99 m) JTT; the anodal stimulation increased the object (9.17 m) but not the other (8.99 m) JTT.

In summary, our results suggest that cognitive perspective taking acts as a modulator of the tDCS effect on the social scaling of extrapersonal space.

Discussion

In a series of previous studies (Fini et al. 2015a, b) we have shown that the distance between another person and an object is judged as compressed compared to the distance between two objects. Here, we aimed to investigate the neuronal correlate of this perceptual effect. Starting from the assumption that our perceptual effect implies to categorize a human as a biological agent and to filter the space by considering the perceptual consequences of the afforded action (e.g., walking), we individuate the inferior frontal cortex (IFC) as a candidate area to be modulated.

Indeed, IFC is a brain area assumed to be involved in the semantic categorization (Mazoyer et al. 1993; Thompson-Schill et al. 1997, 1998; Wagner et al. 1997, 2001) and also recruited during mechanisms of interpersonal motor resonance (IMR; Uithol et al. 2011). In presence of a human, we remap the space by considering the action (e.g., walking) that the other person would perform to cover the distance. In the current work, we modulated (with tDCS) the activity of this area while participants performed the extrapersonal space categorization task with an object (nonsocial condition) or a person (social condition) as reference. Importantly, tDCS of the IFC has been previously shown to modulate motor resonance as indexed by psychophysiological measures of motor activation (Enticott et al. 2012). We are aware, however, of the methodological limitations of tDCS, primarily its relatively low spatial resolution. The IFC includes the ventral premotor cortex (vPMC) and the inferior frontal gyrus (IFG). Ventral PMC responds both to action observation and performance (Gazzola et al. 2006, 2007; Vogt et al. 2007), and IFG is recruited during the matching of motor plans (Iacoboni et al. 1999; Rizzolatti et al. 2001) through the encoding and representation of goals and intentions from observed actions (Cattaneo et al. 2009; Rizzolatti and Sinigaglia 2010; Gallese and Sinigaglia 2011). Future investigations with other techniques, such as fMRI and TMS, are therefore needed to further specify the neural substrate of our effect. Our results, as in Fini et al. (2015b), are calculated on an index that corresponds to the subtraction of the Near space threshold for the object as RF from the Near space threshold for the person as RF [JTT_(other-object)]. We used this index as dependent variable, because it is more sensitive to capture the relation between the social and nonsocial conditions. We found that when IFC activity was increased by the anodal stimulation, there was a space compression (i.e., a greater portion of space judged as "Near," corresponding to a greater JTT threshold) for the social versus nonsocial condition, compared to when IFC activity was inhibited through the cathodal stimulation. The described results were only found during the stimulation, which is in accordance with the observation that tDCS effects over motor areas are not very long lasting (Nitsche et al. 2008). Our results suggest that compression

of space in a social context could be associated with the categorization of a human as a biological agent, and the space would be judged by implicitly considering the other's inferred motor plan. Interestingly, the opposite effect of anodal and cathodal stimulation on the JTT_(other-object) ratio was in part driven by a general perturbation of the other RF perception (longer distance between the person and the object). The unspecific effect of transcranial direct stimulation on biological action representation is in line with Enticott et al. (2012) and also with several studies reporting a disruption of processes following both stimulation polarities (Marshall et al. 2005; Ferrucci et al. 2008). Conversely, the effect of the stimulation on the object RF perception was specific: while the cathodal stimulation increased the object RF perception (shorter distance between the two objects), the anodal stimulation worked in the opposite direction (longer distance between the two objects). Our speculation is that the perception of a biological appearance and the associated space representation is a hard-wired mechanism, not very flexible and easy to be manipulated. The object RF perception would be a neutral condition where the specific effects of the stimulation polarities are rather manifested. We also found that the impact of the stimulation over IFC was modulated by perspective-taking ability: The lower the PT score at the IRI, the greater the impact of the brain stimulation. Specifically, only those participants with lower PT score were sensitive to the brain stimulation. There is evidence that people automatically take the other's spatial perspective to describe the physical world and that in order "to understand" the other, we often need to physically assume his/ her position in the environment [see Tversky and Hard (2009)]. In this regard, Erle and Topolinski (2015) have shown that cognitive perspective-taking ability measured with IRI correlates with visuospatial perspective taking measured with the Tube figure Test (TFT; Stumpf and Fay 1983). This suggests that "being in the other's body entails being in the other's mind" or vice versa. In other words, assuming the other's perspective can be not just a "metaphor" but an embodied process, framed in sensorimotor mechanisms [for a review see Creem-Regehr et al. (2015)]. When we judge the space by considering another body as reference frame, we probably promote three processes: (1) we categorize a human as a biological agent; (2) we assume the other's physical and cognitive perspective and (3) we process the space as a function of the other's bodily capabilities and goals. In those with a weak cognitive perspective taking, there would be space for improving interpersonal motor resonance by brain stimulation over IFC. By contrast, participants who scored high on the perspective-taking scale probably already showed interpersonal motor resonance, which could not be further improved by anodal stimulation. This interpretation is supported by the differences in the baseline effect between the high PT group and the low PT group: In the high PT group, the space compression was significantly greater for the social versus nonsocial condition compared with the low PT group. Thus, the ability to take the other's perspective seems to be a prerequisite of the social scaling of extrapersonal space and to determine the effect of tDCS. In conclusion, our results suggest that: (a) IFC is recruited during the extrapersonal space categorization task, (b) the underlying mechanisms behind the reduced perceived distance could be the semantic attribution of the biological nature to a human, an automatic visual-spatial perspective taking and consequently the promotion of the interpersonal motor resonance, (c) these processes are modulated by the individual level of cognitive perspective taking, with a weak level allowing responsivity to IFC activity boosting.

Acknowledgements This study has been supported by FWO Research Project G.0223.13.

References

- Abdullaev YG, Bechtereva NP (1993) Neuronal correlate of the higher-order semantic code in human prefrontal cortex in language tasks. Int J Psychophysiol 14(3):167–177
- Bloesch EK, Davoli CC, Roth N, Brockmole JR, Abrams RA (2012) Watch this! Observed tool use affects perceived distance. Psychon Bull Rev 19(2):177–183
- Cardellicchio P, Sinigaglia C, Costantini M (2011) The space of affordances: a TMS study. Neuropsychologia 49(5):1369–1372
- Cattaneo L, Caruana F, Jezzini A, Rizzolatti G (2009) Representation of goal and movements without overt motor behavior in the human motor cortex: a transcranial magnetic stimulation study. J Neurosci 29(36):11134–11138
- Coello Y, Delevoye-Turrell Y (2007) Embodiment, spatial categorisation and action. Conscious Cogn 16(3):667–683
- Costantini M, Ambrosini E, Sinigaglia C, Gallese V (2011) Tool-use observation makes far objects ready-to-hand. Neuropsychologia 49(9):2658–2663
- Creem-Regehr SH, Gagnon KT, Geuss MN, Stefanucci JK (2015) Relating spatial perspective taking to the perception of other's affordances: providing a foundation for predicting the future behavior of others. Perspective taking: building a neurocognitive framework for integrating the "social" and the "spatial"
- Davis MH (1983) Measuring individual differences in empathy: evidence for a multidimensional approach. J Pers Soc Psychol 44(1):113
- Enticott PG, Arnold SL, Fitzgibbon BM, Hoy KE, Susilo DA, Fitzgerald PB (2012) Transcranial direct current stimulation (tDCS) of the inferior frontal gyrus disrupts interpersonal motor resonance. Neuropsychologia 50(7):1628–1631
- Erle TM, Topolinski S (2015) Spatial and empathic perspective-taking Correlate on a dispositional level. Soc Cogn 33(3):187
- Ferrucci R, Marceglia S, Vergari M, Cogiamanian F, Mrakic-Sposta S, Mameli FEEA, Priori A (2008) Cerebellar transcranial direct current stimulation impairs the practice-dependent proficiency increase in working memory. J Cogn Neurosci 20(9):1687–1697
- Fini C, Costantini M, Committeri G (2014) Sharing space: the presence of other bodies extends the space judged as near. PLoS ONE 9(12):e114719

- Fini C, Brass M, Committeri G (2015a) Social scaling of extrapersonal space: target objects are judged as closer when the reference frame is a human agent with available movement potentialities. Cognition 134:50–56
- Fini C, Committeri G, Müller BC, Deschrijver E, Brass M (2015b) How watching Pinocchio movies changes our subjective experience of extrapersonal space. PLoS ONE 10(3):e0120306
- Galea JM, Celnik P (2009) Brain polarization enhances the formation and retention of motor memories. J Neurophysiol 102(1):294–301
- Gallese V, Sinigaglia C (2011) What is so special about embodied simulation? Trends Cogn Sci 15(11):512–519
- Gazzola V, Aziz-Zadeh L, Keysers C (2006) Empathy and the somatotopic auditory mirror system in humans. Curr Biol 16(18):1824–1829
- Gazzola V, Rizzolatti G, Wicker B, Keysers C (2007) The anthropomorphic brain: the mirror neuron system responds to human and robotic actions. Neuroimage 35(4):1674–1684
- Holland R, Leff AP, Josephs O, Galea JM, Desikan M, Price CJ, Rothwell JC, Crinion J (2011) Speech facilitation by left inferior frontal cortex stimulation. Curr Biol 21:1403–1407
- Hsu TY, Tseng LY, Yu JX, Kuo WJ, Hung DL, Tzeng OJ, Juan CH (2011) Modulating inhibitory control with direct current stimulation of the superior medial frontal cortex. Neuroimage 56(4):2249–2257
- Iacoboni M, Woods RP, Brass M, Bekkering H, Mazziotta JC, Rizzolatti G (1999) Cortical mechanisms of human imitation. Science 286(5449):2526–2528
- Iyer MB, Mattu U, Grafman J, Lomarev M, Sato S, Wassermann EM (2005) Safety and cognitive effect of frontal DC brain polarization in healthy individuals. Neurology 64(5):872–875
- Jang SH, Ahn SH, Byun WM, Kim CS, Lee MY, Kwon YH (2009) The effect of transcranial direct current stimulation on the cortical activation by motor task in the human brain: an fMRI study. Neurosci Lett 460(2):117–120
- Marshall L, Mölle M, Siebner HR, Born J (2005) Bifrontal transcranial direct current stimulation slows reaction time in a working memory task. BMC Neurosci 6(1):1
- Mazoyer BM, Tzourio N, Frak V, Syrota A, Murayama N, Levrier O, Mehler J (1993) The cortical representation of speech. J Cogn Neurosci 5(4):467–479
- Nitsche MA, Paulus W (2000) Excitability changes induced in the human motor cortex by weak transcranial direct current stimulation. J Physiol 527(3):633–639
- Nitsche MA, Doemkes S, Karakoese T, Antal A, Liebetanz D, Lang N, Paulus W (2007) Shaping the effects of transcranial direct current stimulation of the human motor cortex. J Neurophysiol 97(4):3109–3117
- Nitsche MA, Cohen LG, Wassermann EM, Priori A, Lang N, Antal A, Pascual-Leone A (2008) Transcranial direct current stimulation: state of the art 2008. Brain Stimul 1(3):206–223
- Proffitt DR (2006) Embodied perception and the economy of action. Perspect Psychol Sci 1(2):110–122

- Proffitt DR, Stefanucci J, Banton T, Epstein W (2003) The role of effort in perceiving distance. Psychol Sci 14(2):106–112
- Rizzolatti G, Sinigaglia C (2010) The functional role of the parietofrontal mirror circuit: interpretations and misinterpretations. Nat Rev Neurosci 11(4):264–274
- Rizzolatti G, Fogassi L, Gallese V (2001) Neurophysiological mechanisms underlying the understanding and imitation of action. Nat Rev Neurosci 2(9):661–670
- Schnall S, Zadra JR, Proffitt DR (2010) Direct evidence for the economy of action: glucose and the perception of geographical slant. Perception 39(4):464–482
- Stagg CJ, O'shea J, Kincses ZT, Woolrich M, Matthews PM, Johansen-Berg H (2009) Modulation of movement-associated cortical activation by transcranial direct current stimulation. Eur J Neurosci 30(7):1412–1423
- Stumpf H, Fay E (1983) Schlauchfiguren: ein Test zur Beurteilung des räumlichen Vorstellungsvermögens. Verlag für Psychologie, Hogrefe
- Sugovic M, Witt JK (2013) An older view on distance perception: older adults perceive walkable extents as farther. Exp Brain Res 226(3):383–391
- Thompson-Schill SL, D'Esposito M, Aguirre GK, Farah MJ (1997) Role of left inferior prefrontal cortex in retrieval of semantic knowledge: a reevaluation. Proc Natl Acad Sci 94(26):14792–14797
- Thompson-Schill SL, Kurtz KJ, Gabrieli JD (1998) Effects of semantic and associative relatedness on automatic priming. J Mem Lang 38(4):440–458
- Tversky B, Hard BM (2009) Embodied and disembodied cognition: spatial perspective-taking. Cognition 110(1):124–129
- Uithol S, van Rooij I, Bekkering H, Haselager P (2011) Understanding motor resonance. Soc Neurosci 6(4):388–397
- Vogt S, Buccino G, Wohlschläger AM, Canessa N, Shah NJ, Zilles K, Fink GR (2007) Prefrontal involvement in imitation learning of hand actions: effects of practice and expertise. Neuroimage 37(4):1371–1383
- Wagner AD, Desmond JE, Demb JB, Glover GH, Gabrieli JD (1997) Semantic repetition priming for verbal and pictorial knowledge: a functional MRI study of left inferior prefrontal cortex. J Cognitive neurosci 9(6):714–726
- Wagner AD, Paré-Blagoev EJ, Clark J, Poldrack RA (2001) Recovering meaning: left prefrontal cortex guides controlled semantic retrieval. Neuron 31(2):329–338
- Witt JK, Proffitt DR (2008) Action-specific influences on distance perception: a role for motor simulation. J Exp Psychol Hum Percept Perform 34(6):1479
- Witt JK, Proffitt DR, Epstein W (2004) Perceiving distance: a role of effort and intent. Perception 33(5):577–590
- Witt JK, Proffitt DR, Epstein W (2005) Tool use affects perceived distance, but only when you intend to use it. J Exp Psychol Hum Percept Perform 31(5):880