Impaired semantic categorization during transcranial direct current stimulation of the left and right inferior parietal lobule

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ABSTRACT

We investigated whether semantic knowledge is organized according to domain- or feature-dimensions during a semantic categorization task. In addition, using transcranial direct current stimulation (tDCS), we assessed whether the left or right inferior parietal lobule is differentially engaged based on these dimensions. To this end, four different tDCS electrode montage groups were employed (anodal left, cathodal left, anodal right, cathodal right). Reaction times and accuracy were recorded in response to visually presented words (living and non-living concepts with a high or low number of features). In line with our expectations, living concepts elicited faster reaction times compared with non-living concepts and concepts with a high number of features elicited faster reaction times compared with concepts with a low number of features. In addition, a general, regionally and polarity-unspecific, deteriorating effect of tDCS emerged, with stimulation slowing down reaction times compared with sham. The results are discussed in the frameworks of major theories on the organization of semantic knowledge, including the Distributed Domain-Specific Hypothesis.

1. Introduction

Semantic memory is a part of human long-term memory and represents the meaning of all types of acquired information (Collins & Loftus, 1975; Tulving, 1972). This includes the meaning of words, geographical relationships and mathematical knowledge (among others). The constitutive elements of semantic memory are “concepts”, which are mental representations of classes of objects or other entities (Murphy, 2002). A further notion occurring in this context is “category”. A category refers to a group of entities sharing common features or referring to a certain prototype (e.g., “cat” and “lion” belong to the category “feline”, which, in turn, belongs to the category “animal”, which, in turn, belongs to the category “living”). Concepts incorporate all information linked to the objects they represent. For example, information belonging to the concept “cat” is “is a living being”, “has a fur” or “is domestic”. This information is defined as “properties” or “features” (Farah & McClelland, 1991; McRae, Cree, Seidenberg, & McNorgan, 2005; Warrington & Shallice, 1984).

Despite numerous studies investigating the organization of semantic memory, the question of how conceptual knowledge is structured and organized in the brain remains a controversial issue (e.g., Kemmerer, 2015, 2017). The main assumption of feature-based models is that conceptual representations are multi-modal and stored in distributed semantic networks (e.g., Martin & Chao, 2001). These networks consist of units each representing a specific type of information related to the concepts. The different

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units are jointly activated to allow the coherent conceptual representation of the information as a whole. The central assumption of feature-based approaches such as Sensory/Functional Theories (SFT) is that the semantic system is organized via modality-specific sensory features (e.g., form, color, motion, smell, taste) and functional properties of objects (e.g., motor habits related to the use of the object, its typical location or social value) (Martin & Caramazza, 2003). The second assumption of SFT is that living objects are recognized and named depending on visual/perceptual information, whereas non-living objects are recognized and named depending on functional/associative information. Empirical evidence in support of SFT comes from lesion studies as well as from functional imaging studies (e.g., Gainotti, 2000; Marques, Canessa, Siri, Catricalà, & Cappa, 2008; Proverbio, Del Zotto, & Zani, 2007).

Many studies revealed facilitating effects for words with a high number of features (NOF) compared to a low NOF during semantic, lexical and concreteness decision tasks (McRae, de Sa, & Seidenberg, 1997; Pexman, Lupker, & Hino, 2002, 2003). In particular, Amsel and Cree (2013) found that the domain “animals” resulted in significantly faster reaction time (RT) compared to the domain “objects”. In addition, words with a high number of features (NOF+) resulted in faster RTs relative to words with a low number of features (NOF-). There was, however, no interaction between the two factors. Within each domain, semantically rich concepts (i.e., NOF+) elicited the fastest RTs. Amsel and Cree (2013) concluded that semantic memory organization is based on both semantic categories and semantic features.

The question about the organization of conceptual knowledge still remains the subject of intense debate and there are many clinical cases which cannot be explained by SFT (Caramazza & Shelton, 1998; Laiacona, Barbarotto, & Capitani, 1993; Lambon Ralph, Howard, Nightingale, & Ellis, 1998; Miceli et al., 2001). Based on the inconsistent empirical evidence, Caramazza and Shelton (1998) put forward the Domain-Specific Knowledge Hypothesis (DSKH). The main assumption of DSKH is that the first-order constraint of the organization of conceptual knowledge is the object category or domain. Consequently, impairments should be limited to the affected category (Martin & Caramazza, 2003; Samson & Pillon, 2003; Tyler & Moss, 2001). Evidence for a neural differentiation based on semantic domains comes from functional neuroimaging studies (e.g., Mahon & Caramazza, 2009; Martin & Chao, 2001).

Since the middle of the 19th century, the superiority of the left over the right hemisphere regarding linguistic processing has been demonstrated (e.g., Broca, 1865; Wernicke, 1874). A growing body of neuroimaging and neuropsychological studies, however, suggests an important role of the right hemisphere during semantic processing (Beeman & Chiarello, 1998; Beeman et al., 1994; Jung-Beeman, 2005; Peretz & Lavidor, 2013; Proverbio et al., 2007; Weltman & Lavidor, 2013). In their meta-analysis of 120 functional imaging studies focusing on semantic processing Binder, Desai, Graves, and Conant (2009) reported that 68% (771) of all described activation foci were situated in the left hemisphere, whereas 32% (362) were found in the right hemisphere. Seven principal areas forming the fundamental semantic network were defined: 1) inferior parietal lobule (IPL) including the angular gyrus (AG) and the adjacent supramarginal gyrus (SMG); 2) the lateral temporal lobe, including the middle temporal gyrus (MTG) and posterior portions of the inferior temporal gyrus (ITG); 3) a ventromedial region of the temporal lobe centered on the mid-fusiform gyrus (FFG) and adjacent parahippocampus; 4) dorso medial prefrontal cortex (DMPC) in the superior frontal gyrus (SGF) and adjacent middle frontal gyrus (MFG); 5) the inferior frontal gyrus (IFG); 6) ventromedial and orbital prefrontal cortex (PFC); and 7) the posterior cingulate cortex (PCC) and adjacent ventral prefrontal. Although their data indicated a moderate left hemisphere lateralization, activation was observed at the homologous locations in the right hemisphere, mainly in the IPL, posterior MTG, and PCC. Complementary to these results, several other studies showed an active participation of the fronto-temporal network in the right hemisphere during processing of sentence-level prosody (Friederici, 2011) and specific unilateral right temporal involvement during sentence and text processing tasks, likely related to contextual processing (Vigneau et al., 2011).

In an fMRI study by Leube, Erb, Grodd, Bartels, and Kircher (2001) visual words were presented and participants were asked to perform a semantic categorization task (living vs. non-living). The results showed overlapping activation for living and non-living items in the bilateral inferior occipital gyri, as well as in the left IFG and left IPL. In addition, words referring to living objects elicited higher activation in right IFG, FFG, and medial temporal regions. Conversely, in the PET study by Cappa, Perani, Schnur, Tettemanti, and Fazio (1998) bilateral activation for visually presented words denoting to animals was observed, whereas tools elicited left hemispheric activation.

Marques et al. (2008) reported similar findings in their fMRI-study. They presented statements regarding features (e.g., form, color, size, motion) of living and non-living objects and asked participants to judge whether these statements were correct or incorrect. Responses to living concepts were significantly faster compared to non-living concepts. The fMRI results revealed that the retrieval of semantic features activated a bilateral brain network including IPL, occipital and inferior frontal brain regions.

In the light of these empirical findings and based on the theoretical views of SFT and DSKH, the present study aimed at providing evidence for a possible differential involvement of the left and right IPL during semantic processing. Specifically, we were interested in (1) whether the IPL is differentially involved in the processing of words during semantic categorization (living vs. non-living) and (2) whether it is relevant regarding the representation of features of semantic concepts. Since data from functional neuroimaging studies about the involvement of certain areas is correlational in nature, we sought to assess the causal relationship between IPL engagement and semantic processing by means of non-invasive brain stimulation. To this end, we used transcranial direct current stimulation (tDCS) – a well-established technique in the domain of language research (Monti et al., 2013; Price et al., 2015, 2016; Wirth et al., 2011).

Many studies demonstrated the differential influence of anodal and cathodal tDCS on semantic processing (e.g., De Vries et al., 2010; Föbel, Roesser, Michka, Knecht, & Breitenstein, 2008; Marshall, Mölle, Siebner, & Born, 2005) and targeting particularly the IPL (see review by Joyal & Fecteau, 2016; Price et al., 2016). Therefore, anodal and cathodal stimulation was separately applied to the left and right IPL and adjacent cortical regions, since these regions were proposed to play a central role in the semantic network by numerous functional neuroimaging and lesion studies (e.g., meta-analysis by Binder et al., 2009; Dronkers, Wilkins, Van Valin, Redfern, & Jaeger, 2004). Anodal tDCS typically leads to depolarization of the resting membrane potential, which increases neuronal
excitability, whereas cathodal tDCS typically causes hyperpolarization of the resting membrane potential, which decreases neuronal excitability (e.g., Nitsche et al., 2008). In previous tDCS language studies, anodal IPL stimulation was used to facilitate semantic processing, whereas cathodal IPL stimulation was used to inhibit semantic processing (see review by Joyal & Fecteau, 2016; Brückner & Kammer, 2017; Price et al., 2016). The exact relationship between neuromodulation by means of tDCS and behavior, however, is still unclear (e.g., Almeida et al., 2017; Bestmann, de Berker, & Bonaiuto, 2015; Jacobson, Koslowsky, & Lavidor, 2012).

The experimental procedure consisted of a real and a sham stimulation session. The participants were divided in four groups with different electrode montages (anodal left, anodal right, cathodal left, cathodal right) and took part in both sessions while performing a visual semantic categorization task. The stimulus set used for this study was the same as utilized by Zauner, Gruber, Himmelstoß, Lechinger, and Klimesch (2014). Words belonging to the category living and non-living were subdivided according to their semantic richness having either a high or low NOF.

In order to investigate feature-vs. domain-based semantic processing, two contrasting hypotheses were formulated: (1) Words referring to living objects should generally result in faster RTs compared with words referring to non-living objects. Moreover, even stronger differentiation between living objects compared with non-living objects were expected during stimulation compared with sham. (2) In addition, NOF+ words should result in faster RTs compared with NOF- words. Again, stronger effects between NOF+ and NOF- words were expected for stimulation compared with sham. In addition, since we hypothesized the left IPL to be particularly relevant for the processing of non-living concepts, we expected faster RTs for non-living concepts during anodal stimulation (which typically increases neuronal excitability) applied over the left IPL compared with the other experimental electrode montage conditions (anodal-right stimulation; cathodal-right stimulation; cathodal-left stimulation; sham).

2. Materials and methods

2.1. Participants

The study was conducted at the University of Salzburg. Participants received compensation of ten Euro and students of the university were also rewarded with course credits. Seventy-two participants took part in the study (65 females, 90.28%; 7 males, 9.72%; M age = 25.49 years, SD age = 7.28 years; age range = 19–47 years). The number of participants was calculated a-priori by means of G*Power 3.1 software (Faul, Erdfelder, Lang, & Buchner, 2007) and assuming a medium effect size of \( f = 0.25 \) for a within-between interaction in a repeated measures ANOVA with four groups (alpha error probability = 0.05; power = 0.95). All participants were right-handed, native German speakers, with normal or corrected-to-normal vision. None of the participants reported any brain injuries, psychological or neurological disorders, or intake of psychotropic medication. Before taking part in the study, all participants signed an informed consent according to the Declaration of Helsinki and approved by the local Ethics Committee of the University of Salzburg (IRB number EK-GZ 28/2014).

2.2. Stimuli and task

Participants performed a semantic categorization task, which required deciding whether a visually presented word represented a living or a non-living concept. Animals and fruits constituted the “living” category, whereas tools and objects of daily life constituted the “non-living” category. The stimulus set consisted of 280 words taken from McRae’s et al. (2005) “semantic feature production norms” that were translated to German. The stimulus set used for this study was the same as utilized by Zauner et al. (2014). For living concepts, the mean NOF was 4.15 (SD = 2.13, min = 1, max = 11). For non-living concepts, the mean NOF was 4.98 (SD = 2.29, min = 1, max = 11). The 280 words were evenly divided between the two main categories, with 140 words for the living and 140 words for the non-living concepts. Subsequently, the living and non-living categories were split into two further groups of 70 items each, depending on NOF: NOF+ living words (>4 features per item) and NOF- living words (<4 features per item), and NOF+ non-living words (>5 features per item) and NOF- non-living words (<5 features per item). For stimulus presentation a counterbalanced measures design was used: the stimuli were randomly ordered in two lists (each list containing all 280 words) which were assigned alternately to the stimulation and sham sessions of the experiment.

2.3. Transcranial direct current stimulation

Anodal and cathodal tDCS was separately applied to the IPL and adjacent cortical regions of the left and right hemisphere. This resulted in four electrode montage stimulation groups: anodal left, anodal right, cathodal left, cathodal right. Participants were randomly assigned to one of the groups and were stimulated while carrying out the semantic categorization task. Each participant took part in a stimulation and a sham session (as described below). Following tDCS safety guidelines (Bikson, Datta, & Elwassif, 2009; Nitsche et al., 2008), a direct current of 1.5 mA intensity was induced by two saline-soaked, synthetic sponge electrodes and delivered by a battery-driven, constant-current stimulator (tDCS Stimulator Plus, neuroConn GmbH, Germany). While the active electrode (5 × 7 cm) was placed over the IPL, the reference electrode (10 × 10 cm) was placed over the contralateral supraorbital region with respect to the actually stimulated site.

According to the EEG 10–20 system, P3 and P4 positions corresponding to the IPL were marked on the scalp in order to indicate the stimulated areas. The current had a ramp-up time of 30 s, was held at 1.5 mA for 20 min, and then ramped down for 30 s. Fig. 1 represents the tDCS set-up of the study.

For the sham session the electrodes were placed as during the stimulation session but the current was ramped up for 30 s at the
beginning followed by a ramp down for 30 s with no stimulation taking place during the experiment. The tDCS application was double-blind since neither the participants nor the experimenter knew whether stimulation or sham was applied.

2.4. Experimental design and procedure

Each participant took part in two counterbalanced sessions: a stimulation session and a sham session. The two sessions were separated by a minimum of two days and a maximum of seven days in order to avoid any possible carry-over effects. Four different electrode montage groups (anodal left, anodal right, cathodal left, cathodal right) were employed with each group consisting of 18 participants. Each participant was randomly assigned to one of the groups. At the beginning of the experiment, after the informed consent had been read and signed by the participant, the tDCS electrodes were applied according to the experimental group and the stimulation started. During the first 5 min of stimulation (warm-up-phase), participants were instructed and performed a training session to familiarize themselves with the stimulus presentation and task procedures. If there were no further questions the experiment started.

Participants were seated in front of a 24-inch BenQ XL2411Z LED monitor (60 Hz refresh rate, 1920 × 1080 pixels resolution) at a distance of 60 cm. Stimulus presentation and data collection were controlled by Presentation (version 0.71, Neurobehavioral Systems Inc., CA, US) running on an IBM compatible computer and lasted for 20 min. A gray fixation cross appeared in the center of a black screen and subsequently a word written in upper-case letters was presented (50-point dark gray Verdana font, RGB = 50, 50, 50).

In order to reduce stimulus onset expectancy effects, the interval between the onset of the fixation cross and the onset of the word varied in 50 ms steps between 400 and 600 ms. The words were presented for 1000 ms in a dark gray color (RGB = 50, 50, 50) within a bright gray box (RGB = 100, 100, 100) to ensure comfortable reading and to hold visual surface features constant between trials. After stimulus presentation, a blank screen was displayed for 1500 ms and participants had to indicate whether the word represented a living (left key – right index finger) or non-living concept (right key – right middle finger) by pressing the arrow keys on the keyboard with their right hand. After completing the experiment, the electrodes were removed and participants were asked about their awareness of the real purpose of the experiment and the stimulation conditions.

2.5. Statistical analyses

Statistical analyses were performed using Statistical Package for Social Sciences (IBM SPSS, version 26.0 for Windows). The data were screened for outliers, which were defined as exceeding three standard deviations above or below each participant’s mean RT and percentage of correctly categorized concepts (hits). This resulted in elimination of 1.35% of the data, which is within the normal

Fig. 1. Illustration of the tDCS electrode montages for the four different experimental groups. Active tDCS electrodes (5 × 7 cm) were placed over the IPL in the left and right cerebral hemispheres (P3/P4 in the EEG 10–20 system) and reference electrodes (10 × 10 cm) were placed contralateral supraorbital to the actively stimulated site. A direct current intensity of 1.5 mA was applied for 20 min. A = anodal, C = cathodal.
recommended limits (Ratcliff, 1993). RT means are expressed in milliseconds (ms); accuracy is reported in percentage correct responses.

Statistical analyses were computed for accuracy (hits) and RT based on correct responses. A mixed-design 4 × 2 × 2 × 2 ANOVA on RT was carried out with the between-participants-factor “electrode montage” (anodal left/AL vs. cathodal left/CL vs. anodal right/AR vs. cathodal right/CR) and the within-participant-factors “session” (stimulation vs. sham), “semantic category” (living vs. non-living), and “NOF” (NOF- vs. NOF+).

3. Results

3.1. Post-experiment questionnaire

After taking part in the experiment, the participants were asked about their awareness of the real purpose of the experiment and the stimulation conditions. Generally, tDCS was well tolerated and few side effects were reported, specifically a light itching sensation under the electrodes (n = 3, 4.17%). None of the participants recognized the real purpose of the experiment. When asked whether sham stimulation had been applied, 50 of the overall 72 participants (69.44%) stated that it was not. Twenty-two participants (30.56% overall) declared that a sham condition had been applied but only half of them (n = 11, 15.28% overall) correctly identified the actual session concerned, indicating that the correctness of these “guesses” was at chance level. Importantly, there were no differences between the four stimulation groups regarding side effects or awareness of the sham stimulation.

3.2. Semantic categorization task

Table 1 shows the RT means and standard deviations in milliseconds for each of the electrode montage groups and stimulus categories during real stimulation and sham. Conversely, Table 2 shows the accuracy means and standard deviations in percentage of correct decisions following the same structure. Overall, accuracy was reasonably high (ranging from 91.90% to 97.54% correct decisions), indicating that the task was easy and unambiguous for the participants.

The mixed-design 4 × 2 × 2 × 2 ANOVA revealed a significant main effect for “session”, F(1,68) = 5.946, p = .017, ηp2 = 0.080, with slower RTs for stimulation compared with sham (see Fig. 2). In addition, a highly significant main effect of “semantic category” was found, F(1,68) = 86.143, p < .000, ηp2 = 0.559, with faster RTs for living concepts compared with non-living concepts. Finally, a highly significant main effect of “NOF” was found, F(1,68) = 123.404, p < .000, ηp2 = 0.645, with faster RTs for NOF+ words compared with NOF- words. None of the interaction effects were statistically significant. The between-participants main effect of “electrode montage” was also not statistically significant, F(3,68) = 0.517, p = .672, ηp2 = 0.022.

4. Discussion

The present study was aimed at investigating whether the representation of conceptual knowledge is feature- or domain-based, and whether differences during the processing of objects belonging to the semantic categories living or non-living are subject to differential effects of tDCS over the left and right IPL. In line with previous evidence, our results indicate that words denoting to living concepts were categorized faster than words referring to non-living concepts. In addition, NOF+ words were categorized faster than NOF- words. These effects were observed regardless of the type of stimulation and electrode montage. Contrary to our expectations, tDCS globally worsened participants’ performance during semantic categorization. That is, there were no regionally or polarity-specific effects of tDCS on the categorization of living and non-living concepts.

4.1. Semantic categorization

Concerning feature-vs. domain-based knowledge representation, we hypothesized that living concepts elicit faster RTs than non-living concepts and, furthermore, that words denoting to concepts with a high NOF elicit faster RTs relative to those with a low NOF. In

Table 1

Reaction time means and standard deviations (in parentheses) in milliseconds for each of the electrode montage groups and stimulus categories during real stimulation and sham.

| Group           | N   | tDCS condition |                  | Sham                     |
|-----------------|-----|----------------|-------------------|--------------------------|
|                 |     | Stimulation    | Living            | Non-living               |
|                 |     |                | NOF-               | NOF+                     |
| Anodal left     | 18  | 667 (87)       | 652 (84)          | 689 (79)                |
| Anodal right    | 18  | 666 (60)       | 653 (64)          | 707 (64)                |
| Cathodal left   | 18  | 663 (81)       | 648 (81)          | 696 (101)               |
| Cathodal right  | 18  | 642 (87)       | 626 (94)          | 673 (95)                |

Notes. NOF− = low-features concepts, NOF+ = high-features concepts.
line with our first hypothesis, living concepts lead to significantly faster RTs compared with non-living ones. In addition, tDCS lead to slower RTs compared with sham. This effect was unspecific with respect to electrode montage (AL, CL, AR, CR). The findings are consistent with previous studies outlined in the introduction (Amsel & Cree, 2013; Marques et al., 2008; Proverbio et al., 2007).

In line with our second hypothesis, according to which NOF+ words should result in faster RTs compared with NOF- words, and in line with previous studies (Amsel & Cree, 2013; McRae et al., 2005; Pexman et al., 2002, 2003; Zauner et al., 2014), the results provided support for SFT. That is, words representing concepts with a high NOF elicited significantly faster RTs relative to words with a low NOF. Again, there was a generally deteriorating effect of tDCS on RTs but no specific effect of electrode montage. Taken together, our results support both SFT and DSKH.

A dichotomous division of semantic knowledge into sensory and functional features as proposed by SFT (Farah & McClelland, 1991; Warrington & Shallice, 1984) is probably too reductive to reflect all the different category-specific deficits described in the literature as discussed in the Introduction. Vinson, Vigliocco, Cappa, and Siri (2003) pointed out this issue, showing that features of non-visual nature (e.g., taste or texture) are relevant not only for non-living concepts like clothing but also for living/natural concepts such as fruits and vegetables. In this regard, Cree and McRae (2003) showed that at a later stage of a hierarchical cluster analysis, features of fruits and vegetables clustered together with non-living objects due to functional properties not easily detectable early in the analysis. They demonstrated that it is impossible to capture and explain an entire semantic category through a single knowledge type, but that more dimensions are needed, and, more importantly, that the interaction between all of them could much better depict the structure of semantic knowledge.

SFT predict an interaction effect between semantic category and features on the basis of the different weighting of the semantic categories considered, with living objects characterized by a larger number of sensory features, and non-living objects by a larger number of functional features. The results of our study showed no significant interaction between these two factors. In contrast, DSKH

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### Table 2
Accuracy means and standard deviations (in parentheses) in percentage of correct decisions for each of the electrode montage groups and stimulus categories during real stimulation and sham.

| tDCS condition | Stimulation | Sham |
|----------------|-------------|------|
|                | Living | Non-living | Living | Non-living |
|                | NOF-  | NOF+  | NOF-  | NOF+  | NOF-  | NOF+  | NOF-  | NOF+  |
| Anodal left    | 18    | 93.41 (6.20) | 94.68 (3.88) | 94.37 (3.23) | 95.48 (5.03) | 91.90 (9.68) | 92.94 (6.40) | 94.05 (4.58) | 95.63 (3.38) |
| Anodal right   | 18    | 94.76 (4.36) | 95.40 (4.03) | 94.94 (4.57) | 96.67 (3.43) | 93.41 (6.12) | 94.84 (4.04) | 95.40 (3.68) | 97.22 (3.08) |
| Cathodal left  | 18    | 94.05 (4.39) | 94.36 (3.34) | 94.68 (5.06) | 95.16 (7.69) | 95.87 (2.18) | 96.03 (2.22) | 95.95 (3.77) | 97.30 (2.44) |
| Cathodal right | 18    | 95.40 (3.55) | 95.40 (4.09) | 96.19 (2.08) | 97.54 (2.18) | 96.27 (2.46) | 96.75 (2.72) | 95.48 (3.30) | 96.59 (3.26) |

Notes. NOF- = low-features concepts, NOF+ = high-features concepts.

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**Fig. 2.** Reaction time means in milliseconds for each of the electrode montage groups and stimulus categories during real stimulation and sham.
consider uniquely semantic categories as the main constraint of semantic knowledge. In our study, however, a significant effect was also observed for features. Taking the shortcomings of both principal theoretical positions described here into account, the results of the present study may be best viewed from a different perspective.

In the Distributed Domain-Specific Hypothesis (Mahon & Caramazza, 2009) the object domain and the sensory/motor/emotional properties jointly organize the conceptual knowledge system. The object domain is a constraint on the organization at the conceptual level as well as at modality-specific visual input representations. The main assumption of the Distributed Domain-Specific Hypothesis is that the network binds different processes based on different types of information (visual form vs. visual motion vs. emotion) is focused on those domains which had a crucial role during human evolution. From this point of view, the model further predicts that such a network, if damaged, causes strong category-specific semantic impairments.

Moreover, the model predicts that at the object recognition level, impairments in abstract conceptual knowledge are disjointed from those related to a specific category. That means that impairments at the level of conceptual knowledge are not necessarily related to impairments in visual processing at a modality-specific input level. Furthermore, patients who suffer from prosopagnosia show impairments in recognizing visually presented faces but they are able to retrieve knowledge about the people they cannot recognize (e.g., Damasio, Damasio, & Van Hoesen, 1982). Taking these results into consideration it is possible that the domain-as well as the features-dimension are not single and distinct entities but are coexisting and synergistically operating at a structural and functional level within the semantic system.

The Distributed Domain-Specific Hypothesis is compatible with a semantic structure emerging through the combination of the semantic domain (living vs. non-living) with the feature domain, which characterized the results of the present study. Specifically, a crucial finding of our study was the differentiation regarding the number of features within the semantic dimensions of living and non-living, with NOF + concepts showing significantly faster RTs compared with NOF- concepts. The assumption of the Distributed Domain-Specific Hypothesis stating that the first main constraint of the semantic system is the semantic domain and that within each domain the conceptual representations are feature based fits the results of the present study in a comprehensive way.

4.2. Transcranial direct current stimulation

The application of tDCS has provided interesting results, albeit contrary to our initial expectations. Throughout all four electrode montage groups (AL, CL, AR, CR), a regionally and polarity-unspecific effect denoted by a general deterioration of participants’ performance was observed during stimulation compared with sham.

In line with functional neuroimaging and non-invasive brain stimulation studies on semantic knowledge (e.g., Bonner, Peelle, Cook, & Grossman, 2013; Cappa et al., 1998; Joyal & Fecteau, 2016; Liuzzi, Aglinskas, & Fairhall, 2020; Mummery, Patterson, Hodges, & Price, 1998; Price et al., 2016), we hypothesized a performance enhancement with respect to RTs of correctly assigned words of the category non-living in response to anodal stimulation applied over the left IPL. Furthermore, we expected that anodal tDCS over the right IPL would result in faster RTs of correctly categorized words belonging to the category living concepts (e.g., Chao, Weisberg, & Martin, 2002; Leube et al., 2001; Martin & Chao, 2001). The results, however, showed no significant differences elicited by tDCS during the semantic categorization task among the two stimulated hemispheres. Instead of an expected performance benefit, a general slowdown in RTs under both anodal and cathodal tDCS was observed.

The targeted region of the IPL was selected according to previous findings pointing to this region as key part of a bilateral semantic network (meta-analyses by Binder et al., 2009; Vigneau et al., 2011; Price, 2012). Despite the fact that the IPL is considered to be involved in semantic processing, it might be that some of the underlying structures are specialized for a particular type of semantic processing (Davis & Yee, 2019; Humphreys & Lambon Ralph, 2015). In their review, Binder and Desai (2011) pointed out that the IPL is a convergence zone for information coming from the visual, spatial, somatosensory and auditory processing streams, and that it is involved in depicting the objects in the semantic memory in a recognizable manner.

The IPL is surrounded by the dorsal attention network responsible for spatial cognition, by anterior parietal regions involved in action representation, and by posterior temporal regions supporting movement perception (Kravitz, Saleem, Baker, & Mishkin, 2011). This special location could suggest that the IPL may play a very specific role during semantic processing, namely the representation of events (Binder & Desai, 2011). Some studies provided support for this hypothesis, suggesting that the IPL plays a crucial role in the retrieval of episodic memories and in understanding theory-of-mind stories (Ferstl, Rinck, & Cramon, 2005; Ferstl & von Cramon, 2007; Schurz, Radua, Aichhorn, Richlan, & Perner, 2014). The observed deterioration in performance during stimulation compared with sham might be attributable to interference due to enhanced activation in a larger cortical network causing interactions between cortical processing dynamics of this larger area and of a more specific area specialized for performing the cognitive processes of interest (Bussey, Saksida, & Murray, 2005; Clarke & Tyler, 2014; Marshall et al., 2005; Martin, Douglas, Newsome, Man, & Barense, 2018; Penolazzi et al., 2010).

4.3. Limitations

Another reason why the participants’ RTs slowed down during stimulation compared with sham could be explained by considering the interaction between tDCS and cortical excitation. In their review, Miniussi, Harris, and Ruzzoli (2013) observed that the neuro-modulatory effects of tDCS are strongly influenced by the cortical excitation of the system of interest to which the stimulation is applied. Specifically, the neural noise induced by the tDCS influences task performance, depending on the cortical excitation of the specific system, which is itself mainly determined by the task input. Therefore, the final behavioral result is shaped by the tDCS neuro-modulation interacting with the level of excitation of the target system induced by the task.
Moreover, anodal tDCS may induce facilitation when the task is well trained or familiar. In contrast, in a novel task, more background noise is present because the neural networks involved are not consolidated and many signals close to the target signal are present. In this case, anodal tDCS will increase the signal as well as the noise, which is already close to the excitation threshold. Cathodal tDCS, on the other hand, during performance of a novel task, may induce facilitation by reducing the general noise and helping the signal to emerge (Miniussi et al., 2013; see also; Antal et al., 2004; Dockery, Hueckel-Weng, Birbaumer, & Plewnia, 2009).

Considering our results in relation to a recent (critical) meta-analysis on the efficacy of tDCS (Westwood & Romani, 2017), it is interesting to note that, contrary to what was reported in the meta-analysis, our single-session tDCS did show a significant effect on performance. Westwood and Romani (2017) found that there was no significant effect of tDCS on healthy participants through all the considered studies, including outcomes such as RTs and accuracy. In their moderator analysis, they found that time and duration of stimulation had a small but significant effect, particularly for offline stimulation and shorter durations (<15 min). In the present study, in contrast to what Westwood and Romani (2017) found, the results were observed regarding healthy participants’ RTs during online tDCS in a single session of 20 min.

Westwood and Romani (2017) stated that mainly tDCS studies involving brain-damaged patients have shown reliable results. With these patients, the levels of cortical excitability may become low or dysfunctional compared with the levels in healthy-brain participants, and tDCS may help in achieving more optimal cortical activation levels (see also De Aguiar, Paolazzi, & Miceli, 2015; Miniussi et al., 2013). We entirely agree with the authors about the importance of defining the exact conditions under which the levels of cortical excitation are considered optimal for performance modulation by means of tDCS in language tasks. We also agree and emphasize that there is a need for continued research into the efficacy of tDCS in healthy participants in order to develop reliable application protocols using this method including high-definition tDCS and neuronavigation based on both functional and structural neuroimaging. Considering the limited sample size per group, our study can only be considered as a first attempt in investigating possible laterality effects during semantic processing by means of tDCS.

5. Conclusions

The present investigation was aimed at the structure of the semantic system and the role of the left and right IPL during semantic processing. No differential tDCS effects between the brain hemispheres were observed. Instead, the results showed an overall deteriorating effect of tDCS: both anodal and cathodal stimulation lead to a slowdown of RTs compared with sham. Concerning the organization of semantic knowledge, the results showed that words denoting to living concepts were categorized faster than words referring to non-living concepts and that words with a high number of features were categorized faster than words with a low number of features. Contrary to what has been hypothesized by SFT (stating that conceptual representations are multi-modal and stored in distributed semantic networks) and DSKH (stating that the first-order constraint of the organization of conceptual knowledge is the object domain), the results are in line with the Distributed Domain-Specific Hypothesis. This hypothesis postulates that both the semantic domain (as the first constraint) and the feature domain (as the second constraint) constitute the structure of the semantic system.

Disclosure of interest

The authors report no conflict of interest.

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Data availability

The data that support the findings of this study are available from the corresponding author, FR, upon reasonable request.

References

Almeida, J., Martins, A. R., Bergström, F., Amaral, L., Freixo, A., Ganho-Ávila, A., et al. (2017). Polarity-specific transcranial direct current stimulation effects on object-selective neural responses in the inferior parietal lobe. Cortex, 94, 176–181. https://doi.org/10.1016/j.cortex.2017.07.001
Amsel, B. D., & Cree, G. S. (2013). Semantic richness, concreteness, and object domain: An electrophysiological study. Canadian Journal of Experimental Psychology/Revue Canadienne de Psychologie Expérimentale, 67(2), 117. https://doi.org/10.1037/a0029807
