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The role of the lateral occipital cortex in aesthetic appreciation of representational and abstract paintings: A TMS study

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ABSTRACT

Neuroimaging studies of aesthetic appreciation have shown that activity in the lateral occipital area (LO)—a key node in the object recognition pathway—is modulated by the extent to which visual artworks are liked or found beautiful. However, the available evidence is only correlational. Here we used transcranial magnetic stimulation (TMS) to investigate the putative causal role of LO in the aesthetic appreciation of paintings. In our first experiment, we found that interfering with LO activity during aesthetic appreciation selectively reduced evaluation of representational paintings, leaving appreciation of abstract paintings unaffected. A second experiment demonstrated that, although the perceived clearness of the images overall positively correlated with liking, the detrimental effect of LO TMS on aesthetic appreciation does not owe to TMS reducing perceived clearness. Taken together, our findings suggest that object-recognition mechanisms mediated by LO play a causal role in aesthetic appreciation of representational art.

1. Introduction

The eighteenth century philosopher Friedrich Schiller believed that beauty had the potential to reconcile what he viewed as humans' inherently conflicting sensual (material) and formal (spiritual) essences. The appreciation of beauty, Schiller (1895) argued, emerges from a harmonious relation between intellectual contemplation and bodily sensation, between thinking and feeling. Converging psychological and neurophysiological evidence accumulated during the last fifty years supports Schiller's insight: aesthetic appreciation indeed involves a complex interaction among cognitive, sensorimotor, and emotional processes (Chatterjee, 2011; Chatterjee & Vartanian, 2014; Leder, Belke, Oeberst, & Augustin, 2004; Nadal & Skov, 2013). Neuroimaging and neurophysiological studies continue to shed light on the distributed network of brain regions that underlies aesthetic appreciation (e.g., Cela-Conde et al., 2004, 2009, 2013; Cupchik, Vartanian, Crawley, & Mikulis, 2009; Ishizu & Zeki, 2011; Kawabata & Zeki, 2004; Lacey et al., 2011; Salimpoor et al., 2013; Vartanian & Goel, 2004). However, the specific role of the component regions, and the factors that modulate their activity, require further clarification (Nadal, 2013).

Here we focus our attention on the lateral occipital area (LO). Although LO is a key region within the object recognition pathway, involved in many aspects of objects processing (for reviews, Grill-Spector, 2003; Lacey & Sathian, 2011), such as extracting shape information from both two- and three-dimensional objects (Kourtzi & Kanwisher, 2000; Malach et al., 1995), object size judgments (Eger, Ashburner, Haynes, Dolan, & Rees, 2008; Pourtois, Schwarts, Spiridon, Martuzzi, & Vuilleumier, 2009), and even semantic aspects (i.e., object categorization and naming) (Eger et al., 2008), its functions may go beyond mere shape detection and object recognition. Specifically, LO is one of the brain regions whose activity has been related to aesthetic experience of visual art in neuroimaging studies (Cupchik et al., 2009; Ishizu & Zeki, 2013; Lacey et al., 2011; Vartanian & Goel, 2004). Importantly for our study, Lacey et al. (2011) found that activity in right LO correlated positively with aesthetic evaluation of artistic images. Therefore, it seems that LO activity during the viewing of artworks is not strictly related to the extraction of low-level shape/object information: it is also related to the aesthetic appreciation of an image, at least when the image

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is artistic, and hence more naturally fosters an aesthetic orientation (Huang, Bridge, Kemp, & Parker, 2011; Kirk, Skov, Hulme, Christensen, & Zeki, 2009; Noguchi & Murota, 2013).

However, whether LO plays a *causal* role in aesthetic appreciation of art is currently not known, as available neuroimaging evidence is by definition only correlational. In this study, we aimed to address this issue by using transcranial magnetic stimulation (TMS), given that brain stimulation allows the assessment of causal links between brain activity and behavior (Pascual-Leone, Walsh, & Rothwell, 2000). Previous work has shown the potential of TMS to clarify the role of target brain regions in aesthetic appreciation. For instance, the aesthetic appreciation of human bodies is altered by applying TMS over sensory and motor brain regions (Calvo-Merino, Urgesi, Orgs, Aglioti, & Haggard, 2010; Cazzato, Mele, & Urgesi, 2014). In our study, we presented participants with a series of images, and asked them to indicate whether they liked each of them or not, and to further indicate the extent to which they liked them on a 1–7 Likert scale, while interfering with LO activity using TMS. The images were representational and abstract paintings. Lacey and colleagues only used representational paintings, but there is evidence that aesthetic appreciation of abstract and representational paintings may rely on at least partially different brain mechanisms (e.g., Cattaneo et al., 2014a,b; Lengger, Fischmeister, Leder, & Bauer, 2007). Hence, if the contribution of LO to aesthetic processing is strictly related to object-recognition mechanisms, then TMS over LO should selectively interfere with the appreciation of representational but not abstract artworks, given that the latter lack all discernible object content. If, on the contrary, applying TMS to LO also decreases liking of abstract paintings, the role of LO in aesthetic appreciation must go beyond the mere processing of object information.

2. Experiment 1

2.1. Method

2.1.1. Participants

Fourteen right-handed (Oldfield, 1971) participants (6 males, age: $M = 24.3$ years, $SD = 3.1$) with no previous training or special knowledge about art, volunteered to take part in the study. All had normal, or corrected to normal, vision including color perception (based on self-report) and did not present any contraindications related to the use of transcranial magnetic stimulation (Rossi, Hallett, Rossini, & Pascual-Leone, 2011). Prior to the experiment, participants signed an informed consent. The protocol was approved by the local ethical committee, and participants were treated in accordance with the Declaration of Helsinki.

2.1.2. Stimuli

Stimuli consisted of 80 paintings (see Appendix A for list). Forty abstract and 40 representational paintings were selected from a set of images used in previous work (Cela-Conde et al., 2004, 2009). Twenty-two of the representational stimuli were realistic, and 18 were impressionist or postimpressionist. All of them were created by renowned artists and belonged to the catalogues of European or American museums. In order to avoid the undesired effects of familiarity, only relatively unfamiliar works were selected. Whenever possible, for instance, we chose pictures that have not commonly been exhibited in the museum that owns them. Thus, this set of images is generally unfamiliar to laypeople (Cela-Conde et al., 2004, 2009, 2013). The paintings had been homogenized in terms of pictorial complexity, color spectrum, luminosity, and reflected light (for details, see Cela-Conde et al., 2004). Abstract stimuli lacked any discernible representation of objects, whereas all representational stimuli contained depicted objects, but no close view of human faces or bodies to avoid the activation of facial-recognition brain mechanisms.

2.1.3. Procedure

Participants were seated in front of a 17″ PC (1280×800 pixels) screen, at an approximate distance of 57 cm, in a quiet room with normal illumination, and asked to perform a computerized rating task. Fig. 1 depicts the timeline of an experimental trial. Each trial started with a fixation cross presented for 2500 ms on a white background, after which a painting (20×15 degrees visual angle) was presented at the center of the screen. Participants were instructed to press the left or right keys on a keyboard as soon as possible, using their right index and middle finger, to indicate whether they liked that image or not. Response key assignment for yes/no responses was counterbalanced across participants. Immediately after responding, participants were asked to indicate the extent of their preference for the painting just viewed on a 7-point Likert scale, where 1 was "I do not like it at all" and 7 was "I like it very much". There was no time restriction on the 7-point response. After the response, a new trial started. Stimuli within the experimental block were presented in random order. The same stimuli were presented twice, once for each of the two TMS sites (see next section).

2.1.4. Transcranial magnetic stimulation

TMS was delivered using a Magstim Rapid^2 stimulator (Magstim Co Ltd, Whitland, UK) connected to a 70 mm butterfly coil at a fixed intensity of 60% of the maximum stimulator output (as in previous TMS studies targeting LO, e.g. Mullin & Steeves, 2011). TMS was delivered to the right LO and to the vertex (control site). The right LO was localized on the basis of Talairach coordinates ($x = 37$, $y = -76$ $z = -5$) taken from previous fMRI research on the neural correlates of aesthetic appreciation (Lacey et al., 2011) showing that aesthetic appreciation for artistic images was directly correlated with activity in right (but not left) LO. The targeted site was identified by means of stereotaxic navigation on individual estimated magnetic resonance images (MRI) obtained through a 3D warping procedure fitting a high-resolution MRI template with the participant's scalp model and craniometric points (Softaxic, EMS, Bologna, Italy). The vertex was localized as the midpoint between the inion and the nasion and equidistant from the left and right intertrachial notches. For the vertex the coil was oriented tangentially to the scalp parallel to the nasion-inion line, while for the LO the coil orientation was such that the coil handle was pointing upwards and parallel to the midline. 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 onset of each painting, given prior TMS evidence showing that contribution of LO to object processing takes place within the first 180 ms of stimulus onset (e.g. Mullin & Steeves, 2011), and that triple-pulse 10 Hz TMS has been used before to interfere with underlying cortical activity (e.g., Cohen Kadosh et al., 2007; see Bona, Herbert, Toneatto, Silvanto, & Cattaneo, 2014 for triple-pulse 10 Hz TMS over LO region). Stimulation order was counterbalanced across participants. Prior to the experiment, participants performed a short practice block with 3 different paintings not used in the main experiment, so they could familiarize themselves with the task and sensations generated by TMS. The software E-prime 2.0 (Psychology Software Tools, Pittsburgh, PA) was used for stimulus presentation, data collection and TMS triggering. The whole experiment lasted approximately 90 min.

2.1.5. Data analyses

We analyzed the effects of TMS site (vertex vs. LO) and image category (abstract vs. representational) on participants' responses and response times by means of generalized linear mixed effects models (Hox, 2010; Snijders & Bosker, 2012). This method

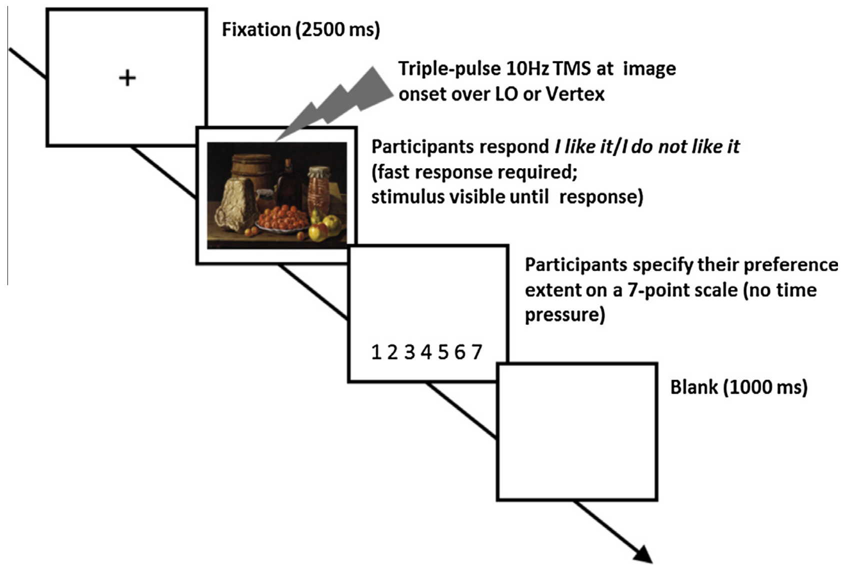

Fig. 1. Schematic overview of an experimental trial of Experiment 1 showing a Realistic painting ("Still Life with Fruit and Cheese" by Luis Egidio Meléndez, oil on canvas, courtesy of Museo del Prado, Madrid). Each trial started with a fixation cross on a white background, after which a painting was centrally presented. Participants had to respond as fast as possible whether they liked or they did not like the painting, by left/right key pressing using their right index and middle finger. Following this first response, participants had to indicate how much they liked the same painting on a 7-point Likert scale (1 = "I do not like it at all"; 7 = "I like it very much"). There was no time restriction on the 7-point response. After the second response, a new trial started. Representational and abstract paintings within the experimental block were presented in random order.

accounts simultaneously for the between-subjects and within-subjects effects of the independent variables (Baayen, Davidson, & Bates, 2008). It is thus especially suitable for understanding aesthetic appreciation, which may vary from person to person, and from image to image (Silvia, 2007). The models were primarily set up to study the impact of TMS site and image category, as well as their interaction. However, in order to control for the effects of TMS site order in each participant, we also included the variable stimulation order (vertex-LO vs. LO-vertex) in the models. All predictor variables were categorical, and the reference levels were vertex for TMS site, abstract for image category, and LO-vertex for stimulation order. In setting the model up, we followed Barr, Levy, Scheepers, and Tily's (2013) guidelines. They suggest modeling the maximal random effects structure justified by the experimental design, which, in addition to avoiding the loss of power and reducing Type-I error, enhances the possibility of generalizing results to other participants and stimuli. However, as noted by Barr et al. (2013), when using maximal models, the process of parameter estimation will occasionally fail to produce a solution. In these cases, they recommend simplifying the model's structure stepwise. Thus, unless specified otherwise, the models included the interaction between TMS site and image category, as well as the control variable stimulation order, as fixed effects, and random intercepts and slopes for the interaction between TMS site and image category within participants, and random intercepts and slopes for TMS site and stimulation order within stimuli. All analyses were carried out within the R environment for statistical computing (R Development Core Team, 2008), using the *glmer()* or *lmer()* functions of the 'lme4' package (Bates, Maechler, & Bolker, 2013), depending on the nature of the outcome variable (dichotomous or scale). The 'lmerTest' package (Kuznetsova, Brockho, & Christensen, 2012) was used to estimate the *p*-values for the *t*-test based on the Satterthwaite approximation for degrees of freedom.

2.2. Results

For the sake of clarity and conciseness, in all analyses only those results directly relevant to understanding the effect of TMS site and its interaction with image category are reported here.

2.2.1. Dichotomous liking response ("I like: Yes/No")

After obtaining the first model, we performed a study of influential cases based on Cook's distance (Cook's *D*). This measure evaluates each case's influence (in this instance, each participant) on the results by examining the impact of its removal from the data set. This analysis revealed one influential case whose Cook's D value exceeded the recommended cut-off point, which in this case was 0.4, calculated as $4/(n - k - 1)$, where n is the sample size and k the number of predictor variables. Thus, this participant was excluded from the analysis of the dichotomous liking response and, for coherence, from the analyses of the associated response times and subsequent Likert liking ratings.

Linear mixed effects modeling of the dichotomous liking response revealed that in the baseline vertex condition participants gave significantly more liking responses in the case of representational images (73.8%) than in the case of abstract images (18.9%) [$\beta = -2.49$; $z = 3.001$; $p < 0.003$]. The model also showed that TMS over LO significantly reduced the number of liking responses for representational stimuli from 73.8% in the baseline vertex condition to 66.1% [$\beta = -0.37$; $z = 2.189$; $p < 0.03$] (note that this effect was still significant even when keeping the influential case in the analysis, [$z = 2.050$; $p < 0.05$]). Conversely, participants' liking for abstract stimuli was unaffected by LO TMS (20.9% of stimuli) compared to the control vertex condition (18.9% of the stimuli), [$\beta = 0.12$; $z = 0.539$; $p = 0.59$] (see Fig. 2). The difference between the magnitude of the effect induced by LO TMS on liking for abstract and representational artworks approached significance [$\beta = 0.49$; $z = 1.773$; $p = 0.0763$]. The analysis of the random effects in the model indicated that variation of the effect of TMS site among participants and among stimuli was not significant [among participants: $\chi^2(3) = 0.00$; $p = 1$; among stimuli: $\chi^2(3) = 1.849$; $p = 0.604$], suggesting that this effect is highly stable over participants and stimuli.

We performed an additional analysis to verify whether the selective effect of LO TMS on representational artworks owed merely to the fact that participants generally like these more than abstract artworks, and that therefore there is a larger margin for TMS effects in the case of representational stimuli than in the case of abstract stimuli. This analysis, thus, aimed to disentangle the possible confound between the presence of objects in representational images and their

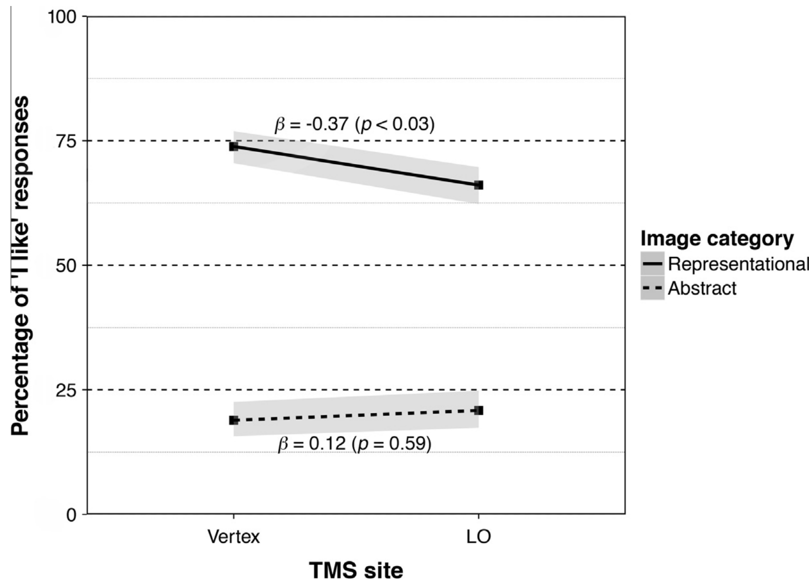

Fig. 2. Effects of TMS site on the percentage of 'I like' (yes/no) dichotomous responses given by participants to representational and abstract stimuli in Experiment 1. Shaded areas represent the 95% confidence intervals.

higher baseline likeability. Using a median split, we divided the participants into two groups: those who under control condition (i.e., vertex stimulation) showed the lowest liking for abstract stimuli, and those who under control condition showed the highest liking for abstract stimuli. Thereafter we used linear mixed effects modeling to determine whether the effect of TMS observed above in the case of representational stimuli occurs also in the case of abstract stimuli in both subsamples of participants. Thus, the model aimed to predict participants' responses from the interaction between TMS site, image category, and participant group (abstract likers vs. abstract dislikers). The variable stimulation order was not included in the model to avoid convergence problems.

Reflecting the median split, in the baseline vertex condition appreciation of abstract paintings was significantly higher in abstract likers than in abstract dislikers [$\beta = -3.19$; $z = 5.352$; $p < 0.001$]. In addition, the analysis revealed three crucial results. First, in the control (vertex) condition, abstract likers responded that they liked abstract (44.7%) and representational (57.2%) artworks to a similar extent [$\beta = 0.50$; $z = 0.7491$; $p = 0.503$]. Second, LO TMS had no effect on abstract likers' responses to abstract stimuli (44.7% liked in both control/vertex and LO conditions). Third, the interaction between the effects of TMS site and participant group was not significant [$\beta = 0.71$; $z = 1.307$; $p = 0.191$], and neither was the triple interaction between TMS site, image category and participant group [$\beta = 0.67$; $z = 1.095$; $p = 0.274$], indicating that independently of whether participants generally liked abstract artworks or not, TMS had the same effect.

Taken together, thus, these results indicate that the selective reduction in liking for representational artworks caused by TMS over LO does not owe to a floor effect in the case of liking for abstract artworks, or a difference in the baseline liking for abstract and representational stimuli. Even though the group of abstract likers had comparable baseline liking for abstract and representational stimuli, TMS only had an effect on their liking for representational stimuli. Moreover, this effect was similar in magnitude to the effect of TMS on the liking for representational stimuli of the group of abstract dislikers.

2.2.2. Response times (RT) in the dichotomous liking response task

Table 1 reports response latencies for the different experimental conditions of Experiment 1. The full model, as described above, did not converge satisfactorily, so it was decided to remove the random effect for the slope of order within stimuli. The new model converged without further problems. None of the independent variables (TMS Site, Image Category, Stimulation Order) had any significant effect on response times. The time it took participants to respond to abstract and representational stimuli did not differ significantly [$\beta = -10.67$; $t = 0.344$; $p = 0.736$]. The effects of TMS on response times did not reach significance in the case of representational stimuli [$\beta = -59.80$; $t = 2.040$; $p = 0.063$] or abstract stimuli [$\beta = -93.69$; $t = 2.057$; $p = 0.062$]. There was, however, a trend towards significance in both cases. The difference in RT between LO TMS and control stimulation was comparable for representational (64 ms) and abstract (94 ms) conditions [$\beta = -33.89$; $t = 1.137$; $p = 0.2720$].

2.2.3. Likert liking ratings

The model revealed that at baseline (vertex) participants liked representational artworks ($M = 3.81$) significantly more than abstract ones ($M = 2.65$) [$\beta = -1.16$; $t = 2.473$; $p < 0.03$]. The effects of TMS were not significant for either representational ($M = 3.67$ for LO TMS) [$\beta = -0.139$; $t = 1.798$; $p = 0.076$], or abstract artworks ($M = 2.71$ for LO TMS), [$\beta = 0.066$; $t = 0.634$; $p = 0.537$]. The interaction between TMS site and image category was not significant [$\beta = 0.204$; $t = 1.712$; $p = 0.099$]. The analysis of the random effects indicated that there was little variation among stimuli and participants in the magnitude of the TMS effect [among participants: $\chi^2(3) = 5.77$; $p = 0.123$; among stimuli: $\chi^2(3) = 2.62$; $p = 0.454$]. As in the case of the dichotomous (like yes/no) response, there was little variation in the effect of TMS site on liking for representational stimuli among participants and stimuli.

Table 1
Response times (ms) in the dichotomous liking response task collapsed over stimulation order.

Image category	TMS site	
	Vertex	LO
Representational	1040.7	983.0
Abstract	1025.1	938.2

3. Experiment 2

Experiment 1 revealed that TMS over LO caused a significant reduction in the appreciation of representational paintings (whereas appreciation of abstract paintings was unaffected). Previous evidence suggests that higher resolution photographs are liked more than lower resolution ones (Tinio & Leder, 2009; Tinio, Leder, & Strasser, 2011). In line with this, we reasoned that LO TMS may have decreased the perceived "clearness/sharpness" of the images in Experiment 1, and that this effect was greater for representational artworks in which objects—whose recognition is specifically mediated by LO—are present. Indeed, contour detection is impaired by LO TMS (Bona, Cattaneo, & Silvanto, 2015; Bona et al., 2014; Wokke, Vandenbroucke, Scholte, & Lamme, 2013). Accordingly, we hypothesized that depicted objects may appear less clear/more blurred following LO TMS. Our abstract paintings could also contain shapes, but they were meaningless (there were no recognizable objects) and mainly defined by changes in color/texture rather than by object-defining contours. LO is known to respond more strongly to objects than to global surfaces or disconnected edges (e.g., Vinberg & Grill-Spector, 2008), so LO disruption may have only marginal effects on visual processing of our abstract paintings. In order to investigate the possibility of LO TMS decreasing the perceived sharpness of the representational paintings, we performed a second TMS experiment in which participants were required to evaluate the same images used in Experiment 1 in terms of their clearness, with TMS applied over LO or vertex (control condition). In addition, to verify whether clearness of the images affects their aesthetic evaluation, we carried out a behavioral experiment. There, we asked an additional group of participants to evaluate the same set of images used in Experiment 1, both in terms of how much they liked them and in terms of how clear they found them. Understanding whether and how the perceived clearness of the images used in Experiment 1 related to their aesthetic appreciation is critical for interpreting the effect, reported above, of TMS over LO during aesthetic appreciation.

3.1. Method

3.1.1. Participants

Ten right-handed (Oldfield, 1971) participants (2 males, mean age: 22.5 years, *SD*: 1.8) were recruited for the TMS part of this study. Inclusion criteria were the same as for Experiment 1. Twenty additional right-handed participants (4 males, mean age: 25.5 years, *SD*: 4.3), with no special expertise in art, took part in the behavioral part of this study. None of the participants in Experiment 2 had taken part in Experiment 1. Participants were treated in accordance with the Declaration of Helsinki, they all signed an informed consent prior to the experiment, and the protocol was approved by the local ethical committee.

3.1.2. TMS experiment: procedure

The experimental paradigm was identical to that used in Experiment 1. The same TMS parameters were used. The only difference with Experiment 1 was in the type of evaluation participants were required to provide. Participants were instructed to look at each painting and to answer (as fast as possible) whether they found it clear (the specific adjective used in Italian was "nitido", which translates into English as clear, sharp, defined). After this first response, participants were required to indicate on a 7-point Likert scale how clear that image was (1 = "not clear at all", 7 = "absolutely clear"). More specifically, the experimenter told participants that for clearness they should take as reference the kind of sensation they may have experienced when viewing a movie on a blueray DVD vs. a standard VHS videotape. Three images (similar to those used in the main experiment) were shown to participants before the experiment to give them an idea of the type of image-quality they would have been presented with. Stimuli were presented as in Experiment 1, following the same counterbalancing of TMS conditions and response key-assignment.

3.1.3. TMS analysis

As in Experiment 1, linear mixed effects models were computed to determine the impact of TMS site and image category on clearness judgments. Again, we included the order of stimulation site as a control variable. Thus, the models included the interaction between TMS site and image category, as well as the control variable stimulation order, as fixed effects, and random intercepts and slopes for the interaction between TMS site and image category within participants, and random intercepts and slopes for TMS site and stimulation order within stimuli. We performed two analyses: one for the dichotomous response, and one for the Likert rating.

3.1.4. Behavioral experiment: procedure

The stimuli used were the same as those used in Experiment 1. In one block, participants were asked to express their liking for each of the 40 abstract and 40 representational paintings, presented in random order. As in Experiment 1, they had to first indicate whether they liked the image or not (yes/no fast response required) and then how much they liked it on a 7-point Likert scale. Thereafter, in another block, participants were presented with the same images and asked to evaluate whether and how much they find the images clear (see "TMS experiment procedure" of Experiment 2 for details on the type of evaluation required). The order of tasks (clearness first vs. liking first) was counterbalanced across participants. Response key assignment for yes/no responses was also counterbalanced across participants. Three practice trials were presented before each task.

3.2. Results

3.2.1. Dichotomous clearness response ("Clear: Yes/No")

An analysis of influential cases revealed that the results of the first model were biased by two highly influential outlier participants. Therefore, it was decided to exclude these two participants from the analysis and re-run the model. In this case, the full model did not converge, so we opted to remove the random slope for order within stimuli. After this, the model converged without further problems. This model revealed that in the vertex control condition responses did not differ between representational stimuli (86.3% identified as clear) and abstract stimuli (82.4% identified as clear) [$\beta = 0.298$; $z = 0.352$; $p = 0.725$]. The model also showed that LO TMS did not significantly affect clearness responses for either representational stimuli (91.8% identified as clear with LO TMS) [$\beta = 0.571$; $z = 0.973$; $p = 0.331$], or abstract stimuli (91.2% identified as clear with LO TMS) [$\beta = 0.801$; $z = 1.832$; $p = 0.067$], though there was a trend in the latter category. Accordingly, the effects of LO TMS for representational and abstract stimuli were not statistically different [$\beta = 0.230$; $z = 0.470$; $p = 0.639$]. Note that the same pattern was obtained even when both influential cases were kept in the analysis: in particular, LO TMS did not affect dichotomous responses either for representational ($z = 0.112$; $p = 0.911$) or abstract ($z = 1.645$; $p = 0.100$) artworks.

3.2.2. Response times (RT) in the dichotomous clearness response task

Table 2 reports response times for the different experimental conditions of Experiment 2. None of the independent variables (TMS Site, Image Category, Stimulation Order) had any significant effect on response times. The model shows that response times to abstract and representational stimuli were not significantly different [$\beta = -51.27$; $t = 1.426$; $p = 0.198$]. Likewise, LO TMS did not

Table 2
Response times (ms) in the dichotomous clearness rating task collapsed over stimulation order.

Image category	TMS site	
	Vertex	LO
Representational	1004.5	1009.3
Abstract	937.9	955.5

affect RT compared to the vertex control stimulation for either representational [$\beta = -9.91$; $t = 0.179$; $p = 0.863$] or abstract [$\beta = -16.18$; $t = 0.297$; $p = 0.775$] artworks. Accordingly, the effect of LO TMS did not differ between both art categories [$\beta = -6.269$; $t = 0.181$; $p = 0.860$].

3.2.3. Likert clearness ratings

The full model (excluding the influential cases from the dichotomous response analysis) predicting Likert clearness ratings did not converge satisfactorily, so it was decided to remove the random effect for the slope of order of stimulation site within stimuli. The results of this model indicated that there was no difference in the clearness ratings awarded to representational ($M = 3.83$) and abstract ($M = 3.87$) stimuli in the control vertex TMS condition [$\beta = 0.043$; $t = 0.098$; $p = 0.924$]. The model also showed that, compared to vertex TMS, LO TMS did not alter the clearness ratings awarded to representational stimuli ($M = 4.15$ with LO TMS) [$\beta = 0.322$; $t = 1.826$; $p = 0.109$], though it increased them in the case of abstract stimuli ($M = 4.22$ with LO TMS) [$\beta = 0.348$; $t = 2.796$; $p = 0.019$]. Still, the TMS and art category interaction was not significant [$\beta = -0.026$; $t = 0.125$; $p = 0.903$]. Note that the same pattern was obtained even including the influential cases in the analysis: in particular, LO TMS did not increase clearness responses for representational stimuli [$t = 1.770$; $p = 0.109$], but it did in the case of abstract stimuli [$t = 3.132$; $p = 0.007$].

3.2.4. Behavioral experiment

Participants reported greater appreciation for representational than abstract art, both when percentage of "I like it" responses were considered, $t(19) = 3.11$, $p = 0.006$ ($M_{\text{representational}} = 59.1\%$, $SD = 24.7$; $M_{\text{abstract}} = 33.6\%$, $SD = 18.1$), and when Likert scores ($M_{\text{representational}} = 4.08$, $SD = 0.77$; $M_{\text{abstract}} = 3.10$, $SD = 0.82$) were considered, $t(19) = 3.77$, $p = 0.001$. Clearness evaluations did not differ for representational and abstract art neither when yes/no responses were considered, $t(19) < 1$, $p = 0.43$ ($M_{\text{representational}} = 39.1\%$, $SD = 12.9$; $M_{\text{abstract}} = 42.8\%$, $SD = 15.2$), nor for Likert scores, $t(19) < 1$, $p = 0.34$ ($M_{\text{representational}} = 3.75$, $SD = 0.60$; $M_{\text{abstract}} = 3.60$, $SD = 0.60$).

Fig. 3 shows how aesthetic appreciation judgments, both in terms of frequency of "yes" responses (Fig. 3a) and Likert scores (Fig. 3b), related to clearness evaluation for abstract and both representational image categories (realistic and impressionist/postimpressionist). Correlational analyses were corrected for outlier and influential artworks, based respectively on standardized residuals (those with standardized residuals above 2 or below −2 were excluded) and Cook's distances. The results of the analysis (Pearson, two-tailed) for the yes/no dichotomous responses revealed that clearness and liking evaluations were significantly positively correlated for abstract artworks [$r(37) = 0.66$, $p < 0.001$, after removal of one influential outlier artwork] (see Fig. 3a), but not for representational artworks (realistic and impressionist/postimpressionist together) [$r(37) = 0.005$, $p = 0.98$, after removal of one influential outlier artwork]. Since lack of defined contours is an intrinsic characteristic of Impressionism, separate additional

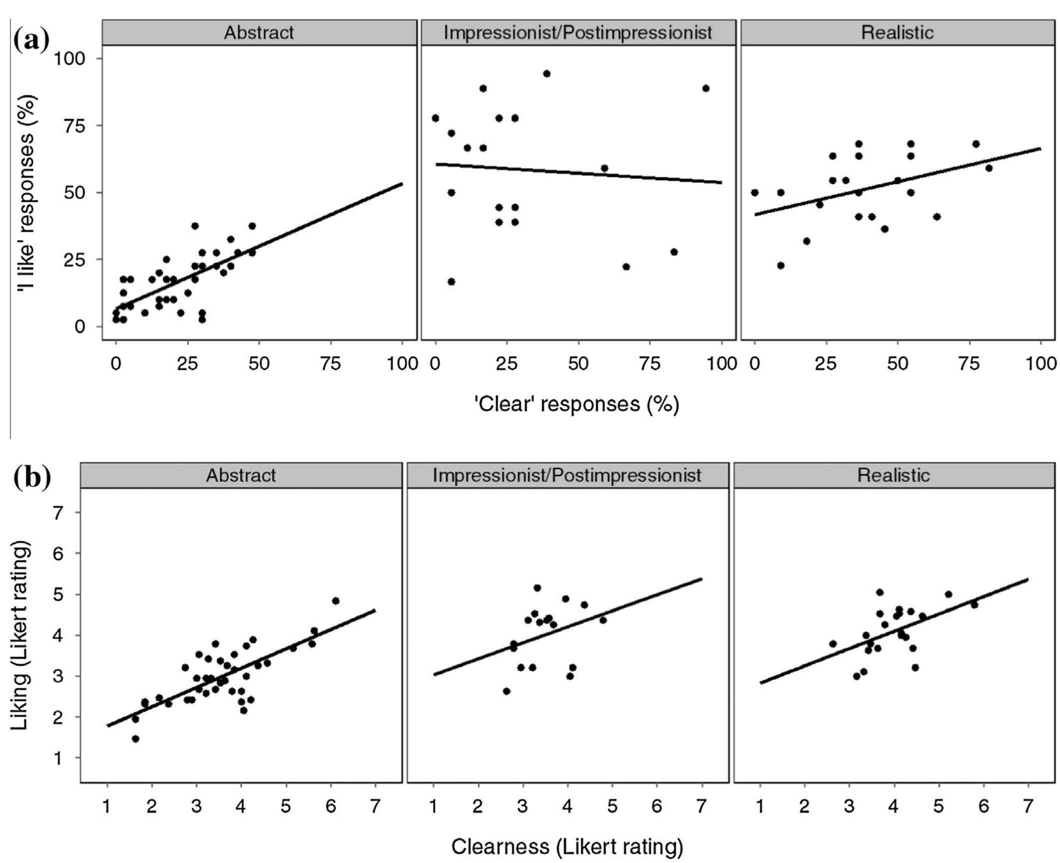

Fig. 3. Relation between (a) dichotomous (yes/no) and (b) Likert-scale liking and clearness responses for abstract, impressionist/postimpressionist and realistic stimuli in the behavioral assessment of Experiment 2. Outlier influential cases are not shown.

correlational analyses were carried out on realistic and impressionist/postimpressionist paintings. The results revealed that liking and clearness judgments did not correlate for impressionist artworks [$r(16) = -0.08$, $p = 0.76$], whereas the two types of judgments were significantly positively correlated for realistic artworks [$r(20) = 0.52$, $p = 0.013$] (see Fig. 3a).

Similar analyses carried out on Likert scores found a positive significant correlation between liking and clearness judgments for both abstract artworks [$r(36) = 0.74$, $p < 0.001$, after removal of two influential outlier artworks] (see Fig. 3b), and representational artworks [$r(38) = 0.42$, $p = 0.007$]. A more detailed analysis showed that the positive correlation reported for representational paintings was mainly driven by realistic artworks [$r(20) = .51$, $p = .016$], whereas when only impressionist/postimpressionist paintings were considered, the correlation between liking and clearness judgments was non-significant [$r(16) = .33$, $p = .18$] (see Fig. 3b).

4. Discussion

We found that TMS-induced interference with LO activity during visual aesthetic appreciation selectively reduced liking for representational paintings, leaving liking for abstract paintings unaffected (Experiment 1). In particular, analyses of dichotomous responses ("I like it" vs. "I do not like it") showed that TMS over LO decreased aesthetic appreciation of representational artworks (this pattern emerged as a weak trend [$p = 0.076$] also in the Likert responses). Overall, results of Experiment 1 point to a selective causal role of LO in aesthetic appreciation of representational art. Interestingly, a control experiment (Experiment 2) showed that LO TMS increased perceived clearness of abstract paintings as measured by the Likert scale, whereas clearness of the representational paintings was not affected.

Previous neuroimaging and TMS evidence suggests that LO is involved in object recognition (for reviews, Grill-Spector, 2003; Lacey & Sathian, 2011). Our results support prior neuroimaging findings that indicated that object-processing in LO also plays a critical role in aesthetic evaluation of objects—at least, artistic ones (Lacey et al., 2011; see also Vartanian & Goel, 2004). Indeed, our findings are in line with previous research showing that activity in sensory brain regions selective for certain classes of visual processing correlates with subjective preference for those stimuli, possibly related to a gradient of μ-opioid receptor density along the ventral visual pathway (Biederman & Vessel, 2006; Lewis et al., 1981). For instance, preference ratings for images of visual scenes and their novelty vary with activity in the parahippocampal place area, a visual area selective to visual scenes (Biederman & Vessel, 2006; Yue, Vessel, & Biederman, 2007). More closely related to the present study, LO activity correlates positively with preference for simple shapes (Amir, Biederman, & Hayworth, 2011) and even funniness ratings for humorous visual riddles (Amir, Biederman, Wang, & Xu, 2013). Our findings, thus, extend this literature by showing that there is a causal relation between activity in such higher-level visual regions (LO in our case) and preference. Moreover, our results are also in line with the finding that repetitive TMS over the extrastriate body area and over the ventral premotor cortex—two regions known to be involved in body perception (Urgesi, Calvo-Merino, Haggard, & Aglioti, 2007)—significantly modulated aesthetic appreciation for body stimuli (Calvo-Merino et al., 2010; Cazzato et al., 2014).

Overall, in the baseline condition (vertex stimulation) our participants indicated liking more representational (73.8%) than abstract paintings (18.9%). This finding is in line with previous evidence reporting a higher preference for representational artworks in participants with no specific art-background (Flexas, Rossello-Mir, de Miguel, Nadal, & Munar, 2014; Vessel & Rubin, 2010). It could be argued that LO TMS only affected aesthetic judgments for representational artworks, because of a floor effect in the liking for abstract ones. However, we were able to rule out this possibility. In an additional analysis we showed that even in participants who appreciated representational and abstract artworks to a similar extent, LO TMS selectively affected appreciation of representational paintings. This analysis enabled us to disentangle the effects of general likeability and the presence of objects in the images. It showed that the effects of LO TMS are specific to images that contain meaningful objects, independently of how much abstract and representational stimuli are liked under the control vertex condition.

But why does interfering with LO activity reduce aesthetic liking for representational artworks? LO is known to be involved in object processing. However "object processing" refers to a large set of sub-processes (grouping Gestalt processes, figure-ground segregation, object/scene processing, semantic components involved in object recognition and so on, see Chouinard, Whitwell, & Goodale, 2009; Malach et al., 1995). We designed Experiment 2 to test the possibility that the effects of LO TMS on aesthetic evaluation were caused by a stimulation-induced reduction in the sharpness/clearness of images. The possibility that a reduction in clearness might lead to a reduction in liking is suggested by previous studies that have shown that high-resolution representational images are liked more than lower quality ones (Tinio & Leder, 2009; Tinio et al., 2011). Although no previous studies have directly assessed whether LO TMS affects scene clearness, it has been shown that LO TMS impairs contour detection (Bona et al., 2014, 2015; Wokke et al., 2013): accordingly, we hypothesized that depicted scenes containing objects may appear more blurred/less sharp to participants following LO TMS. The results of Experiment 2 did not meet our expectations. LO TMS did not affect dichotomous clearness responses for representational or abstract stimuli, though it selectively increased Likert scores of perceived clearness for abstract paintings (a counterintuitive result that we will further consider below). Experiment 2, thus, refutes the possibility that a reduction in clearness was the cause of the lower liking for the representational art under TMS LO, suggesting that sharpness/clearness and liking do not go hand-in-hand in LO. This is not to say that they are unrelated, but that their relationship does not appear to be mediated by LO. Indeed, we found a positive correlation between liking and perceived clearness for both abstract and representational realistic paintings.

Why, then, was the aesthetic appreciation of representational paintings selectively reduced following LO TMS? Eye movement studies of art appreciation offer a promising answer. When viewing representational paintings, laypeople tend to rely more on a local than on a global viewing strategy. That is to say, they fixate mostly on recognizable objects, at the expense of background and framing elements and the relations among objects. Moreover, their liking is linked to the identity and meaning attached to those objects (e.g., Kapoula & Lestocart, 2006; Kapoula, Yang, Vernet, & Bucci, 2008; Nodine, Locher, & Krupinski, 1993; Vogt, 1999; Vogt & Magnussen, 2007; Zangemeister, Sherman, & Stark, 1995). While we cannot offer this as a conclusive explanation, the selective decrease in our art-naïve participants' liking for representational artworks following LO TMS might owe to TMS affecting processing of the individual objects depicted. If this were the case, it would also explain why liking for abstract artworks was unaffected by LO TMS. Given that this class of images contained no meaningful objects—again, the main source of aesthetic appreciation in lay participants—LO TMS did not interfere with any process that was relevant to deciding about their liking for these images. It could be objected, however, that the abstract paintings we used also contained shapes (though not meaningful objects), whose processing is susceptible to LO TMS (e.g., Ellison & Cowey, 2006, 2009; see also Ales, Appelbaum, Cottereau, & Norcia, 2013; Ferber, Humphrey, & Vilis, 2005; Kourtzi & Kanwisher, 2000). Nonetheless, our data show that interfering with shape processing itself is not sufficient to affect liking for abstract art. Indeed, abstract art appreciation in art-naive participants likely relies on evaluation of a number of visual characteristics other than shape, such as color, texture or dynamism. Thus, even if LO TMS did interfere with grouping mechanisms (such as contour detection mediating the processing of shape), this was not critical enough for the aesthetic experience of this class of artworks.

Contrary to our expectations, the control experiment showed that LO TMS increased perceived clearness of abstract paintings as measured using a Likert scale. This result might seem counterintuitive at a first glance. However, prior research has reported similar "paradoxical" facilitation effects on visual performance following disruption of LO via TMS. For instance, Mullin and Steeves (2011) found that LO TMS impairs object processing, but facilitates scene processing. In their view, this finding suggests a release of inhibitory connections between object-selective area LO and the scene processing pathway. More recently, Wokke, Scholte, and Lamme (2014) showed that LO TMS resulted in increased performance in motion-defined figure-ground segregation, supporting the existence of a "push–pull" mechanism in which dorsal and ventral extrastriate areas are activated or inhibited depending on stimulus and task characteristics. Accordingly, it is possible that interfering with LO in our clearness experiment favored the processing of features mainly mediated by the dorsal stream, such as luminance, spatial arrangement and implied dynamism of the image, leading to increased clearness of paintings in which these cues were more salient (i.e., abstract paintings lacking object content). Moreover, in debriefing, participants reported that their clearness ratings (for both abstract and representational paintings) reflected their perception of the picture as a whole, rather than meaningful objects within the picture. Thus, in our experiment, clearness seems to reflect the extent to which participants are able to process not any individual items of the paintings, but their overall content and the relationship between its components (scene processing, facilitated by LO TMS, see Mullin & Steeves, 2011). Overall though, the effect of LO TMS on clearness judgments was small, not being able to affect less fine-grained responses, as those required by the dichotomous response. Also, the aspects that drive the perception of clearness in abstract and representational artworks are not well understood on their own. Further research is required to address these interesting issues. One possibility would be to selectively interfere with other regions along the dorsal and ventral streams (possibly including other "control" regions in the visual cortex beyond vertex, to better control for possible unspecific effects of visual cortex stimulation).

Finally, TMS did not significantly affect response latencies. We only observed a (non-significant) trend toward faster responses in the aesthetic task (Experiment 1) following lateral occipital region (LO) TMS, irrespective of art category. This finding is unlikely to reflect unspecific effects of TMS, since no such trend was evident in the clearness task (Experiment 2). The time required to decide about whether a painting is liked or not is likely to be affected by participants' viewing strategy (e.g., Day, 1968; Leder, Tinio, Fuchs, & Bohrn, 2010). When confronted with paintings, individuals likely look for objects in the scene, engaging in a sort of "object search" (as suggested by Pihko et al., 2011). LO is known to play a key role during visual search of objects in scenes (e.g., Pantazatos, Yanagihara, Zhang, Meitzler, & Hirsch, 2012; Preston, Guo, Das, Giesbrecht, & Eckstein, 2013). Thus, it is possible that interfering with LO activity during aesthetic evaluation interfered with usual visual exploration strategy of paintings' content, this affecting timing of exploration. Future studies may better address this hypothesis, maybe combining TMS with eye movement recording.

In sum, our findings suggest that the lateral occipital region, a key node in the object processing network, is also recruited in such higher-level processes as those at play during aesthetic appreciation of paintings. The fact that a region is specialized in the basic processing of a given stimulus feature, does not automatically imply that it also plays a role in higher-level processes, such as aesthetic evaluation. For instance, previous evidence has shown that using TMS to interfere with activity in the occipital face area (OFA), a key region in face detection/discrimination processing, clearly affected face gender discrimination but had only a minimal effect on face trustworthiness judgments (Dzhelyova, Ellison, & Atkinson, 2011). However, our data support the notion that LO is involved in aesthetic appreciation, of at least representational artworks (in which meaningful objects are depicted). This adds to the already existing work that has shown that aesthetic appreciation is mediated by a broad network of cortical and subcortical regions related to sensory, attentional, cognitive and reward-related processes (Chatterjee & Vartanian, 2014). Our study supports the view that brain regions specialized for the processing of certain stimuli may also respond to those stimuli's higher attributes, including their aesthetic qualities (e.g., Amir et al., 2013; Calvo-Merino et al., 2010; Cazzato et al., 2014; Lacey et al., 2011; Yue et al., 2007).

Appendix A

Abstract artworks

Giacomo Balla (1913) *Velocità astratta – l'auto è passata*
Antoni Clavé *Trois Fruits*
Antoni Clavé *Sans Titre*
Antoni Clavé *Peinture*
Antoni Clavé (1976) *Trois Points*
Georgi Daskaloff *Colors*
Robert Delaunay (1912) *Windows Open Simultaneously (First Part, Third Motif)*
Will Faber (ca. 1950) *El Dadasoph*
Jean Fautrier (1945) *Tête D'Otage No. 24*
Juana Francés (1967) *Sin Título*
Juana Francés (ca. 1955) *Sin Título*
Helen Frankenthaler (1952) *Mountains and Sea*
Arshile Gorky (1947) *The Betrothal*
Carles Guasch (ca. 2000) *Sense Títol*
Stanley William Hayter (1972) *Claduegne*
Howard Hodgkin (1984) *Dinner in Palazzo Albrizzi*
Wassily Kandinsky (1913) *Black Lines*
Wassily Kandinsky (1910) *Improvisation 19*
Wassily Kandinsky (1910–1) *Cossacks*
Wassily Kandinsky (1942) *Reciprocal Agreement*
Paul Klee (1915) *Side Panels for Anatomy of Aphrodite*
Paul Klee (1937) *Ofrenda Ajada*
Paul Klee *Intervención*
Frantisek Kupka (1912) *Fugue à deux couleurs*
Morris Louis (1959–1960) *Number 99*
Piet Mondrian (1913) *Oval composition*
Robert Motherwell (1961) *Mallarme's Swan*
Robert Motherwell (1962) *Chi Ama, Crede*
Ben Nicholson (1951) *Feb 28–53 (vertical seconds)*
Serge Poliakoff (1950) *Composition*
Lyubov Popova (1921) *Space force construction (5)*

(*continued on next page*)

Juli Ramis i Palau (ca. 1950) *Espacial 1*
Chaim Soutine (1920–1) *Landscape at Céret*
Nicolas de Staël (1949) *Rue Gauguet*
Antoni Tàpies (1961) *Relleu Ocre*
Antoni Tàpies (1958) *Ocre Gris*
Antoni Tàpies (1973) *Gran marró sobre fusta foradada*
Jacoba van Heemskerck (1919) *Abstract composition*
Manuel Viola (1959) *Orquídea*
Edward Wadsworth (1915) *The open window*

Representational artworks

Lubin Baugin (1630–1635) *Le dessert de gaufrettes*
Georges Braque (1927) *Still life (with clarinet)*
Pieter Bruegel the Elder (1567) *The Adoration of the Kings in the Snow*
Canaletto (1725) *The Stonemason's Yard*
Canaletto (late 1730s) *Venice: The Doge's Palace and the Riva degli Schiavoni*
Paul Cézanne (1902–04) *Mont St. Victoire*
Paul Cézanne (1873) *View of Auvers-sur-Oise (The Fence)*
Paul Cézanne (1875) *Trees in the park of Jas de Bouffan*
Paul Cézanne (1876) *Landscape. Study after nature*
Paul Cézanne (ca. 1894) *Bathers*
Ángel Mateo Charris (1997) *Intimate Biography*
William Davis (1860–1870) *At Hale, Lancashier*
Aureliano de Beruete y Moret (1905) *El Tajo (Toledo)*
Aureliano de Beruete y Moret (1910) *Otoño en Madrid*
Juan de Espinosa (ca. 1630) *Bodegón de uvas, manzanas y ciruelas*
Wilfred Fairclough (1945–7) *High Wycombe, Buckinghamshire*
Carlos de Haes (1864) *Paisaje del Delfinado*
Carlos de Haes (ca. 1872) *Paisaje de montaña*
Carlos de Haes (ca. 1881) *Rompientes (Guethary)*
Carlos de Haes (1883) *Barco Naufragado*
Richard Hamilton (1958–61) *She*
Willem Claeszoon Heda (1633–37) *Still Life: Pewter and Silver Vessels and a Crab*
John William Hill (1867) *Bird's Nest and Dogroses*
Edward Hopper (1930) *Highland light*
William Holman Hunt (1862) *Asparagus Island, Kynance, Cornwall*
Julius Caesar Ibbetson (1798) *A Phaeton in a Thunderstorm*
Ernst Ludwig Kirchner (ca. 1909) *Strassenbahn (Dresden)*
Claude Lorrain (1639) *Seaport at Sunset*
Luis Egidio Melendez (1759) *Bodegón con manzanas, nueces, cajas de dulces y otros recipientes*
Luis Egidio Meléndez (ca. 1770) *Bodegón: granadas, manzanas, tarros y cajas de dulce*
Joaquim Mir i Trinxet (ca. 1898) *El huerto de la Ermita*
Claude Monet (1874) *The Bridge at Argenteuil*
John Charles Moody (1937–9) *Barnard Castle*
Sir William Nicholson (1940) *Mushrooms*
Luis Paret y Alcazar (ca. 1780) *Ramillete de flores*
Camillo Pissarro (1873) *La Gelée Blanche (Hoarfrost)*
Thomas Rowlandson (1808) *Bartholomew Fair, Smithfield*
Mario Sironi (1928) *Montagne*
Chaim Soutine (1939) *Le retour de l'école après l'orage*
Alexej Georgewitsch Von Jawlensky (1908) *Summer Evening a Murnau*

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