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The role of prefrontal and parietal cortices in esthetic appreciation of representational and abstract art: A TMS study

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ABSTRACT

To explain the biological foundations of art appreciation is to explain one of our species' distinctive traits. Previous neuroimaging and electrophysiological studies have pointed to the prefrontal and the parietal cortex as two critical regions mediating esthetic appreciation of visual art. In this study, we applied transcranial magnetic stimulation (TMS) over the left prefrontal cortex and the right posterior parietal cortex while participants were evaluating whether they liked, and by how much, a particular painting. By depolarizing cell membranes in the targeted regions, TMS transiently interferes with the activity of specific cortical areas, which allows clarifying their role in a given task. Our results show that both regions play a fundamental role in mediating esthetic appreciation. Critically though, the effects of TMS varied depending on the type of art considered (i.e. representational vs. abstract) and on participants' a-priori inclination toward one or the other.

Introduction

Art is created and appreciated in all human cultures. It is used to convey fundamental spiritual, ethical, and philosophical meaning, and it serves diverse economic, social, political, and symbolic functions all around the world (Anderson, 1989, 2004). Not only is art common to all human groups, it is a uniquely human trait. To explain the biological foundations of art, thus, is to explain a distinctive aspect of our species.

During the last decade, brain lesion and neuroimaging studies have provided insight into the cognitive and neural underpinnings of esthetic appreciation (Cela-Conde et al., 2011; Chatterjee, 2011). These studies have espoused the view – broadly shared within cognitive neuroscience – that "'Mind' can only be regarded, for scientific purposes, as the activity of the brain" (Hebb, 1949, p. xiv). In this sense, their chief aim is to understand how brain activity engenders and modulates esthetic experience. Nevertheless, it does not follow from this that esthetic experience can be regarded a purely biological phenomenon, free from cultural influence. The example of reading provides a clear illustration of the extent to which nature and culture are actually indissoluble (Chatterjee, 2014). Although writing is a recent cultural invention, reading words is consistently related to activity in a remarkably specific brain region of the left fusiform gyrus, known as the *visual word form area*, though obviously only in the case of literate people (McCandliss et al., 2003). Thus, it is not by nature that this region is involved in reading. Still, its structural and functional features are coopted to solve the cognitive challenges posed by writing and reading, only when these activities are part of the individual's cultural environment. Although much less is known about the environmental susceptibility of the neural underpinnings of esthetic experience, training and experience have a significant modulating effect on them (Pang et al., 2013; Wiesmann and Ishai, 2010, 2011). This suggests that, like reading, the cultural milieu, personal experience, and learning, shape the development of esthetic experience and its neural foundations.

Esthetic appreciation relies on the activity in a broadly distributed network of brain regions. In addition to cortical and subcortical regions related to pleasure and reward (e.g., Ishizu and Zeki, 2011; Kawabata and Zeki, 2004; Lacey et al., 2011; Salimpoor et al., 2013), frontal cortical areas involved in decision-making and evaluation (e.g., Cela-Conde et al., 2004; Cupchik et al., 2009), as well as various cortical areas related to perception (e.g., Cela-Conde et al., 2009; Lacey et al., 2011; Vartanian and Goel, 2004), have been identified as key neural substrates of esthetic appreciation (Nadal and Pearce, 2011).

More specifically, several studies have observed increased activity in the left dorsolateral prefrontal cortex (L-DLPFC) and in the posterior parietal cortex (PPC) (especially in the right hemisphere, R-PPC) while participants viewed esthetically pleasing images (Cela-Conde et al., 2004, 2009; Cupchik et al., 2009; Lengger et al., 2007; Vartanian and

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Goel, 2004; Vessel et al., 2012). Whereas DLPFC activity is usually interpreted as reflecting evaluation processes involved in esthetic preference and the orientation toward esthetic qualities of the stimuli (Cela-Conde et al., 2004; Cupchik et al., 2009; Lengger et al., 2007), parietal activation has been related to enhancement of spatial processing and the elaboration of object representations (Cela-Conde et al., 2009; Cupchik et al., 2009). Both the lateral prefrontal and the posterior parietal cortices appear to be integral elements of a frontocaudal network whose synchronized activity is related with the detailed appraisal of visual esthetic features (Cela-Conde et al., 2013). Nevertheless, there are at least three issues that call for further research.

First, the pattern of prefrontal and parietal activity registered in neuroimaging studies during esthetic evaluation seems to vary depending on the abstract-representational dimension of the stimuli (Fairhall and Ishai, 2008). Lengger et al. (2007) found greater activity in left DLPFC and PPC while participants viewed representational images than while they viewed abstract ones. However, most of the studies investigating neural correlates of art appreciation used exclusively (or mostly) representational stimuli (e.g., Cupchik et al., 2009; Vessel et al., 2012), and studies that included a balanced set of stimuli, collapsed both categories for subsequent analysis (e.g., Cela-Conde et al., 2004, 2009). This makes it impossible to determine whether activity in prefrontal and parietal activity associated with the esthetic appreciation is related specifically with representational stimuli, or with any sort of visual stimuli that are appreciated esthetically.

Second, the aforementioned neuroimaging studies have overlooked well-known individual differences in preference for abstract and representational art (Vessel and Rubin, 2010). Clearly, only limited headway can be made by sidestepping what Dewey (1934) referred to as the human contribution to the experience of art: The spectator's agency in the elaboration of a response to an artwork, and the key role of certain personal aspects in this constructive process, including prior experience, knowledge and personal preferences (Leder et al., 2004). In relation to the latter, it is well known that people generally prefer representational to abstract artworks (Furnham and Walker, 2001; Kettlewell et al., 1990; Knapp and Wulff, 1963; Pihko et al., 2011). Many people, however, also value and enjoy abstract art. The reasons for this difference in the appreciation of abstract art relate to the degree of art interest and knowledge, to the extent to which people engage in art-related activities, and to certain personality traits, especially openness to experience and non-conformity. Research shows that openness to experience, certain early learning events and parental attitudes can encourage people to engage in art-related activities, such as visiting museums and galleries or taking art classes (Chamorro-Premuzic et al., 2009; Feist and Brady, 2004; Furnham and Walker, 2001; McManus and Furnham, 2006). In time, such experiences shape people's attitudes toward art and enrich their knowledge about art forms, movements, and artists. In turn, these attitudes and knowledge lead to differences in the depth with which people are able to engage with art. Cupchik and Gebotys (1988) showed that artistically naïve people's approach to art can be viewed as an extension of everyday perception. Thus, they operate mainly with object schemes and search for recognizable elements that can elicit pleasant associations. Experienced art viewers, on the other hand, are able to approach art with deeper sensory schemes that enable them to derive meaning from the art medium and the sensory effects it affords. These differences in the way naïve and experienced people search for meaning in art are intertwined with their attitudes and beliefs about art. Winston and Cupchik's (1992) results indicate that naïve people's tendency to respond to qualities of art that provide pleasant feelings is related to their belief that art should please, evoke peaceful feelings and positive memories, and appeal to many people. In contrast, experienced people's response to stylistic and expressive qualities of art is related to their belief that art should challenge the viewer's conception of the world, express the artist's deep feelings, and require some effort from the viewer. This tightly interwoven complex of beliefs about art, additional schemas, and openness, enhances some people's appreciation and enjoyment of abstract art (Silvia, 2006). At present, however, very little is known about how such personal general preferences are related with brain activity involved in esthetic appreciation.

Finally, most of the neuroimaging and electrophysiological findings related to the neural underpinnings of esthetic appreciation have involved the recording of brain activity under certain conditions or while performing certain tasks. Although certainly valuable in itself, this strategy does not allow drawing conclusions about the causal efficiency of brain regions in esthetic experience. Colas and Hsieh (2013), for instance, did demonstrate that prefrontal cortices have a causal role in esthetic appreciation. Their study showed that esthetic evaluation of abstract fractal art could be predicted from pre-stimulus patterns of BOLD fMRI signals across a distributed network of frontal regions before the stimuli were presented. However, as acknowledged by the authors themselves, pre-stimulus frontal activity may significantly bias value-based decisions only when stimuli are ambiguous, as in case of fractal flames (Colas and Hsieh, 2013). Conversely, in evaluating stimuli for which individuals may already have strong preferences (as in the case of our study in which paintings were used), pre-stimulus activity per se is unlikely to be significantly predictive of the esthetic decision (Colas and Hsieh, 2013). In a recent study employing brain stimulation, Cattaneo et al. (2013) used direct current stimulation (tDCS) to explore the direct relation between brain activity and art appreciation. Their results showed that increasing activity in the left DLPFC caused an enhancement of the esthetic appreciation of figurative images (Cattaneo et al., 2013). However, the spatial and temporal resolution of tDCS is lower than other techniques, such as Transcranial Magnetic Stimulation (TMS), and participants' a priori preference for a specific art style was not taken into account.

The present study aims to surpass the aforementioned shortcomings by using Transcranial Magnetic Stimulation (TMS) to determine the causal role of prefrontal and parietal cortices in mediating esthetic appreciation of art. Specifically, we applied triple-pulse TMS to induce transient disruption in the underlying neural activity (e.g., Kadosh et al., 2007), over the left DLPFC and right PPC of participants engaged in evaluating whether, and how much, they liked a series of representational and abstract paintings. Critically, individual preference for abstract and representational art was considered by recruiting an equal number of participants that showed a biased inclination for either category. In light of neuroimaging evidence showing a positive correlation between activity in prefrontal regions and visual esthetic appreciation (e.g., Cela-Conde et al., 2004) we expected TMS delivered to DLPFC to decrease participants' overall appreciation of the presented artworks. In addition, we expected TMS over PPC to also decrease liking, but mainly so for representational art, in light of previous evidence suggesting that the PPC involvement in esthetic evaluation may be related to the activation of objects' recognition mechanisms, with objects typically being not as discernible in abstract compared to representational artworks (Cela-Conde et al., 2009; Cupchik et al., 2009; Lengger et al., 2007).

Method

Participants

Twenty participants (13 F, mean age = 22.6 ys, SD = 2.2, range = 19–27) with no previous training or special interest in art, volunteered to participate in this study. All were right handed, as assessed by a test for handedness (Oldfield, 1971), and all had normal, or corrected to normal, vision including color perception. A short test administered at the recruitment stage (see Supplementary material) ensured that an equal number of participants preferring representational to abstract paintings vs. preferring abstract to representational paintings were recruited. Henceforth we use the term *general preference* to refer to this classification. The term *liking* will be used to refer to the responses participants gave in the experiment described below. Prior to the experiment, each participant filled out a questionnaire (translated from Rossi et al., 2011) to evaluate any contraindications related to the use of TMS. Written informed consent was obtained from all participants before the experiment was conducted. The protocol was approved by the local ethical committee and participants were treated in accordance with the Declaration of Helsinki.

Stimuli

Stimuli consisted of 72 reproductions of artistic representational paintings and 72 abstract paintings belonging to a set of images used in previous magnetoencephalography (MEG) studies of esthetic appreciation (Cela-Conde et al., 2004, 2009). All representational stimuli contained depicted objects, whereas all abstract stimuli lacked any discernible representation of objects. This distinction is grounded on the fact that abstraction in art aims to break with the traditional representation of visible reality, and to free itself from the portrayal of objects (Barasch, 1998). Thus, by definition, abstraction implies the lack of representation, and the exclusive reliance on purely formal elements, such as color, stroke, line, composition, or texture (Townsend, 2006). Representational paintings comprised realist, impressionist and postimpressionist artworks. None of the paintings contained close views of humans in order to avoid the activation of facial-recognition brain mechanisms. Stimuli were adjusted for level of luminance, color spectrum, and visual complexity (see Cela-Conde et al., 2004, for details). The 144 paintings used in the experiment were selected from a larger set of 200 paintings (100 representational and 100 abstract) on the basis of a pilot rating study (see Supplementary Material).

Procedure

The timeline of an experimental trial is shown in Fig. 1. Participants were seated in front of a 17″ PC (1280 ∗ 800 pixels) screen at an approximate distance of 57 cm, in a normal-lightened and silent room, and asked to perform a computerized rating task. Each trial started with a fixation cross presented for 2500 ms on a white background. This was followed by a 250 ms white screen after which a painting (subtending approximately 10 × 10 degrees of visual angle) was presented in the central field of view. Participants were instructed to indicate as fast as possible whether they liked the painting or not by left/right key pressing with their right index and middle finger. Response key assignment for yes/no responses was counterbalanced across participants. Response was immediately followed by a white screen with the sequence "1 2 3 4 5 6 7" (Likert scale) presented at the bottom. Participants were asked to use a keyboard to select the number that corresponded to their appreciation of the previously shown image, where 1 meant "I do not like it at all" and 7 "I like it very much". There was no temporal restriction on this second response. After the response, a new trial started. Stimuli were split into two sets (matched in terms of liking scores as assessed in the rating experiment), comprising of 36 representational and 36 abstract images each. Participants were first presented with the same set three consecutive times (one for each TMS condition). After a short break, the second set was presented with the order of stimulated sites being reversed compared to the first half of the experiment. The order of set and TMS sites was counterbalanced across participants so as to exclude any carry over effects related to stimulation site or previously viewed sets.

Transcranial magnetic stimulation

In TMS, the rapidly changing electric field induced by the magnetic pulse causes depolarization of cell membranes and the initiation of an action potential. The behavioral effects of TMS have been described in terms of induction of noise in the neural mechanisms that underlie specific cognitive processes (Miniussi et al., 2013), and are dependent on the activation state of the targeted regions (Silvanto and Cattaneo, 2014). Because of the temporal and spatial precision of these transient alterations, TMS can be used to characterize the involvement of a specific cortical brain region in the performance of motor, perceptual or cognitive tasks (Robertson et al., 2003).

TMS was delivered using a Magstim Rapid2 stimulator (Magstim Co Ltd, Whitland, UK) connected to a 70 mm butterfly coil at a fixed intensity of 60% of the maximum stimulator output. A fixed intensity was used in accordance with previous studies on visual perception (Pitcher

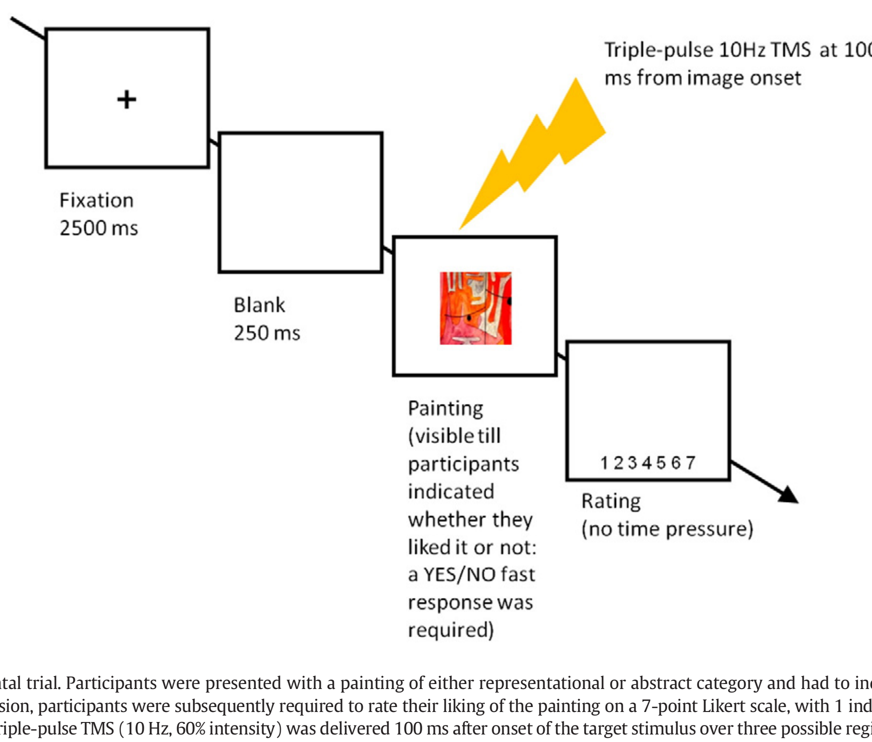

Fig. 1. Timeline of an experimental trial. Participants were presented with a painting of either representational or abstract category and had to indicate whether they liked it as fast as possible. After the yes/no decision, participants were subsequently required to rate their liking of the painting on a 7-point Likert scale, with 1 indicating "I do not like it at all" and 7 indicating "I like it very much". Triple-pulse TMS (10 Hz, 60% intensity) was delivered 100 ms after onset of the target stimulus over three possible regions: the left dorsolateral prefrontal cortex (L-DLPFC), the right posterior parietal cortex (R-PPC) and the vertex.

et al., 2007). TMS was delivered to the left DLPFC and to the right PPC on the basis of previous MEG evidence investigating esthetic appreciation of visual artworks (Cela-Conde et al., 2004, 2009). To localize the left DLPFC and the right PPC, we placed the TMS coil over F3 and P4, respectively, according to the 10–20 electroencephalogram (EEG) coordinate system (Herwig et al., 2003) using commercially available 10–20 EEG stretch caps. Importantly, previous TMS studies demonstrated the reliability of this localization method for the areas we targeted (Knoch et al., 2009; Prime et al., 2008). In addition to the two target sites, vertex was used as a control site for nonspecific effects of TMS caused by noise and tactile sensations. The vertex was localized as a midpoint between the inion and the nasion and equidistant from the left and right intertrachial notches. For the left DLPFC and the right PPC, the coil was initially oriented with an angle of approximately 45° from the nasion-inion line and the handle pointing outwards, and hence adjusted for each participant in order to minimize discomfort. For the vertex, the coil was oriented tangentially to the scalp parallel to the nasion-inion line. The pitch and roll angles were set in order to minimize the distance between the scalp and the cerebral target. Three TMS pulses were delivered at 10 Hz (pulse gap of 100 ms) 100 ms after the onset of each painting. We chose to use triple-pulse 10 Hz TMS on the basis of previous studies showing that these stimulation parameters were effective in interfering with underlying cortical activity (see Kadosh et al., 2007; Saad and Silvanto, 2013). Moreover, triple-pulse 10 Hz TMS allows to cover an early time window in which a first esthetic impression is likely to be formed: indeed, previous electrophysiological and MEG evidence suggests that a first esthetic evaluation of visual stimuli may occur as early as 300–400 ms from stimulus onset (e.g., Cela-Conde et al., 2009; de Tommaso et al., 2008; Jacobsen and Hofel, 2003; Sbriscia-Fioretti et al., 2013; Wang et al., 2012). Prior to the experiment, short practice blocks (with stimuli different compared to those used in the experiment) were performed in order to familiarize participants with the task and sensations generated by TMS pulses. The software E-prime 2.0 (Psychology Software Tools, Pittsburgh, PA) was used for stimuli presentation, data collection and TMS triggering. The whole experiment lasted approximately 90 min.

Results

Mean frequencies (percentage scores) of “I like it” responses were calculated for each participant in each TMS condition. Mean response latencies (RT, ms) for all responses were also registered. Finally, mean rating scores for the second more detailed judgment (Likert scale) were calculated.

Dichotomous liking response (“I like it”/“I do not like it”)

The percentage of “I like it” responses in the control (vertex) condition confirmed that participants had been appropriately assigned to either the “representational-preferred” vs. “abstract-preferred” group. Indeed, *all* participants that had shown higher general preference for representational/abstract over abstract/representational art in the pre-experiment test manifested the same pattern here. This was also confirmed by correlational analyses showing a highly significant positive correlation between general preference, as assessed by the pre-test experiment, and liking scores awarded in the control condition of the TMS experiment for both yes/no responses (Pearson two-tailed $r = .901$, $p < .001$), and the Likert-scale rating scores ($r = .828$, $p < .001$).

Mean percentages of “I like it” responses for each group of participants and the two art categories in the different TMS conditions are reported in Fig. 2. A repeated-measures ANOVA with TMS condition (vertex, L-DLPFC, and R-PPC) and art category (representational vs. abstract) as within-subjects variable and group (i.e., general preference for one art category) as between-subjects variable was carried out on percentages of “I like it” responses. As hypothesized, the ANOVA revealed a significant interaction art category by group, $F(1,18) = 48.82$, $p < .001$, $\eta_p^2 = .73$: participants classified on the basis of the pre-experiment test as generally preferring representational art showed overall higher liking for representational over abstract art in the TMS experiment, $t(9) = 5.52$, $p < .001$; participants with a greater a priori general preference for abstract art showed overall higher liking for abstract art over representational art in the TMS experiment, $t(9) = 4.29$, $p = .002$. The main effect of TMS, $F(2,36) = 10.31$, $p < .001$, $\eta_p^2 = .36$, the interaction TMS by group, $F(2,36) = 5.33$, $p = .009$, $\eta_p^2 = .23$, and the three-way interaction art category by TMS condition by group, $F(2, 36) = 8.81$, $p = .001$, $\eta_p^2 = .33$, were significant. Neither the main effect of group ($p = .65$) nor the main effect of art category ($p = .14$) reached significance. The effect of TMS and the interaction of TMS by group were analyzed in light of the three-way significant interaction. In particular, we looked at the effect of TMS on appreciation of abstract and representational artworks in the two different groups of participants.

In participants generally preferring representational art, a repeated-measures ANOVA with art category and TMS condition as within-subjects variable indicated a significant effect of art category, $F(1,9) = 30.43$, $p < .001$, $\eta_p^2 = .77$, a significant effect of TMS, $F(2,18) = 8.36$, $p = .003$, $\eta_p^2 = .48$, and a significant interaction TMS condition by art category, $F(2,18) = 4.70$, $p = .023$, $\eta_p^2 = .34$. Post-hoc comparisons (Bonferroni–Holm correction applied) showed that TMS over

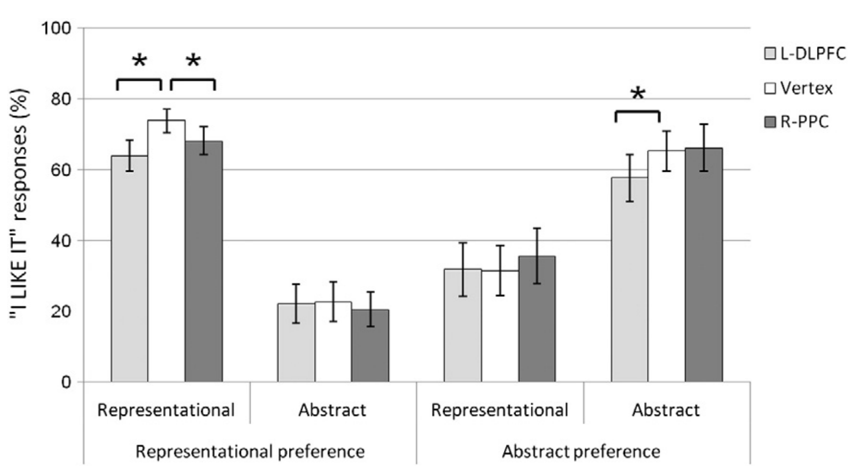

Fig. 2. Frequency histograms for “I like it” responses as a function of participants' general preference for representational or abstract art and art category. TMS over the L-DLPFC selectively reduced appreciation for the preferred type of art. TMS over the R-PPC selectively reduced appreciation for representational artworks, but only in participants preferring representational art. Error bars depict ± 1 SEM. Asterisks indicate that the difference between two conditions reached significance.

the L-DLPFC significantly reduced liking for representational artworks compared to the vertex control stimulation, $t(9) = 3.53$, $p = .018$, whereas it did not affect liking for abstract artworks ($p = .63$). Similarly, TMS over the R-PPC significantly reduced number of "I like it" responses for representational paintings compared to the vertex condition, $t(9) = 4.16$, $p = .008$, but left liking for abstract artworks unaffected ($p = .25$).

In participants generally preferring abstract paintings, a similar analysis showed a significant effect of art category, $F(1,9) = 18.42$, $p = .002$, $\eta_p^2 = .67$, a significant effect of TMS, $F(2,18) = 7.46$, $p = .004$, $\eta_p^2 = .45$, and a significant interaction TMS condition by art category, $F(2,18) = 4.11$, $p = .034$, $\eta_p^2 = .31$. Post-hoc comparisons (Bonferroni–Holm correction applied) showed that TMS over L-DLPFC significantly reduced liking for abstract paintings compared to the vertex control stimulation condition, $t(9) = 3.53$, $p = .012$, whereas it did not affect liking for representational paintings ($p = .78$). TMS over the R-PPC did not significantly affect liking in these individuals for either representational paintings ($p = .26$) or abstract paintings ($p = .71$).

Mean response latencies

Mean response latencies (for all responses) for participants preferring representational art and participants preferring abstract art in each TMS condition and for each art category are reported in Fig. 3a. A repeated-measures ANOVA with TMS condition (L-DLPFC, R-PPC and vertex) and art category (representational vs. abstract) as within-subjects variable and group (i.e., general preference for representational or for abstract art) as between-subjects variable only revealed a significant interaction art category by group, $F(1,18) = 7.34$, $p = .014$, $\eta_p^2 = .29$. Post-hoc comparisons (Bonferroni–Holm correction applied) showed that participants who generally preferred representational art took significantly longer to judge representational artworks than abstract artworks, $t(9) = 3.66$, $p = .005$, whereas no difference in RT for the two art categories was reported in participants who generally preferred abstract art ($p = .61$). None of the main effects or of the remaining interactions reached significance (all $ps > .05$). Further analyses considering the type of response given and collapsing for TMS condition showed that, overall, liking responses took longer than disliking responses, $t(19) = 2.24$, $p = .038$. Moreover, participants who generally preferred abstract art were significantly slower in expressing their liking for representational than for abstract art, $t(9) = 4.28$, $p = .002$, and tended to be faster (but not significantly so) in expressing dislike for representational than abstract paintings ($p = .17$). Participants who generally preferred representational art were equally fast in deciding that they liked a painting irrespective of its category ($p = .46$), but they were significantly faster in disliking abstract than representational paintings, $t(9) = 5.09$, $p = .001$.

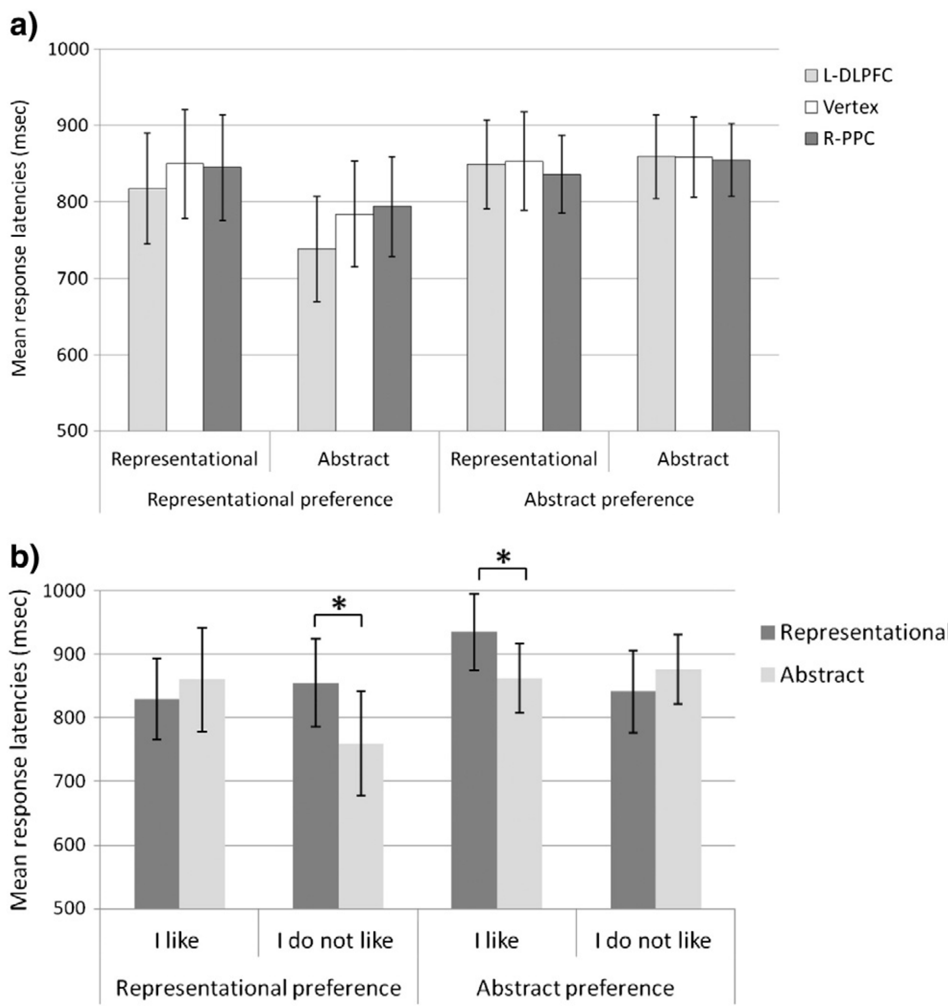

Fig. 3. a) Participants' mean response latencies (RT, ms) in deciding whether they liked a painting or not as a function of participants' general preference for representational or abstract art and art category. TMS did not affect RT. b) Participants' RT (ms) as a function of participants' preference for representational or abstract art and art category (collapsed across TMS conditions). Error bars depict ± 1 SEM. Asterisks indicate that the difference between two conditions reached significance.

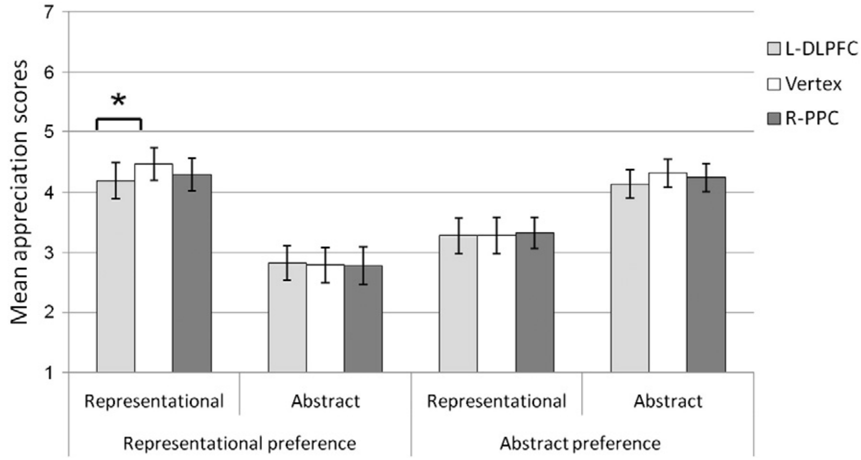

Fig. 4. Participants' mean rating scores on a 7-point Likert scale expressing how much they liked a particular painting. For participants generally preferring representational art, TMS over the L-DLPFC significantly reduced appreciation of representational artworks, with a similar trend observed for stimulation of R-PPC. No effect of TMS was observed in participants preferring abstract art. Error bars depict ± 1 SEM. Asterisks indicate that the difference between two conditions reached significance.

Mean liking scores

Mean liking scores (Likert scale 1–7) for abstract and representational paintings as a function of general preference are shown in Fig. 4. A repeated-measures ANOVA with TMS condition (vertex, L-DLPFC, and R-PPC) and art category (representational vs. abstract) as within-subjects variable and group (i.e., general preference) as between-subjects variable showed a significant interaction art category by group, $F(1,18) = 38.61$, $p < .001$, $\eta_p^2 = .68$, confirming the pattern reported with yes/no responses: participants classified on the basis of the pretest as generally preferring abstract art gave overall higher liking scores to abstract paintings than to representational ones, while the opposite pattern emerged for participants generally preferring representational art. The main effect of TMS was significant, $F(2,36) = 4.28$, $p = .022$, $\eta_p^2 = .19$. The three-way interaction art category by TMS by group was also significant, $F(2,36) = 5.65$, $p = .007$, $\eta_p^2 = .24$. None of the other main effects or interactions reached significance (all *ps* > .16). The main effect of TMS was considered in light of the significant three-way interaction. In particular, we looked at the specific effects of TMS for each art category within the two groups, separately.

In participants who generally prefer representational art, a repeated-measures ANOVA with TMS and art category as within-subjects factors showed a significant effect of art category, $F(1,9) = 30.69$, $p < .001$, $\eta_p^2 = .77$, and a significant interaction TMS by art category, $F(2,18) = 5.14$, $p = .017$, $\eta_p^2 = .36$. The main effect of TMS only approached significance ($p = .058$). Post-hoc comparisons (Bonferroni–Holm correction applied) showed that TMS over the L-DLPFC compared to the vertex condition significantly reduced appreciation of representational artworks in these participants, $t(9) = 3.35$, $p = .036$. A similar trend was observed for R-PPC compared to vertex, $t(9) = 2.28$, $p = .14$ (without correction, $p = .048$). No effect of TMS over either L-DLPFC ($p = .48$) or R-PPC ($p = .82$) compared to vertex was observed on liking scores for abstract artworks.

In participants who generally prefer abstract art, the ANOVA only revealed a significant effect of art category, $F(1,9) = 10.85$, $p = .009$, $\eta_p^2 = .55$, no significant effect of TMS ($p = .229$), and no significant interaction TMS × art category ($p = .285$) for their liking ratings.

Discussion

In this study, we stimulated participants' left DLPFC and right PPC while they decided whether, and how much, they liked abstract and representational paintings. Applying TMS over the left DLPFC caused a reduction in liking for the kind of artwork participants generally preferred, but not the other. When compared to the control condition (i.e., vertex stimulation), thus, participants who generally preferred representational paintings expressed lower liking for representational stimuli (see also Cattaneo et al., 2013), and participants who generally preferred abstract paintings expressed lower liking for abstract stimuli. TMS over the PPC had less clear-cut effects. Only for participants preferring representational paintings did stimulation over this site cause a reduction in liking for the preferred kind of art. Control for a priori preferences has not been included in previous studies investigating the neural correlates associated with art appreciation. Nonetheless, models of esthetic appreciation point to individual stylistic preference as an important factor to be considered (Jacobsen, 2004; Leder et al., 2004). The selective effect of brain stimulation that depended not only on the type of viewed artworks but also on the observer's a priori preference is in line with Leder and colleagues' model (Leder et al., 2004), as well as Dewey's (1934) emphasis on the human contribution to the experience of art.

Our findings show that activity in the left DLPFC has a causal role in the liking for the sort of artworks that are generally preferred, independent of whether the object of appreciation is representational or abstract. What is the functional significance of this finding? It has been suggested that the role of the left DLPFC in esthetic appreciation is to engage an "esthetic orientation" toward the presented stimuli (Cupchik et al., 2009). This view agrees with other studies highlighting the role of the prefrontal cortex in cognitive control over other brain regions, directing attention to the relevant environmental features for the task (Miller and Cohen, 2001; Soga and Kashimori, 2009). Our results suggest that TMS over the left DLPFC interfered with the adoption of an esthetic orientation toward the features that would otherwise have fostered it. Owing to the disruption of top-down processing, cognitive resources might not have been allocated to the search and evaluation of the esthetic qualities of the kind of stimuli that were generally preferred. Such an effect was not observed for the less generally preferred sort of stimuli, presumably because participants orient esthetically toward them to a lesser extent.

Our results show that PPC activity also causally contributes to the liking for representational paintings, though, only in the case of participants who generally prefer representational art. Consistent evidence suggests that conscious perception of global Gestalt (i.e., grouping single features in a meaningful object) is associated with PPC integrity (Culham and Kanwisher, 2001; Zaretskaya et al., 2013). Indeed, patients with bilateral parietal lesions may present simultanagnosia, that is, they can recognize distinct objects of a scene but are unable to perceive its global picture (Wolpert, 1924). The role of PPC in directing spatial attention toward selective features salient for the ongoing task is also well demonstrated (Gottlieb et al., 2009; Soga and Kashimori, 2009), and recognizable objects and semantic content is what lay people primarily focus on when viewing artworks (Cela-Conde et al., 2004; Nodine et al., 1993; Winston and Cupchik, 1992). Accordingly, previous studies using artworks as stimuli reported that parietal activity is more closely tied with processing representational art (in which objects are visible) than abstract or indeterminate art (Fairhall and Ishai, 2008; Wiesmann and Ishai, 2010). The reduction in liking following PPC stimulation may hence be linked to a disruption of Gestalt-like processing related to holistic spatial processing. The fact that this reduction was selective for participants preferring representational art may be less surprising when considering that their esthetic appreciation relies precisely on literal and structured depictions, and on the meaning conveyed by the portrayed objects and the way they are structured in the scene (Chamorro-Premuzic et al., 2009; Furnham and Walker, 2001; Hekkert and van Wieringen, 1996; McManus and Furnham, 2006; Winston and Cupchik, 1992).

For participants who generally preferred representational art, TMS also had an effect on the Likert-ratings, despite the time interval between the presentation of the stimulus and the response. Again, TMS application over left DLPFC reduced liking ratings for representational but not abstract stimuli (with a similar trend being evident for PPC stimulation). No such effect was found for participants who generally preferred abstract art (although a similar pattern was observed in yes/no responses and Likert scores also in these participants, see Figs. 2 and 4). A possible explanation for the stronger effect for participants who generally preferred representational art is that, both in the literature and in the present study, their general preference is more clear cut that that of participants who generally prefer abstract art. Whereas the former not only prefer representational painting, they even tend to reject abstract art, the latter are merely more open to abstract painting, while not clearly rejecting representational art (Feist and Brady, 2004; Furnham and Walker, 2001). In our study, in participants who generally preferred abstract art this may have resulted in less polarized and more variable responses when a more *continuous* type of response (i.e., Likert) was required, making the data somewhat more noisy and possibly masking TMS effects. Thus, some caveats need to be considered when interpreting TMS effects on Likert liking scores in our study. The Likert evaluation always followed the first discrete evaluation (i.e., “I like” vs. “I do not like”). It is hence possible that Likert scores were directly affected by the first (dichotomous) response due to participants' need to be consistent in their judgment. In this view, TMS effects on Likert scores were an indirect consequence of TMS on the first type of judgment required rather than a direct effect of brain stimulation on the second evaluation. Since different Likert scores are consistent with “I like it” decisions (possibly, 7, 6, 5 but also 4 values) and “I do not like it” decisions (possibly, 1, 2, 3 but also 4 values), this variability may have weaken TMS effects on Likert decisions. Future research may clarify these aspects by testing the effects of TMS on Likert scores directly (i.e., not preceded by yes/no responses), thus avoiding confounding effects depending on the use of multiple evaluation measures.

Response latencies were not affected by TMS. Overall, participants took longer to decide that they liked a painting than when they did not like it, in line with previous evidence finding a positive correlation between preference ratings and response latencies (Vartanian and Goel, 2004). Moreover, irrespective of TMS, participants tended to be slower in liking and faster in disliking paintings of the category they did not generally prefer compared to artworks of the category they generally preferred. Effects of TMS are usually reported on response latencies for correct responses or on accuracy, with TMS affecting different variables depending on the specific task requirements (see Kadosh et al., 2010). However, in tasks in which subjective evaluations are assessed as ours, TMS may be more likely to bias response decisions.

It is important to note that our results cannot be explained as a response bias caused by TMS. Because response keys were counterbalanced across participants, it is highly unlikely that stimulation selectively inhibited the “yes” response in the dichotomous response task. Moreover, TMS did not affect responses in all conditions. It had an effect on only one of the two categories of stimuli, and this varied depending on the participants' general preference. It is also worth mentioning that prefrontal stimulation may be more uncomfortable than vertex stimulation in some participants, and that this may affect their responses. However, previous studies found no correlation between level of stimulation discomfort and TMS effects on performance (e.g., Machizawa et al., 2010). Although recent evidence suggests that non-neural effects of TMS may depend on a complex interplay between stimulation timing, site of stimulation and experimental task (e.g., Duecker and Sack, 2013; Duecker et al., 2013), non-neural effects of TMS should have been comparable for all the stimuli presented in our study and not selective for the preferred art-category. Moreover, response latencies should have also been affected (Duecker et al., 2013), whereas no effect of TMS was reported on participants' response latencies. Unspecific effects of TMS are thus unlikely to have played a considerable role in the pattern of performance we reported.

Converging evidence shows that prefrontal and parietal regions are involved in computation of values and in a broad range of decision-making tasks (e.g., Camus et al., 2009; Costa and Averbeck, 2013; Essex et al., 2012; Gold and Shadlen, 2007; Sugrue et al., 2004). Indeed, preference for other types of stimuli, such as faces or food, also involves the frontoparietal network (e.g., Chatterjee et al., 2009; Fregni et al., 2008). Accordingly, we do not claim that the effects we reported here are specific for esthetic appreciation of visual art. There is no evidence for a specific esthetic system in the human brain; rather, esthetic appreciation of visual art is likely to be mediated by cognitive and neural mechanisms involved in processing other kinds of stimuli (e.g., Brown et al., 2011). However, it is also unlikely that the TMS effects we reported were completely independent from the specific object to be evaluated (i.e., artworks). In fact, the contribution of parietal and frontal cortices in different preference judgments is likely to depend on a complex interaction of the rewarding value of the object to be evaluated, the extent to which it requires cognitive evaluation, and evaluator's experience with, and beliefs about, art (Cupchik and Gebotys, 1988; Silvia, 2006; Winston and Cupchik, 1992).

In sum, this study provides causal evidence for the involvement of frontal and parietal cortices in the appreciation of art. Moreover, it points to a selective role of these regions as a function of both stimuli features and personal preferences. These findings corroborate and extend previous evidence showing different cortical activation elicited by representational and abstract artworks (Lengger et al., 2007). Moreover, our analysis of general predilection for abstract and representational painting adds to a line of research exploring how individual differences, such as expertise, influence the underpinnings of art appreciation (Kirk et al., 2011; Pang et al., 2013; Wiesmann and Ishai, 2011). From a methodological perspective, our results highlight the utility of TMS to advance our understanding of the neural processes underlying the complex interactions between object, person, and context that give rise to art appreciation. Finally, if it is true that the history of art begins with that of humanity (Lorblanchet, 2007), our data contribute to shedding light on a fundamental trait of humankind.

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