Effect of tDCS on task relevant and irrelevant perceptual learning of complex objects

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During perceptual learning the visual representations in the brain are altered, but these changes' causal role has not yet been fully characterized. We used transcranial direct current stimulation (tDCS) to investigate the role of higher visual regions in lateral occipital cortex (LO) in perceptual learning with complex objects. We also investigated whether object learning is dependent on the relevance of the objects for the learning task. Participants were trained in two tasks: object recognition using a backward masking paradigm and an orientation judgment task. During both tasks, an object with a red line on top of it were presented in each trial. The crucial difference between both tasks was the relevance of the object: the object was relevant for the object recognition task, but not for the orientation judgment task. During training, half of the participants received anodal tDCS stimulation targeted at the lateral occipital cortex (LO). Afterwards, participants were tested on how well they recognized the trained objects, the irrelevant objects presented during the orientation judgment task and a set of completely new objects. Participants stimulated with tDCS during training showed larger improvements of performance compared to participants in the sham condition. No learning effect was found for the objects presented during the orientation judgment task. To conclude, this study suggests a causal role of LO in relevant object learning, but given the rather low spatial resolution of tDCS, more research on the specificity of this effect is needed. Further, mere exposure is not sufficient to train object recognition in our paradigm.

Introduction

With intensive training, the ability to extract relevant visual information increases, a process called perceptual learning. Evidence of perceptual learning has been reported in studies using simple stimuli (e.g., Fiorentini & Berardi, 1981; Karni & Sagi, 1991; Yu, Klein, & Levi, 2004) and experiments using complex objects (e.g., Baeck & Op de Beeck, 2010; Furmanski & Engel, 2000). This training-induced improvement in performance on visual tasks is possible due to plasticity in visual cortical areas. For example, orientation discrimination training leads to changes in the characteristics of neurons in the primary visual cortex (Schoups et al., 2001). This is consistent with the properties of V1 neurons, as these neurons are tuned to low-level features such as orientation. For perceptual learning of complex objects, further called object learning, we can expect a similar learning-dependent plasticity in higher-level visual areas, such as the inferotemporal cortex (IT) in monkeys or the lateral occipital complex (LOC) in humans (for a review, see Bi & Fang, 2013; Kourtzi & DiCarlo, 2006). This prediction was confirmed by Grill-Spector, Kushnir, Hendler, and Malach (2000), who found that the fMRI signal in LOC increased with improved recognition of objects after training. These object-selective areas show (to some degree) invariance to changes in low-level properties (e.g., Booth & Rolls, 1998; DiCarlo & Cox, 2007; DiCarlo, Zoccolan, & Rust, 2012; Wallis & Rolls, 1997), leading to the prediction that object learning also would show invariance. Behavioral studies indeed have observed such invariance: Whereas the learning effect is specific for the trained objects (Baeck & Op de Beeck, 2010; Baeck, Rentmeesters, Holtackers, & Op de Beeck, 2013; Furmanski & Engel, 2000), complete or partial

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generalization of the training effect is found over size (Furmanski & Engel, 2000; Lee, Matsumiyo, & Wilson, 2006), exemplar (Baeck, Windey & Op de Beeck, 2012), and orientation (Baeck et al., 2012; Husk, Bennet, & Sekuler, 2007).

In the current study, we aimed to directly test the involvement of the lateral occipital (LO) cortex in object learning, by making use of transcranial direct current stimulation (tDCS), a stimulation technique that modulates cortical excitability by reversibly modifying the resting state neuronal membrane potential area (Bindman, Lippold, & Redfearn, 1964; Purpura & McMurry, 1965). Based on the direction of the current flow, a distinction can be made between anodal and cathodal tDCS. Anodal stimulation results in depolarization of neuronal membranes and thus increases neuronal excitability, whereas cathodal stimulation hyperpolarizes neurons and has the opposite effect. Previously, it has been shown that tDCS applied to the visual cortex can affect performance on visual tasks (Antal, Nitsche, & Paulus, 2006). For example, anodal stimulation of V1 resulted in a reduced surround suppression (Spiegel, Hansen, Byblow, & Thompson, 2012). Kraft et al. (2010) found an increased contrast sensitivity after anodal stimulation of the visual cortex, but not after cathodal or sham stimulation. Regarding visuo-motor learning, participants showed increased performance on a tracking task after anodal stimulation of MT during training (Antal et al., 2004b). Using an object detection task, Clark et al. (2012) showed that anodal stimulation over the right inferior frontal and right parietal cortex resulted in a larger training effect. Further investigation revealed that the enhanced training was caused by an improvement in perceptual sensitivity (Falcone, Coffman, Clark, & Parasuraman, 2012). Although another stimulation technique, namely transcranial magnetic stimulation (TMS), has been used over LO in a few studies (Pitcher, Charles, Devlin, Walsh, & Duchaine, 2009) including in the context of perceptual learning (Chang, Mevorach, Kourtzi, & Welchman, 2014; note that simple stimuli instead of objects were used in this study), to our knowledge, no study has yet investigated the effect of tDCS on LO or on object learning.

When studying object learning, studies mostly require participants to direct their attention to the visual stimuli they are trained to recognize. Performance after training is then compared between the trained objects and objects that were not encountered during training. However, several studies using simple stimuli have provided evidence that conscious effort is not always necessary for perceptual learning to occur. Then, participants' attention is not focused on the to-be-learned stimuli, but is directed elsewhere by presenting them with a task that is irrelevant to the investigated learning process. For example, in one study (Watanabe, Nanez, & Sasaki, 2001), a coherently moving dynamic dot display was presented in the background, with a letter presented in the middle of the screen. Participants were performing a letter identification task. In a later test phase, participants were asked to report the direction of the coherently moving dots. The repetitive exposure to the moving dots displays in the earlier phase had improved the participants' performance in the later test phase. Thus, though participants do not direct their attention to the irrelevant stimuli during the learning sessions, these studies show a learning effect evidenced by improvements in identifying, discriminating, or detecting the irrelevant (for the training task) features (e.g., Dinse, Ragert, Pleger, Schwenkreis, & Tegenthoff, 2003; Seitz & Watanabe, 2003), although this effect has not been found consistently (Ahissar & Hochstein, 1993; Shiu & Pashler, 1992). Task-irrelevant learning only occurs when the irrelevant stimulus is paired with a target (Pilly, Grossberg, & Seitz, 2010; Seitz & Watanabe, 2003) and when the irrelevant feature is weak (Tsushima, Seitz, & Watanabe, 2008). With the current study, we aim to investigate whether task-irrelevant learning also occurs for more complex stimuli, namely pictures of common objects. If not, and if there is a significant difference in learning between relevant and irrelevant objects, then we have evidence that mere exposure is not enough to induce the training effects induced with relevant objects.

The current study was designed to investigate the effect of tDCS targeted at the lateral occipital (LO) cortex on task relevant and irrelevant object learning. Participants were trained in two tasks: one relevant to object recognition (object naming in a backward masking task) and one where the object was presented in the background but not relevant for the training task. The object-irrelevant task had to meet some requirements: It had to be difficult enough, so participants would direct their attention to this object-irrelevant task rather than the objects; it had to be possible to present the stimulus for the irrelevant task simultaneously with the objects, without covering too much of the object image; and we aimed to control for the visual input participants were exposed to during both tasks. An orientation discrimination task on the fixation line was developed. As participants have to report the orientation at each trial, every trial is a "target trial," allowing for task-irrelevant learning on the objects to occur (Pilly et al., 2010; Seitz & Watanabe, 2003). Anodal or sham tDCS targeted at right LO was delivered during the training over multiple days in both the object-relevant and object-irrelevant task. In a test session, participants were tested on their ability to name the objects presented during the object-relevant task, during the object-

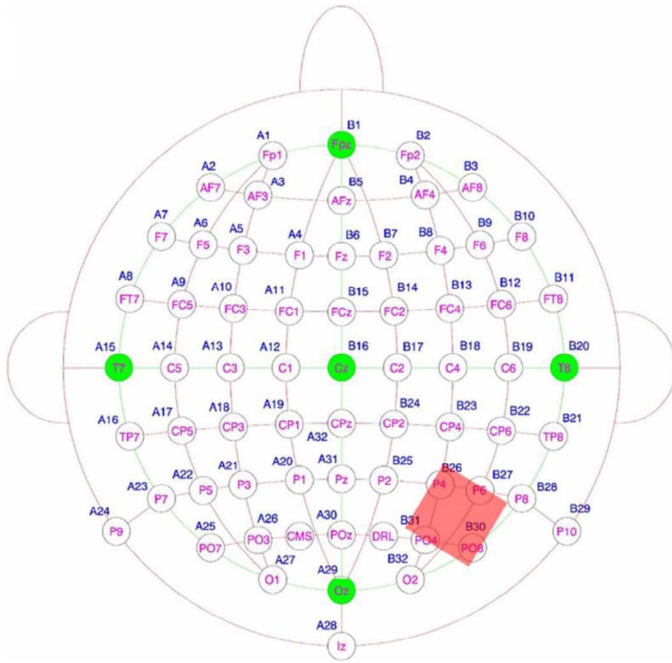

Figure 1. The location of the anode (red patch) was determined using an international 10-20 EEG system cap (BioSemi). Figure retrieved and adapted from http://www.biosemi.com/download.htm.

irrelevant task and a set of objects to which they were not yet exposed. We found that the group of participants stimulated with anodal tDCS during training showed an increased ability to name the trained objects compared to participants in the sham condition. No evidence for irrelevant learning of the complex objects was found.

Method

Participants

Participants were 24 naïve paid volunteers (19 female, five male) aged between 17 and 29 years (mean: 21.208 years) recruited through the social network of the experimenters, the laboratory's participant database, and the online recruitment system of the Faculty of Psychology and Educational Sciences at the University of Leuven (KU Leuven). The two experimental groups were matched in age, $t(22) = 0.857$, $p = 0.401$. All participants had normal or corrected-to-normal vision, had no history of neurological problems, no metal implants other than dental fillings, and were right-handed. In case of doubt on this last criterion, a handedness questionnaire was assessed (Van Strien, 1992). One participant was excluded based on the handedness questionnaire. Data from one other participant were discarded because said participant misunderstood the instructions of the behavioral task. Both participants were not included in the final group of 24 participants. The study was approved by the ethical committee of the Faculty of Psychology and Educational Sciences of KU Leuven. All participants signed an informed consent form prior to each session.

Apparatus

Stimulus presentation was controlled with a Dell desktop (GX-780) running Windows XP on a 16-inch monitor with a resolution of 1024×768 pixels and a frame rate of 100 Hz (Dell, Inc., Round Rock, TX). MATLAB (MathWorks, Inc., Natick, MA) and the Psychophysics Toolbox 3 (Brainard, 1997) were used to program the experiment. Viewing distance was approximately 80 cm. The room was darkened during stimulus presentation.

A NeuroConn DC Stimulator Plus (version 4.1.00.17, neuroConn GmbH, Ilmenau, Germany) was used to deliver a direct current through a pair of 5×5 cm rubber electrodes, placed inside 5.5×5 cm sponges. Before each use, the sponges were soaked in a 0.9% sodium chloride solution. The electrodes were kept in place on the scalp with nonconductive rubber straps. The electrodes, sponges, and straps were from the same manufacturer as the DC Stimulator. The device automatically checks the impedance at the start of stimulation and stimulation does not proceed unless impedance levels are within recommended limits (lower than 55 kΩ) to ensure subject safety. The DC Stimulator continuously monitors the impedance to maintain the user-defined current amplitude throughout the stimulation session.

We used an international 10-20 EEG system cap (BioSemi B. V., Amsterdam, The Netherlands) to locate the stimulation site for each individual participant before the experiment was started. Given that with tDCS only unilateral stimulation is possible, the right LO region was selected for stimulation. There is some evidence that the object learning effect is stronger in right compared with left LOC (Op de Beeck et al., 2006; van der Linden et al., 2008, Vanni, Revonsuo, Saarinen, & Hari, 1996), although the hemispheric difference was not always retrieved (e.g., Gillebert et al., 2009). While participants were wearing the EEG cap, we measured the distance from the nasion to reference point Pz, and the distance from reference point Pz to the center of the square formed by reference points P4, P6, PO4, and PO8 (Figure 1). Participants were asked to take off the cap and the measured distances were used to place the electrode in the correct position. The reference electrode was placed on the left upper arm.

Stimuli

The stimuli comprised four distinct stimulus sets each containing 20 gray-scale pictures of everyday living and nonliving objects with a resolution of 450 by 450 pixels (approximately 10.8 visual degrees). Stimulus contrast was reduced to 12.5% of the original contrast to increase the difficulty of recognizing the objects. The experimenters estimated through pilot testing that all stimulus sets had approximately equal difficulty. Masking stimuli consisted of small fragments (70 by 70 pixels) of all different object pictures. Whole masking stimuli were the same size as the object stimuli (450 by 450 pixels). All stimuli were gamma corrected to create a linear luminescence range. Given that this correction reduced the overall contrast of the images, an inverse gamma-correction was applied to the masking stimuli to create a more robust masking effect.

Experimental tasks

The goal of this study was to provide insight into both relevant and irrelevant perceptual learning of objects. Hence, participants performed alternately two distinct tasks during the experiment: an object-relevant task and an object-irrelevant task.

Object-relevant task

In the object-relevant task, participants were instructed to identify the presented objects (Figure 2). Each trial started with presentation of a fixation point for 400 ms, followed by a stimulus shown for a variable time. Each stimulus was followed by three masks with a total duration of 250 ms to prevent further visual processing. Next, a blank screen was shown, which signaled that a response could be made. Participants were instructed to type the first three letters of the name of the object that was presented. They received feedback after each trial. The duration of presentation of each stimulus was determined through three interleaved two-down, one-up staircases: During the first trial of a run, the stimulus was presented for 120 ms. The duration of the stimulus presentation shortened by 10 ms (one frame at a refresh rate of 100 Hz) after two consecutive correct answers within one staircase, and increased with 10 ms after one incorrect answer. To keep visual input as similar as possible between the two tasks, a small red line (width: 1 pixel, height: 10 pixels or approximately 0.2 visual degrees) also was presented on top of the object stimulus for 120 ms. The orientation angle of this line was determined by the orientation angles of the participant's previous run of the object-irrelevant task, or by the orientation angles of a median staircase of a pilot group (n = 7) if no object-irrelevant run preceded the current object-relevant run.

Object-irrelevant task

The object-irrelevant task was an orientation discrimination task (Figure 2). The stimulus presentation was similar to the presentation during the object-relevant task: Each trial started with the presentation of a fixation point, then a small red line on top of an object image was presented, followed by three mask images (Figure 2). The small red line (width: 1 pixel, height: 10 pixels, i.e., approximately 0.2 visual degrees) with a variable orientation angle was shown for 120 ms. Participants were instructed to report whether the line was oriented rather vertically or horizontally. They responded by pressing one of two buttons ("h" for horizontal and "l" for vertical) when a blank screen at the end of the trial appeared. Participants received feedback after each trial. The orientation angle of the red line was determined through three interleaved two-down, one-up staircases: During the first trial of a run, the orientation angle of the red line was oriented 12° away from the diagonal meridian (thus had an angle of either 33° for a vertical trial, or 57° for a horizontal trial) and orientation shifted 1° closer to diagonal after two consecutive correct answers, and shifted 1° away from diagonal after one incorrect answer (Figure 3). During this task, objects from a different stimulus set than the one used in the relevant task were shown in the background. Since participants had to focus on the orientation discrimination task, attention was not primarily directed towards these objects, to allow for irrelevant learning. Presentation duration of these objects was determined by the presentation duration of the participant's previous run of the object-relevant task, or by the presentation durations of a median staircase of a pilot group of participants (n = 7), if no object-relevant run preceded the current object-irrelevant run. The objects in the background were masked in the same way as during the object-relevant task. This way, visual input was equated as much as possible between the two tasks. Note that presentation duration of the red line was constant at 120 ms, even when the presentation duration of the background objects could be much shorter. In these cases, the red line was presented on top of the masks for as long as was needed to reach 120 ms.

tDCS procedure

For the anodal stimulation group, the current was initially ramped up to an intensity of 1000 μA over 1 s,

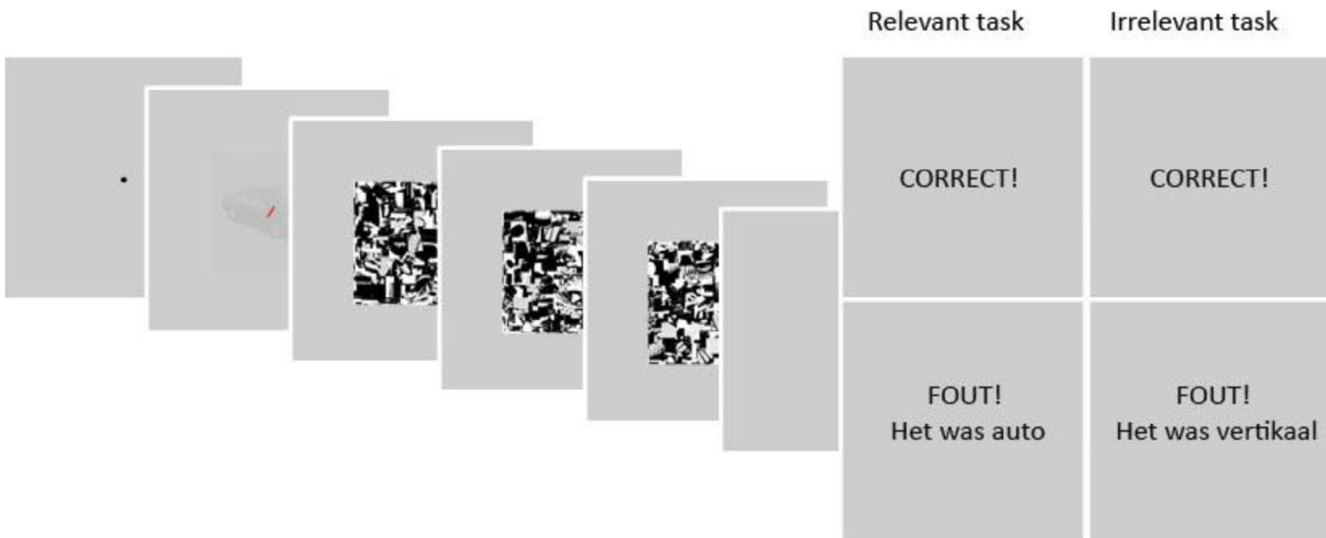

Figure 2. Example of one trial: In either task the presentation of the stimulus and masks were the same, only the required response and corresponding feedback differed over tasks. (A) Object-relevant task: the object stimulus in this example trial is a car ("auto"). If participants typed "aut," this resulted in the feedback "CORRECT!" being shown. If participants gave another response, then "FOUT! Het was auto" (English: "WRONG! It was car") appeared. (B) Object-irrelevant task: The red line presented on the background image is more vertically than horizontally oriented in this trial. If participants typed "l," this resulted in the feedback "CORRECT!" being shown. If participants typed "h" instead, then "FOUT! Het was vertikaal" (English: "WRONG! It was vertical") appeared. The size of the fixation line in the Figure is increased compared with the presentation during the experiment for illustration purposes.

followed by 30 min of anodal stimulation at 1000 μA (density 40 $\mu A/cm^2$) with a similar ramp-down period at the end of the session. For the sham group, the initial ramp-up and final ramp-down were mimicked, but no stimulation was given during the 30-min period in between. Participants were divided in an anodal stimulation and sham group using a double-blind procedure: During training days that included tDCS stimulation, two experimenters were present. Only one of the experimenters handled the tDCS apparatus and knew the participant's group. Except for the initial phase during which the electrodes were attached to the participant's head and stimulation was started, there was no interaction between the first experimenter and the participants. The second experimenter, ignorant to the stimulation condition, instructed the participant. Stimulation was started at the same time as the behavioral experiment. Since the behavioral testing lasted longer than 30 min, a small part of the behavioral test was conducted immediately after the stimulation. Aftereffects of tDCS for the visual cortex have been shown to be relatively short compared with other cortical areas, where aftereffects can last up to 1 hr (Nitsche & Paulus, 2000), and to decay over time (Antal, Kincses, Nische, Bartfai, & Paulus, 2003, Lang et al., 2007). The duration of the behavioral training after the 30-min tDCS stimulation had ended was on average approximately 6 min. As most of the behavioral training was conducted during stimulation, and the remaining (small) part immediately after stimulation, we can assume that the effects of tDCS on cortical excitability were present for almost all or even all of the session. Since the object-relevant and object-irrelevant tasks (and thus also the presentation of the relevant and irrelevant stimulus sets) were alternated and the order was counterbalanced over participants in both groups, any difference in behavioral outcome between performance for the relevant and irrelevant stimulus sets on the last day cannot be attributed to the stimulation duration during training.

Procedure during training and test days

Participants completed three training sessions and one test session on four separate days within one week (Figure 4). The duration of the first training session was approximately one hour and a half. All other sessions lasted for approximately 1 hr.

The first session started with a preview of each of the four stimulus sets (20 stimuli per set). Each object accompanied by its name was shown for 2 s, allowing participants to associate the pictures with their correct names. This preview has also been applied in all previous studies with this paradigm (Baeck et al., 2012, 2013; Furmanski & Engel, 2000). The same preview procedure would be repeated on the following training and testing days, with the exception that the baseline set was only presented on day 1 (leaving 60 of the 80 stimuli to preview again on day 2 to 4). After the preview, instructions for the object-relevant task were

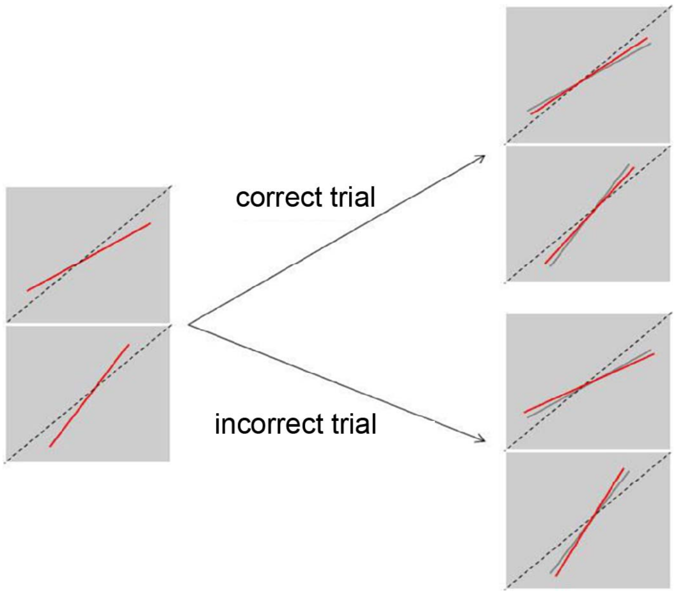

Figure 3. First steps of the orientation angle staircase. Dotted lines represent the diagonal meridian. Gray lines in the panels on the right represent the red line on the previous trial. Note that neither the diagonal meridian nor the gray lines were presented in the experiment. For each pair of panels, the upper one represents a horizontal trial, and the lower one represents a vertical trial. During the first trial (left panels), the orientation angle of the red line is either 33° or 57°. After two consecutive correct trials, orientation shifted towards the diagonal meridian (upper right panels). After an error, orientation shifted away from the diagonal meridian (lower right panels). Sizes in this Figure are for illustration purposes only and do not correspond to those used in the experiment.

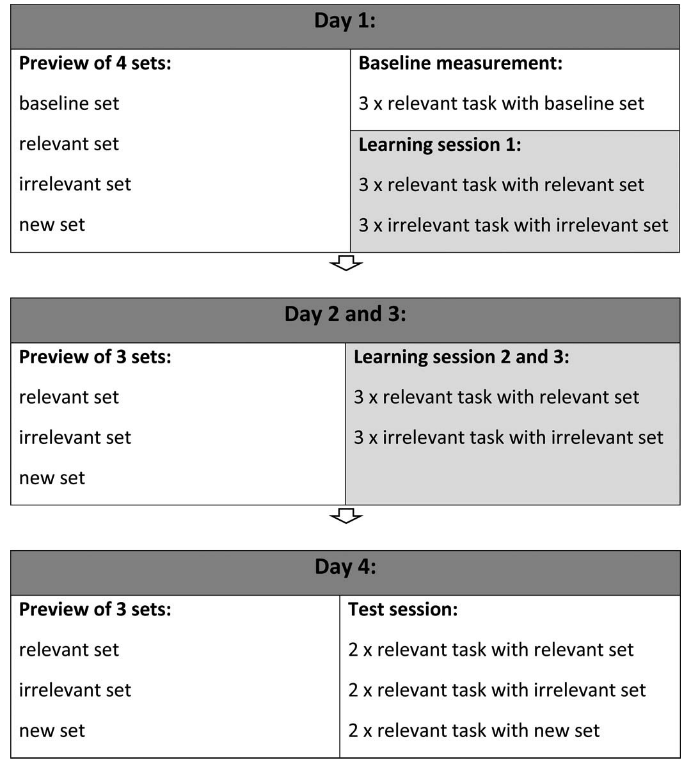

Figure 4. Procedure of the study: overview of the stimulus sets and tasks presented during the training and test days. Stimulation (anodal or sham) was applied during learning sessions, indicated by a light-gray background.

given. Participants first completed three runs of this task each containing 120 trials with one stimulus set. The 120 trials include all three interleaved staircases, i.e., each staircase had 40 trials with each object in the set presented twice. This set will further be called the baseline stimulus set, as these runs were considered a baseline measure to compare initial performance between participant groups. After the baseline measurement, participants received instructions for the following six runs, which alternated between the object-relevant and the object-irrelevant task. Participants had to complete three runs for the object-relevant task and three runs for the object-irrelevant task. The exact alternation order of object sets and tasks was unique for each pair of participants consisting of one person from the stimulation group and one person from the sham group. The object-relevant task had the same characteristics as described for the baseline measure, but a different stimulus set was used. We further refer to this stimulus set as the relevant stimulus set. For the object-irrelevant task, (unattended) objects of a third stimulus set were presented in the background. This stimulus set is called the irrelevant stimulus set. At the start of these last six runs, anodal or sham stimulation was started for a duration of 30 min.

The second and third learning sessions were identical to the first, except that they only consisted of six runs: three runs with the object-relevant task and three runs with the object-irrelevant task. As on the first day, the runs of the object-relevant and object-irrelevant task were interleaved. The baseline stimulus set was no longer presented in the preview. Stimulation was applied during these training sessions.

During the test session on the fourth day, participants completed six runs of the object-relevant task: two runs using the relevant stimulus set, two using the irrelevant stimulus set and two using the remaining stimulus set, further called the new stimulus set. The testing was preceded by a preview of these three stimulus sets. Again, the exact alternation order was unique for each pair of participants consisting of one person from the stimulation group and one person from the sham group. No stimulation was applied during the test session. The stimulus sets were balanced across participants: Each stimulus set was used equally often as baseline stimulus set, relevant stimulus set, irrelevant stimulus set, and new stimulus set. The content of the relevant task and the

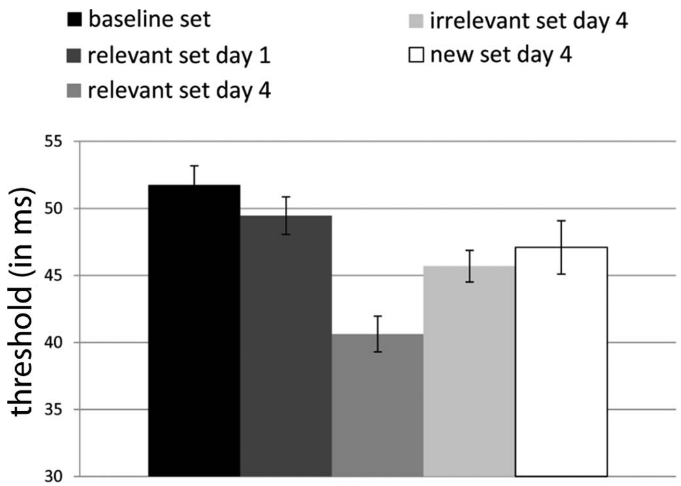

Figure 5. Thresholds from the first and last day are plotted as a function of the stimulus set.

length per run stayed the same during all learning and test sessions.

Data analysis

For each participant, perceptual thresholds were estimated for each run of the object-relevant task on each day. The experiment consisted of adaptive two-down, one-up staircases, which means that the endpoints of these staircases approximate the exposure duration at which participants are able to correctly identify the objects in 70.7% of the trials (Leek, 2001). These endpoints were averaged across the three staircases within a run and across runs of the same task and stimulus set on the same day for each participant, in the same way as done before in earlier studies using the same paradigm (Baeck & Op de Beeck, 2010; Baeck et al., 2013). A mixed-model analysis of variance (ANOVA) with the thresholds for the relevant stimulus set as the dependent variable was used to clarify the overall effect of participant group (anodal stimulation or sham group), time (training and test days, i.e., days 1 to 4) and their interaction on the perceptual thresholds. Two repeated-measures ANOVAs tested for the effect of training within each group. In addition, a priori paired and two-sample *t* tests were used to test for day-to-day improvements, object specificity, and irrelevant learning.

Results

Baseline measurement

When comparing the baseline measurements between both groups, no significant difference was found, $t(22) = 1.232$, $p = 0.227$. Thus, no initial performance difference between both groups was present. In both groups the performance for the baseline set and for the relevant stimulus set during the first day did not differ [anodal stimulation group: $t(11) = 1.639$, $p = 0.129$; sham group: $t(11) = 0.645$, $p = 0.532$], indicating that there was no within-session effect of the tDCS stimulation and no rapid learning effect (Figure 5). Because of the absence of these effects, for further analyses comparing the data from the test day to pretraining performances, the data from the relevant stimulus set on the first day will be used.

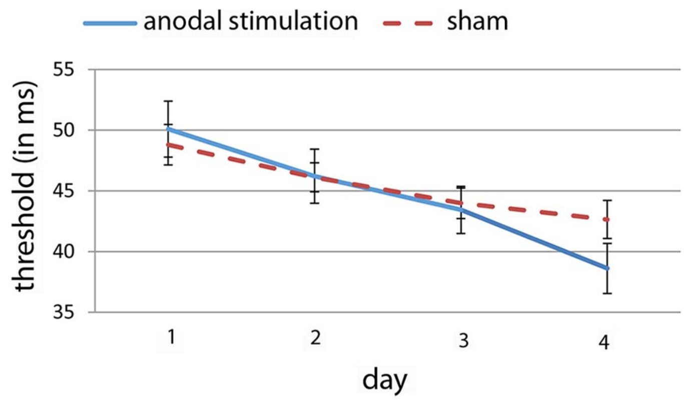

Figure 6. Thresholds for the relevant stimulus set are plotted as a function of time and stimulation group.

Effect of training and tDCS

The mixed-model ANOVA with time (training and test days, i.e., days 1 to 4) as the within-subject variable and group (anodal stimulation or sham) as the between-subject variable revealed a significant main effect of time, $F(3, 66) = 35.743$, $p < 0.001$; no main effect of group, $F(1, 22) = 0.116$, $p = 0.736$; and most interestingly, a significant interaction between time and group, $F(3, 66) = 3.341$, $p = 0.024$, on the thresholds of the relevant stimulus set. This interaction implies that the effect of training was not the same for both groups (Figure 6).

The effect of training in the object-relevant task was evident in both groups, as revealed by two separate repeated-measures ANOVAs [sham group: $F(3, 33) = 15.62$, $p < 0.001$; anodal stimulation group: $F(3, 33) = 21.19$, $p < 0.001$]. In the sham group, thresholds gradually declined from 48.80 ms ($SEM = 1.67$) on the first day to 42.64 ms ($SEM = 1.57$) on the fourth day, $t(11) = 6.297$, $p < 0.001$. In the anodal stimulation group, thresholds declined from 50.09 ms ($SEM = 2.31$) to 38.61 ms [$SEM = 2.06$; $t(11) = 7.332$, $p < 0.001$].

A two-sample *t* test was used to get a better understanding of the interaction between time and group. The improvement of the anodal stimulation

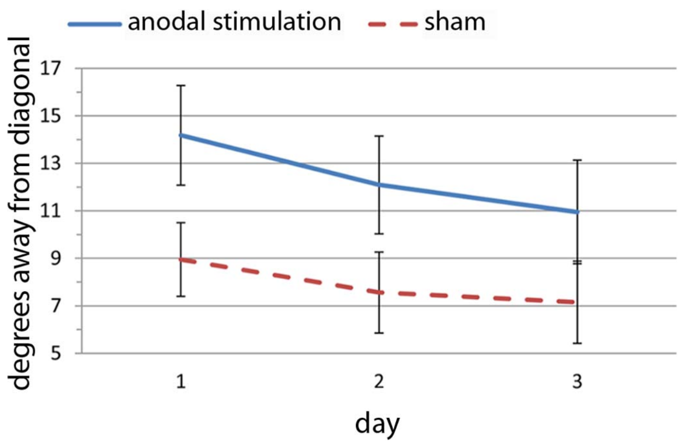

Figure 7. Results of the object-irrelevant orientation task. Thresholds are plotted as a function of time and stimulation group.

group, measured as the difference in threshold between the first and the last day (11.48 ms, $SEM = 1.57$) was significantly higher than the improvement of the sham group [6.16 ms, $SEM = 0.98$; $t(22) = 2.884$, $p = 0.009$]. Thus, anodal stimulation affected how much perceptual learning had occurred after four days.

Additionally, we verified whether participants got better at performing the object-irrelevant task (Figure 7). Although a learning effect in that task is not the focus of interest of this study, its presence would increase our confidence that participants' attention was directed to the object-irrelevant task. Thresholds were calculated for each day, in the same way as was done for the object-relevant task. The thresholds are measured in number of degrees away from the diagonal, and approximate the orientation at which participants are able to correctly discriminate between horizontal and vertical in 70.7% of the trials (Leek, 2001). The repeated-measures ANOVA revealed no effect of group, $F(1, 22) = 2.97$, $p = 0.099$); a main effect of time [day 1 to 3; $F(2, 44) = 12.09$, $p < 0.001$]; and no interaction, $F(2, 44) = 0.92$, $p = 0.408$). We note that there is a trend towards a difference ($p < 0.1$) between the groups, but this trend is nonsignificant, and thus might reflect random fluctuations. In the sham group, the effect of time was significant, $F(2, 22) = 5.82$, $p = 0.009$), with thresholds declining from 8.95° ($SEM = 1.55$) on the first day to 7.15° ($SEM = 1.73$) on the third day. The effect of time also remained significant in the anodal stimulation group, $F(2, 22) = 6.77$, $p = 0.005$, with thresholds declining from 14.18° ($SEM = 2.10$) to 10.95° ($SEM = 2.18$). Performance on the object-irrelevant task thus improved over time with no difference between the groups in the amount of learning, $t(22) = -1.305$, $p = 0.206$), indicating that participants in both groups were sufficiently engaged in the object-irrelevant task.

Irrelevant learning

The testing day naming thresholds for the irrelevant stimulus set were compared with those of the new stimulus set (Figure 5). In this way, it could be verified whether there was evidence for irrelevant learning. In particular, irrelevant learning should be reflected by a better performance for the irrelevant stimulus set than for the completely new stimulus set.

Thresholds for the irrelevant and new stimulus set did not differ in either of the groups [sham group: 47.08 ms, $SEM = 1.45$ (irrelevant) and 49.44 ms, $SEM = 3.17$ (new), $t(11) = -0.866$, $p = 0.405$; anodal stimulation group: 44.31 ms, $SEM = 1.84$ (irrelevant) and 44.72 ms, $SEM = 2.38$, $t(11) = -0.200$, $p = 0.847$]. As the amount of irrelevant learning, measured as the difference in threshold between the irrelevant and the new stimulus set, did not differ between participant groups, $t(22) = 0.56$, $p = 0.578$, the data of both groups were collapsed. No evidence was found for irrelevant learning, as the thresholds for the irrelevant set (45.69 ms, $SEM = 1.18$) and the new stimulus set (47.09 ms, $SEM = 2.00$) did not differ, $t(22) = 0.823$, $p = 0.419$ (Figure 5). We can conclude that being exposed to the stimuli before testing did not make any difference for the performance when participants were not trained in the object-relevant task with this stimulus set.

Object specificity

Performance on the object-relevant task for the new stimulus set was compared with performance for the relevant stimulus set on the first day and on the last day to assess whether the learning effect was specific to the trained objects. As no difference in transfer of performance was found between groups, $t(22) = 1.608$, $p = 0.122$, data of both groups were collapsed.

Thresholds were lower for the trained relevant stimulus set on the last day (40.63 ms, $SEM = 1.33$) than for the new stimulus set (47.09 ms, $SEM = 2.00$) and this difference was significant, $t(23) = 3.916$, $p = 0.001$ (Figure 5). Thus, participants were better at recognizing trained objects than they were at recognizing new objects that were never encountered during training. Thresholds for the new stimulus set did not differ from those for the relevant set on day 1 (49.45 ms, $SEM = 1.40$; $t(23) = 1.224$, $p = 0.223$). The training effect was thus object specific.

For the sake of being complete, we also present the results for the two groups separately. In the sham group, thresholds for the trained relevant stimulus set on the last day (42.64 ms, $SEM = 1.57$) were lower than those for the new stimulus set [49.44 ms, $SEM = 3.17$, $t(11) = -2.619$, $p = 0.024$], while thresholds for the new stimulus set did not differ from those for the relevant set on the first day [48.8 ms, $SEM = 1.67$; $t(11) = -0.207$, $p = 0.84$]. The training effect is thus object specific in the sham group. In the anodal stimulation group, thresholds were again lower for the trained relevant stimulus set on the last day (38.61 ms, $SEM = 2.06$) than for the new stimulus set [44.72 ms, $SEM = 2.38$; $t(11) = -2.849$, $p = 0.016$]. Contrary to the results in the sham group, thresholds for the new stimulus set were lower than those for the relevant set on the first day [50.09 ms, $SEM = 2.31$; $t(11) = 2.644$, $p = 0.023$]. Thus, in the group that received tDCS, the learning effect seems to have slightly transferred to a new stimulus set. Nonetheless, it remains important to not assign too much importance to this effect since, as has been noted previously, the absolute differences in the amount of transfer do not differ between the groups, $t(22) = 1.608$, $p = 0.122$.

Discussion

The aim of this study was twofold. First, we wanted to investigate the effect of tDCS targeted at right LO on object learning. Second, we tested whether task-irrelevant learning is possible when complex everyday objects are used. We found that when participants received anodal stimulation during training, they improved more on the relevant trained objects than participants in the sham group. For neither group, a transfer of performance to untrained stimuli was found, regardless whether participants were already exposed to these new stimuli during the object-irrelevant task or not.

Effect of tDCS on LO

The main finding of the current manuscript was a significantly better learning effect in an object recognition task for participants who were stimulated with anodal tDCS during training compared with participants receiving sham stimulation. The anodal electrode was placed over the square formed by P4, P6, PO4, and PO8 (Figure 1), hence targeting the lateral occipital cortex (LO). This result is in accordance with the abundance of studies pointing to LO as a key area for object learning (for a review, see Bi & Fang, 2013; Kourtzi & DiCarlo, 2006) and the upcoming field of research showing that visual functions can be transiently altered by applying tDCS on the visual cortex (for a review, see Antal & Paulus, 2008). While the modulatory effect of tDCS was previously only tested for lower visual regions as V1 (Antal, Kincses, Nische, Bartfai, & Paulus, 2004a; Antal, Nitsche, Kruse, Hoffman, & Paulus, 2004b; Costa, Nagy, Barboni, Boggio, & Ventura, 2012; Spiegel et al., 2012) and MT (e.g., Antal et al., 2004b), this is the first study targeting lateral occipital cortex during object learning. We localized our target region using the 10-20 EEG system cap. Though this is a rather crude localization measurement, it was widely used in tDCS research and is very likely to select the target area, definitely when the poor spatial resolution of tDCS is considered (Cohen Kadosh, 2015). We must, however, note that this study does not provide evidence that this effect is specific to stimulation of the LO region. Using a double-blind procedure, we compared anodal versus sham stimulation targeting LO, but we did not include control regions in this study. With this study alone, we cannot exclude that stimulation of other regions in the (visual) human cortex would lead to the same results. Further, while some studies (e.g., Holland et al., 2011) found a local effect of tDCS, there is also evidence that, in addition to the targeted area, tDCS can affect a more distributed network that is functionally connected to the stimulated region (Keeser et al., 2011; Meinzer et al., 2013). It is for instance possible that apart from LO the right inferior parietal lobule (IPL) was also affected by our stimulation. TMS over P4—situated very close to the center of our stimulation electrode—has been shown to affect this region that is implemented in visual attention (Rushworth & Taylor, 2006). One observation that suggests at least some degree of neural specificity to our stimulation site is the lack of an effect of tDCS in the orientation discrimination task, a task recruiting early visual regions (V1, V2). Null results are always difficult to interpret and a direct comparison between both tasks is further hampered by the absence of a fourth testing day for the orientation discrimination task. However, it is relevant to note that, as far as a (nonsignificant) difference between both participant groups was found, this trend was in the direction opposite to what would be expected if the anodal stimulation would improve learning in the orientation discrimination task, e.g., because it would also target early visual regions. At the very least, the results of the orientation discrimination task do not provide any suggestive evidence that such a general effect would be occurring. Our study thus suggests that direct stimulation targeted at LO through tDCS influences the amount of object learning, and follow-up research could include control sites and adapt the stimulation parameters to enhance stimulation specificity and further investigate the role of LO in object learning.

Researchers have previously tried to infer the cortical level of learning in a more indirect way, for example by looking at the specificity of perceptual learning. As mentioned in the Introduction, object learning has been found to generalize partially or completely over aspects to which LO shows invariance, such as size (Furmanski & Engel, 2000; Lee, Matsumiyo, & Wilson, 2006), exemplar (Baeck et al., 2012), and orientation (Baeck et al., 2012; Husk et al., 2007).

These indirect inferences are consistent with a role of LO in object learning and thus provide converging evidence for our own results acquired through direct stimulation targeted at LO.

It should be noted that the positive effect of anodal tDCS stimulation only manifested itself in a larger improvement from the first to the last day for the anodal stimulation group than for the sham group, and that the groups' performances did not differ significantly from each other on any of the days [day 1: $t(22) = -0.45$, $p = 0.654$; day 2: $t(22) = -0.04$, $p = 0.971$; day 3: $t(22) = 0.24$, $p = 0.813$; day 4: $t(22) = 1.56$, $p = 0.134$]. We used an online stimulation paradigm, i.e., stimulation was always applied during (the largest portion of the) task performance. A study by Pirulli, Fertonani, and Miniussi (2013) suggests that for visual areas, offline anodal stimulation before the task might result in larger effects than online stimulation. Future studies could verify whether using an offline stimulation paradigm increases the difference between the groups. We did not find evidence for a within-session effect of tDCS, as no difference in performance was found between the baseline stimulus set and the relevant stimulus set on the first day for the anodal stimulation group. This indicates that tDCS did not have immediate effects on performance but instead affected learning overnight. This can also explain why learning in the anodal stimulation group—and as a result the difference in improvement between the groups—still increased from the third to the last day, $t(11) = 2.79$, $p = 0.018$, even when no stimulation was given on that last day. In a study by Peters, Thompson, Merabet, Wu, & Shams (2013), a baseline measure was conducted on both testing days. Similar to our study, no improvement between baseline and stimulation performance on the same day was found, irrespective of the stimulation group (anodal, cathodal, sham). They did find a significant improvement for the cathodal and sham group from day 1 to day 2 baseline measures. Since they did not find a significant improvement from day 1 to day 2 baseline measures in the anodal stimulation group, the researchers hypothesized that anodal stimulation blocked the overnight consolidation of perceptual learning. We must, however, note that their results, where anodal stimulation hinders learning instead of facilitating it, are rather atypical in the literature, and that when performance during anodal stimulation (instead of day 2 baseline) was compared with day 1 baseline measures, they did find evidence for an improvement.

Task-irrelevant learning and transfer to new stimuli

We did not find a transfer of learning performance to a new set of stimuli. This object specificity is in accordance with several earlier studies on object learning, although the degree of specificity varies over studies. In some studies, the same complete object specificity is found (Baeck & Op de Beeck, 2010; Baeck et al., 2012), whereas other studies found evidence for a small transfer towards the new stimuli, although they never reached the same performance as with the trained stimulus set (Baeck et al., 2013; Furmanski & Engel, 2000; Grill-Spector et al., 2000). However, in all studies, large interindividual differences were reported.

For the current study, this stimulus set was most useful as a comparison for the irrelevant stimulus set: In case irrelevant learning is possible for object images, participants should show a better recognition performance for the irrelevant stimulus set compared with the completely new stimulus set. However, when mere exposure to stimuli is not sufficient, and explicit training is needed for a learning effect to occur, no difference in performance between the irrelevant and the completely new object stimulus set will be found. This last effect is what we observed: Participants did not show a transfer of performance towards the irrelevant stimulus set. An alternative way to test for specificity is the comparison between performance for the irrelevant stimulus set and the relevant stimulus set on the first day. When data of both groups were taken together, thresholds for the irrelevant stimulus set (45.69 ms, $SEM = 1.18$) were lower than those for the relevant set on day 1 [49.44 ms, $SEM = 1.40$; $t(23) = -2.505$, $p = 0.02$], suggesting that there is partial transfer of learning to the irrelevant set. We would like to note, though, that this test entangles the effects of irrelevant learning and transfer of learning, and thus its results are difficult to interpret. In earlier studies, the occurrence of task-irrelevant learning has been reported for simple stimuli (e.g., Dinse et al., 2003; Gutnisky, Hanse, Iliescu, & Dragoi, 2009; Ludwig & Skrandies, 2002; Paffen, Verstrate, & Vidnyanszky, 2008; Seitz, Nanez, Holloway, & Watanabe, 2006; Seitz & Watanabe, 2003; but see Ahissar & Hochstein, 1993; Shiu & Pashler, 1992) and for the integration of local elements in contours (Rosenthal & Humphreys, 2010).

This study was one of the first to investigate task-irrelevant learning in complex objects. On that account, the paradigm used here differs from designs used in other studies, including studies with simple stimuli, and we do not intend to generalize our results to draw conclusions about the existence of irrelevant learning in general. A study by Wong, Folstein, and Gauthier (2011), using a different design, suggests that task-irrelevant learning is possible in complex stimuli. Participants' performance at differentiating between similar-looking complex meaningless shapes called Ziggerins improved after receiving training in orientation discrimination of these stimuli. Our study differs from the study by Wong and colleagues in different ways. We use everyday objects as stimuli for the object-relevant task instead of meaningless shapes. In the study by Wong and colleagues, relevant and irrelevant features (shape identity and orientation) are different aspects of the same stimuli. The object-relevant and object-irrelevant tasks are performed on the same set of stimuli, but attending to one of the features while ignoring the other. In our study, on the other hand, relevant and irrelevant features are separated since they belong to different stimuli and performing the object-relevant and object-irrelevant tasks requires attending to one stimulus (either a complex object or a simple red line) while ignoring the other. Possibly task-irrelevant learning occurs more easily when complex task-irrelevant features are part of the relevant stimulus than when they belong to a different stimulus, because the relevant stimulus has already been selected for attention and entered visual short term memory. Following this line of thought, it would be more plausible for the attention system to filter out complete irrelevant background objects compared with shutting out irrelevant features of a stimulus that has already been encoded. Another possibility is that irrelevant learning of objects requires longer presentation times than relevant object learning, and thus equating presentation times of the irrelevant objects to those of the objects of the last object-relevant run in our study might have prevented irrelevant learning. Note that presentation times in the study by Wong and colleagues (150 ms) were longer than the presentation times of the irrelevant objects in our study (ranging from 23 to 120 ms), but that they presented eight objects at once, making it difficult to compare the two studies on this aspect.

Previous studies have found a few conditions the design should meet in order to enable task-irrelevant learning. One condition comes from the finding that task-irrelevant learning is not the result from mere exposure of the irrelevant stimuli, but that learning of the irrelevant stimulus or stimulus feature is related to the task participants were performing during the training phase (Seitz & Watanabe, 2005). For example, when the training task is a target-detection task, task-irrelevant learning only occurs for the irrelevant features that were paired with a target trial (Pilly, Grossberg, & Seitz, 2010; Rosenthal & Humphreys, 2010; Seitz & Watanabe, 2003). However, as in the current study participants have to report the orientation at each trial, every trial can be considered a "target trial." In this task, the irrelevant object image is also presented at the same time as the relevant oriented line. Another condition is the spatial relationship between the stimuli for both tasks: The closer the spatial proximity, the more task-irrelevant learning is found (Nishina et al., 2007). As the object image and the red fixation line in the current study were superimposed, this can also not explain the absence of a task-irrelevant learning effect. Tsushima et al. (2008) suggested that task-irrelevant learning is only possible when the irrelevant feature is weak because of attentional inhibition of suprathreshold irrelevant stimuli or stimulus features. In the current study, object images were presented at very low contrast to impede recognition. Some participants in our study even reported that they were not aware that the object images were presented during the orientation discrimination task. This should not have prevented them from learning the object images, as previous research has shown that task-irrelevant learning is possible for below-threshold stimuli (Watanabe et al., 2001). However, another aspect of the design might have prevented the participants from learning the irrelevant object set: the masking of the object stimuli. Meuwese, Post, Scholte, and Lamme (2013) showed that backward masking can effectively interfere with task-irrelevant learning. We should, however, note that their masking procedure differs from ours, as in the study of Meuwese et al. (2013) masking was used to prevent participants from perceiving the stimuli ("perceptual blindness"), whereas in our study masking was used to increase the difficulty level of object recognition by preventing further visual processing after the object image disappeared. It was thus still possible for our participants to perceive the stimuli if they would attend to them, as the visual presentation of the objects was the same as the presentation during the relevant task, where participants' performance proves they are able to perceive the stimuli. Thus, whether or not the conclusion of Meuwese et al. (2013) applies to the current study remains to be tested, possibly by investigating task-irrelevant learning of complex object images using a different paradigm such as the simultaneous noise addition paradigm (Rainer & Miller, 2000).

Remarks on the object recognition task

The object recognition task depends also upon cognitive processes beyond perception, as it requires accurate name memorization, memory retrieval, and typing skill. When participants correctly identify an object but mistype, their response will be counted as an error. Accordingly, the lack of irrelevant learning and of transfer of object learning might be caused simply by less opportunities of memorization and of name retrieval, or errors in typing. For consistency with the literature it is useful to keep this task paradigm, given that it has been used multiple times in our lab as well as other labs in studies on object learning (Baeck & Op de Beeck, 2010; Baeck et al., 2013; Baeck, Windey, & Op de Beeck, 2012; Furmanski & Engel, 2000). Changing the object-relevant task would preclude clear comparisons with these previous studies. Nevertheless, we performed an additional analysis to verify whether typing errors significantly influenced the results. Given our adaptive design, early trials still reflect asymptotic performance levels, in contrast to the late trials that reflect threshold performance. The difference between this asymptote and perfect performance reflects interfering factors such as distraction, memory failure, semantic aspects, and typing errors. For every participant, we calculated the performance for the first 10 trials per staircase, and averaged across staircases and runs for the same stimulus set on the same day. Mean first-10-trials-performance for the relevant stimulus set across participants was high (day 1: 92.23%, day 2: 97.27%, day 3: 97.84%, day 4: 98.53%), indicating that typing errors were rather uncommon. A mixed-model ANOVA on the first-10-trials-performance of the relevant stimulus set revealed a main effect of time, $F(3, 33) = 49.102$, $p < 0.0001$, no main effect of group, $F(1, 22) = 0.252$, $p = 0.62$, and no interaction between time and group, $F(3, 66) = 0.616$, $p = 0.607$. Although the main effect of time on the first-10-trials-performance could indicate that part of our learning effect is not only present in the thresholds but also in the asymptotes, it has to be noted that only the improvement from day 1 to day 2 was significant, $t(23) = -7.786$, $p < 0.0001$, and that performance was already high on the first day, suggesting that typing errors cannot explain the observed learning effect and are too uncommon to be problematic. The absence of a main effect of and interaction with group indicates that tDCS did not affect performance in the asymptote. This is especially important to note since the two tasks that were used (object recognition and orientation discrimination) do not only differ in their perceptual processes but also in the opportunity for typing errors, semantic processes, and memory retrieval. The lack of an effect of tDCS on the first-10-trials-performance for the object recognition task strengthens our assertion that the effect can be attributed to a change in the perceptual processes, and not a change in one of the potential interfering factors. Moreover, mean asymptotic performance for the irrelevant stimulus set on the last day (94.6%) did not differ from that for the new set [94.14%, $t(23) = 0.69$, $p = 0.497$], which shows that typing errors do not explain the lack of irrelevant learning. On the other hand, asymptotic performance for the new set was worse than that for the relevant set on the last day, $t(23) = 5.145$, $p < 0.0001$, while not being different from that of the relevant set on the first day, $t(23) = -2.031$, $p = 0.054$. As a consequence, the possibility that typing errors partly explain the lack of transfer to the new stimulus set cannot be excluded.

Conclusion

To summarize, participants stimulated with anodal tDCS targeted at right LO during training showed a larger improvement of performance in an object recognition task compared with participants in the sham condition. No within-session benefits of anodal tDCS were found, only a positive learning effect after multiple training sessions. This study thus suggests a causal role of LO in object learning, although more targeted studies on the specific role of LO are needed. Further, no transfer of the learning effect was found on the test day for completely new objects and objects that were previously presented in another task setting, and for which participants were not trained to recognize them. Thus, mere exposure is not sufficient for object learning as implemented in our paradigm.

Keywords: perceptual learning, task irrelevant learning, object recognition, tDCS

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