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Investigating the neural network underlying aesthetic experience

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Summary

The experimental work presented in this dissertation is part of a relatively young field of research in cognitive neuroscience, neuroaesthetics. The main aim of this field is to investigate the neural underpinnings of the aesthetic experience.

The studies I describe in this thesis focus on a particular aspect of the aesthetic experience, namely beauty appreciation. The experiments conducted aimed to investigate the neural correlates of beauty perception using behavioural methods as well as neurostimulation techniques such as transcranial direct current stimulation (tDCS) and transcranial magnetic stimulation (TMS). Non-invasive brain stimulation techniques allow to establish causal relationships between specific brain areas and the underlying processes (for an overview see: Nitsche et al., 2008; Vincent Walsh & Cowey, 2000), adding to neuroimaging evidence.

A first study, using a divided visual field paradigm, investigated hemispheric asymmetries in men and women's preference for abstract and representational artworks (Study 1). Findings of this first experiment showed that both male and female participants liked representational paintings more when presented in the right visual field, and that liking for abstract paintings was unaffected by presentation hemifield.

In Study 2, TMS applied over motion sensitive cortical area V5 while viewing a series of paintings was found to significantly decrease the perceived sense of motion, and also to significantly reduce liking of abstract (but not representational) paintings.

A third study showed that TMS over the superior temporal sulcus, but not the somatosensory cortex (SC) disrupted expressivity judgment in portraits, without affecting though beauty judgments.

Study 4 showed that enhancing excitability via tDCS in the reward system, and in particular in the ventromedial prefrontal cortex (vmPFC), resulted into a slight increase in aesthetic appreciation of paintings.

Finally, findings of Study 5 suggest that the dorsomedial prefrontal cortex causally contributes to mediate the link between moral and aesthetic valuation.

Taken together the present results help to clarify the causal role of different brain regions underlying beauty perception and shed light on the intersection between moral and aesthetic evaluation.

Introduction

In every human culture, it is possible to find a form of art creation and appreciation (Kandel, 2012). Even children appreciate art (Mai & Gibson, 2009). Artworks are intentionally designed to be appealing and induce an emotional and cognitive response in the viewer (Cela-Conde, Agnati, Huston, Mora, & Nadal, 2011). Certain visual elements seem to be objectively pleasant to humans, for instance, in faces, symmetry and average-like traits (Rhodes, 2006), or, in artworks, a certain level of regularity, clarity, novelty, contrast or complexity (see Berlyne, 1974). However, beauty appreciation highly depends on the perceiver, whose aesthetic experience is based on multiple interconnected dimensions. In this dissertation, I will focus on beauty that is just one aspect of the more complex aesthetic experience.

Beauty can be expressed in many ways (beautiful painting, beautiful face, etc.) and can influence a range of cognitive processes. For instance, it is known that people considered physically beautiful are usually perceived and treated more favourably than those less attractive, a phenomenon known as "beautiful is good" stereotype (see Eagly, Ashmore, Makhijani, & Longo, 1991; Langlois et al., 2000). In addition, there is a relation between beauty and emotional state: our mood affects our evaluations of beauty and beautiful things positively affect our emotional state (Flexas et al., 2013; Leder, Belke, Oeberst, & Augustin, 2004). Beauty seems to be the result of a complex interplay between sensation, emotion and cognition (Chatterjee & Vartanian, 2014; Pearce et al., 2016). It goes without saying that aesthetic appreciation is based on the activity of several different brain regions. Converging evidence from neuroimaging, electrophysiological and lesion studies (Chatterjee, 2011; Nadal, 2013) have allowed to identify a cortical-subcortical neural network involved in the perception and processing of aesthetics stimuli. These neural substrates of aesthetic appreciation include cortical and subcortical regions associated with pleasure and reward (Brown, Gao, Tisdelle, Eickhoff, & Liotti, 2011; Tomohiro Ishizu & Zeki, 2011; Jacobsen, Schubotz, Höfel, & Cramon, 2006; Kawabata & Zeki, 2004; O. Vartanian & Goel, 2004), frontal cortical areas involved in decision-making and evaluation (Cattaneo et al., 2014a, 2014b; Cela-Conde et al., 2004; Cupchik, Vartanian, Crawley, & Mikulis, 2009; Yue, Vessel, & Biederman, 2007), as well as various cortical areas related to perception.

The present research focuses on the neural correlates of beauty appreciation and processing of visual artworks. Beauty will be investigated for a restricted range of stimuli, that is paintings and faces, even if beauty experience can also apply to other objects. Moreover, “aesthetic experience” throughout this dissertation will be used to refer to what an individual experiences as beautiful, hence not dealing with other aesthetically engaging experiences. Accordingly, a bipolar beautiful/ugly dimension has been found to be the primary and prototypical descriptive dimension used to address the aesthetics of objects (Jacobsen, Buchta, Kohler, & Schroger, 2004).

Despite the growing literature concerning this topic (see Pearce et al., 2016 for a review) many questions remain unsolved. For example, although the right hemisphere is often regarded as the “aesthetic brain” it is still unclear whether the two hemispheres are equally involved in aesthetic appreciation. In the first study presented here, a divided visual field paradigm was used to test for hemispheric asymmetries in men and women’s preference for abstract and representational artworks. After this first study dealing with hemispheric differences, the dissertation will focus on more specific brain areas trying to shed light on the role of sensory cortices in aesthetic evaluation of paintings.

It is already known that the viewing of painting with depiction of motion activates motion-sensitive areas, like MT + (Thakral, Moo, & Slotnick, 2012), viewing of portraits recruits face area in the fusiform gyrus (FFA) and landscape paintings activate the place area in the parahippocampal gyrus (PPA) (Kawabata & Zeki, 2004; Yue et al., 2007). It seems moreover that these sensory-areas are not just involved in recognition but seem to play a role also in evaluation of paintings. Indeed, neural activity in visual areas increase if the stimuli are beautiful, for example FFA activation is stronger when subjects see attractive faces (Chatterjee, 2009). In study 2 and 3 TMS will be used to investigate the causal role of distinctive brain areas in aesthetic appreciation of different painting’s categories. TMS is a neurostimulation technique that allows induced currents to be focused within the brain based on electromagnetic induction. The electrical field affects the neural activation in the stimulated cortical region allowing direct investigation of brain-behaviour relations. In particular, TMS can be used to establish whether the targeted brain region is causally implicated in the studied function (Walsh & Pascual-Leone, 2003). This approach is methodologically well supported, as brain stimulation has been already successfully used to interfere with subjective decisions (e.g. Jeurissen, Sack, Roebroeck, Russ, & Pascual-Leone, 2014) and has already been demonstrated that brain stimulation is able to affect aesthetic preference (Cattaneo et al., 2014b, 2015).

In study 2 the goal is to investigate the possibility that activity in cortical area V5, a region in the occipital cortex mediating physical and implied motion detection, is related not only to the generation of a sense of motion from visual cues used in artworks, but also to the appreciation of those artworks. To clarify this issue triple-pulse online TMS was applied over V5/MT or over a control site (vertex) while participants were evaluating a set of figurative or abstract paintings. Study 3 aims to explore the relationship between expressivity and aesthetic appreciation in portraits. Two cortical areas, the superior temporal sulcus and the somatosensory cortex involved in expression recognition were stimulated while subjects had to judge the expressivity and beauty of a series of portrait and non-portrait paintings.

Beside sensory areas, beautiful paintings induce the activation of reward related areas, whose role in aesthetic appreciation is yet to be fully explored. Thus, in Study 4 the possible causal role of the ventromedial prefrontal cortex (vmPFC), an essential component of the reward system, will be investigated by means of tDCS. tDCS consists in a non-invasive, transcranial and painless induction of weak direct currents able to modify activation in the targeted region therefore allowing to draw causal inferences.

Finally, Study 5 will address the influence of beauty on other cognitive processes. In particular, this final study aims to shed light on the neural underpinnings of the intersection of aesthetic and ethical evaluation by combining TMS with a priming paradigm designed to reveal the *Beauty-is-Good* stereotype.

What is neuroaesthetics?

The term neuroaesthetics was first used in the 1990s by Semir Zeki in his book "Inner vision". Neuroaesthetics is a discipline who aims to combine neuroscientific methods with our knowledge about art to understand brain involvement in various aspects of aesthetics, from perception to production (Zeki & Lamb, 1994; Zeki, 1999a). When neuroimaging techniques became available, scientists could use them to study healthy participants and were able to correlate the appreciation of music, painting, architecture, sculpture, and dance, with neural activity. In the last few decades a growing number of books and articles was published about this topic, nonetheless is still difficult to consider neuroaesthetics as a defined domain for several reasons (Brown & Dissenayake, 2009). Researchers in the field still do not agree about which are the main objectives and how to study them. The concept of art itself is controversial and does not have a universally accepted definition. Skov (2005) writes: “has proven exceedingly difficult to define what art is in the first place. Even though thousands of authors throughout the ages have tried to pinpoint the properties that set art objects apart from other objects, in general, all such efforts have failed or proven controversial. Frustratingly, any property that has been advanced as unique to artworks has quickly been shown to be found also in non-art objects. The same goes for attempts to define what constitutes the aesthetic experience.”

Neuroaesthetics has received criticisms both from the humanities (art theory, philosophy, art history), as well as from scientific disciplines (neuroscience, psychology,…). Philosophers claim that examining the brain does not give a contribution to knowledge about art (Massey, 2009; Tallis, 2008). Studying art in a lab remove important variables, like the context, the cultural and historical background. Isolating the different components of the process can destroy the aesthetic experience.

On the other hand, also scientific discipline moved criticisms to the highly subjective nature of the judgments measured (liking, preference…) and to “the lack of a cogent, universally accepted definition of beauty” (Conway & Rehding, 2013). However, the lack of a broadly shared definition in other branches of psychology and cognitive neuroscience, like emotions and consciousness, never prevented scientist to study these phenomena.

Cognitive neuroscience of art can be descriptive and experimental, with qualitative observations and quantitative tests of hypotheses. Neuroscientific methods today allow to study what happens in the brain when we see an artwork, helping us to uncover the information processing involved in our psychological engagement with the world. As pointed out at the beginning of the introduction, artworks can be conceived as stimuli intentionally designed to induce an emotional and cognitive response in the viewer. As stimuli, they carry information in their structure and neuroscience of art tries to discover how this information is processed in the brain and how they influence behaviour. Cognitive science “makes possible a meaningful series of dialogues between brain science and other areas of knowledge. Such dialogues could help us explore the mechanisms in the brain that make perception and creativity possible, whether in art, the sciences, the humanities, or everyday life" (Kandel, 2012). Since art is a very important aspect of mankind and a central challenge of science in the twenty-first century is to understand the human mind in biological terms, a cognitive neuroscience of art is not only possible but necessary.

Models of aesthetic appreciation

Aesthetic appreciation emerges from several cognitive and affective processes: perception, attention, familiarity, learning and knowledge, judgment, decision making, affect and emotion. Some models of aesthetic experiences were proposed (Chatterjee 2003, Nadal 2008) but the most comprehensive one, that manage to take all these domains and their relationship into consideration was presented in 2004 by Leder and collegues. This model is very informative and structured in a modular way that works well as a basis for empirical research.

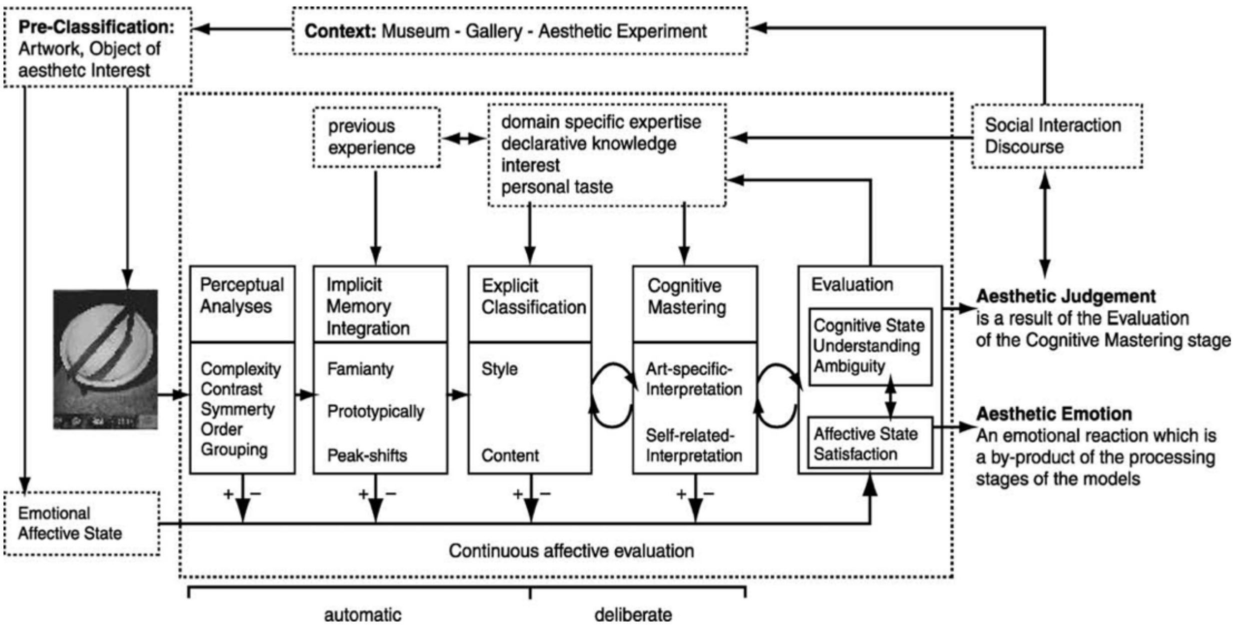


Figure 1. Neural model of the aesthetic experience (reproduced from Leder et al., 2004).

Leder et al. (2004) suggest that aesthetic experience involves five stages: perception, explicit classification, implicit classification, cognitive mastering and evaluation. The evaluation process ends with two parallel and different outputs: aesthetic judgment (a judgment of artwork's beauty) and aesthetic emotion (e.g., feeling of pleasure). In this model, all the processing stages proposed can increase or decrease the affective state and they are all accompanied by emotions. Successful processing results in positive affective states (pleasure or satisfaction), whereas non-successful processing results in negative emotions. Even before perception there are two factors that can influence the judgment. The first is pre-classification, that means that people tend to put what is seeing in a context. If I go in a museum I expect to see works of art of famous artists, so I take for granted that what I will see has some value. Researcher should thus take into consideration that there is a non-trivial difference between that visiting an art gallery and judging painting appearing on a computer screen. The other factor is the emotional state of the subject, that is to say, we are influenced by our mood when we make an aesthetic evaluation (Flexas et al., 2013)

When it comes to the model, the first stage is perception, that involves mostly the occipital cortex where the visual properties of the stimuli are processed. The first publications on neuroaesthetic were focused on the perceptual aspects of works of art. These studies tried to identify which visual characteristics of the stimuli could influence the perception of beauty in art (Conway & Livingstone, 2007; Ramachandran & Hirstein, 1999; Semir Zeki, 1999b). Indeed, many perceptual cues seem to influence aesthetic perception, for example clarity of the image (Reber, Winkielman, & Schwarz, 1998), complexity and symmetry (Berlyne, 1974; 1970; Frith & Nias, 1974), color (Jacobsen, 2002; Maffei & Fiorentini, 2008; Martindale & Moore, 1988)

In the second processing stage, there is the integration of the percept with the implicit memory. The result of this stage affect aesthetic processing even if it doesn't become conscious. The features that are evaluated in this process are familiarity, prototypicality and peak-shift effect. Experiments using "mere-exposure" paradigm showed that familiarity enhance affective preference for a stimulus, even though result with artworks are not always consistent (Hekkert & Van Wieringen, 1996). Prototypicality (Martindale & Moore, 1988), namely the amount to which an object is representative of a class of objects, also seems to affect the judgment of preference. Since prototypicality is built through experience it depends on the expertise of the subject, the more expert the more would be able to judge the work in relation to a style or a historical period. The peak-shift effect is a response that is stronger if the somehow exaggerate the properties of familiar objects, for example caricatures (Ramachandran, 2004).

The explicit classification is specifically dependent from the expertise and has to do with the observer's ability to recognize style and content. This ability make the aesthetic experience deeper and more complete. Moreover, expertise can provide the pleasure of generalization, i.e. the ability to recognize other examples of a style once one learned about it. The last two stages are cognitive mastery and evaluation. Experts subject tend to make judgments based on style, while naïve subject tend rely only (or mostly) on the content (Parsons, 1987). This information processing model has two distinct outcomes outputs: the aesthetic emotion and aesthetic judgment. The aesthetic judgment depends to a large extent by aesthetic emotion: the more pleasurable the emotion elicited by the artwork, the more positive the artwork will be found. The aesthetic judgment again is affected by expertise: laypeople rely more on emotional processing while, while experts perform more cognitive evaluations (Cupchik & Lazlo, 1992). Aesthetic preference is generated by the cognitive state, while aesthetic emotion is based on the affective state.

Neural basis of aesthetics appreciation

Burke in 1757 thought that the foundations of aesthetic experience were the same neural mechanisms of pleasure and pain. “The sense of the sublime, then, has its source in an unnatural tension of the nerves, such as is produced both by fear and by pain” and “beauty acts by relaxing the solids of the whole system”. Since then many theory about beauty where formulated and lately thanks to brain lesion and neuroimaging studies we gain information into the cognitive and neural underpinnings of aesthetic appreciation (Cela-conde, Agnati, Huston, Mora, & Nadal, 2011; Chatterjee, 2011). The firsts insight on the neural correlates come from neurodegenerative diseases that affected both artistic production and appreciation (Chatterjee, 2004; Zaidel, 2010). Cases reported in literature show that despite brain damages artists usually continue to be productive after recovery of diverse forms of disability.

Focal brain lesions produce specific alterations in aesthetic production and appreciation. In case of strokes usually artist's production display some alterations, somehow related to the area affected by the damage, for example when the lesion interest the right hemisphere the depiction of spatial relations is altered, some artist even leave out the left side of images when they draw (Blanke, Ortigue, & Landis, 2003; Schnider, Regard, Benson, & Landis, 1993). Kaczmarek (1991) reported the case of a painter who after a stroke to the left hemisphere, resulting in hemiparesis and aphasia, preserved his drawing skill but lost the ability to create the symbolic pictures he used to paint.

In artists suffering from dementing diseases, where the neurodegenerative damage is extensive, the skills appear to survive for many years into the illness, even after cognitive functions undergo severe deficits (Cummings, Miller, Christensen, & Cherry, 2008; Drago et al., 2006; Fornazzari, 2005; Miller & Hou, 2004) and capacities for appreciation are generally preserved (Graham et al., 2013; Halpern & O'Connor, 2013). People suffering from frontotemporal dementia (FTD) can even develop new artistic skills and enhance productivity despite progression of the disease (Cohen et al., 2016). However neurodegenerative diseases produce alterations in the production of art. Maurer et al. (2004) for example report a German artist and illustrator who suffered from Alzheimer's disease. He presented a gradual loss of the capacity to represent with precision but conserved the ability of using color and form in an aesthetically pleasant way. Neuropsychological approaches to art is anecdotal and qualitative, but make clear that there is no single brain region specifically linked to art or aesthetics (Cela-conde et al., 2011).

The first neuroimaging studies, whose aim was to identify the neural correlates of aesthetic judgment were published in the early 2000s (Cela-Conde et al., 2004; Jacobsen et al., 2006; Kawabata & Zeki, 2004; O. Vartanian & Goel, 2004). Kawabata and Zeki (2004) recorded the brain activity of participants with fMRI while assessing the stimulus beauty. During the observation of the stimuli that the participants found more beautiful, there was a significant activation of the orbitofrontal cortex, whether for the uglier stimuli correlated with activity in the motor cortex. Using the magnetoencephalography Cela Conde and colleagues (2004) have identified a particularly significant activity in the dorsolateral prefrontal areas of the left hemisphere, between 400 and 1000 ms after the onset of the stimuli considered beautiful.

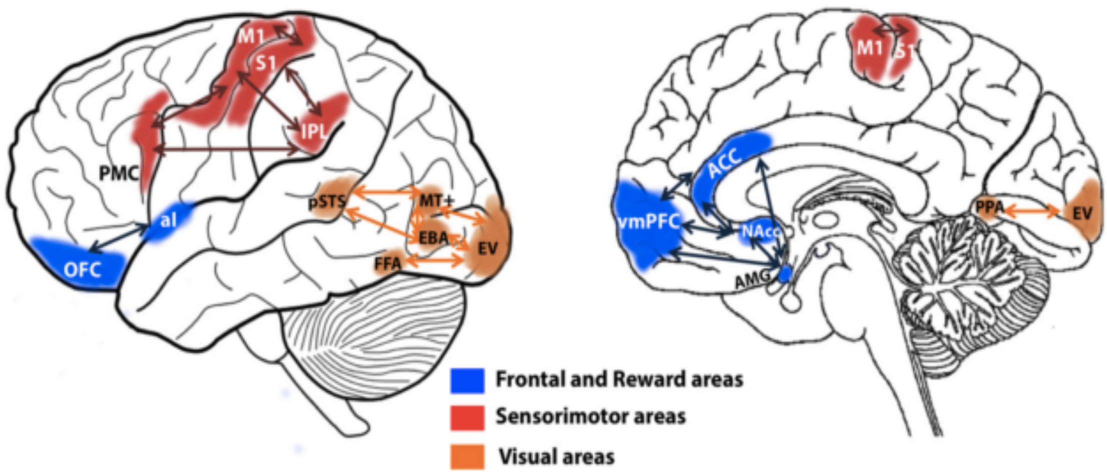


Figure 2. Schematic representation of the neural circuits implicated in aesthetic judgement tasks. In blue, brain regions associated with reward processing, in red, sensorimotor areas, in orange, visual areas, part of the occipitotemporal cortex. Reproduced from Kirsch et al. 2016.

Vartanian and Goel (2004) in their study of fMRI, observed a deactivation of the right caudate nucleus with decreasing preference for the stimulus and an increase in the fusiform gyrus and occipital areas with increasing preference. Another study is the one of Jacobsen et al. (2006), that is however a bit different form the other because he compares a beauty judgment task with a symmetry judgment, using not artworks but black and white figures of different complexity. They found activation in the anterior cingulate cortex and in the frontomedian cortex during the observation of stimuli considered beautiful. After these pioneering studies, many other followed, and many areas were identified as neural substrates in aesthetic appreciation. Nadal and Pearce (2011) report a summary of areas that seem to play a role in aesthetic experience. They suggest that the distributed neural system involve areas responsible for low-level cortical sensory processing, areas for high-level top-down processing and involved in evaluative judgment and an engagement of the reward circuit, including cortical and subcortical regions. This is also in line with Chatterjee (2003) who proposed that that processing aesthetic stimuli involves similar visual brain regions as processing any other kind of visual stimuli thus activation of the visual cortex (occipital areas for early, and ventral for later visual processing stages) but also an engagement of additional non perceptual processes like decision making and affection, then areas mediating emotions such as the anterior medial temporal lobe, medial, and orbital cortices and subcortical structures, but also areas involved in decision-making namely dorsolateral frontal and medial frontal cortices. Indeed several studies confirmed activation in occipital cortex (Cupchik et al., 2009; O. Vartanian & Goel, 2004), temporal cortex (Jacobsen et al., 2006; Yue et al., 2007), and in parietal cortex (Cela-Conde et al., 2009; Fairhall & Ishai, 2008; Lengger, Fischmeister, Leder, & Bauer, 2007), in cortical and subcortical regions associated with pleasure and reward (Tomohiro Ishizu & Zeki, 2011; Jacobsen et al., 2006; O. Vartanian & Goel, 2004), and in frontal cortical areas involved in decision-making and (Cattaneo et al., 2014a, 2014b; Cela-Conde et al., 2004; Cupchik et al., 2009; Vessel, Starr, & Rubin, 2012). Another system that seem to play a role is the motor system. On one hand art, and in particular depiction of humans, may activate the mirror system (Freedberg & Gallese, 2007; Umilta', Berchio, Sestito, Freedberg, & Gallese, 2012) On the other hand it seems that even abstract art can engage motor system because people tend to mimic the gesture that the painter used to paint (Ticini, Rachman, Pelletier, & Dubal, 2014; Umilta' et al., 2012).

Even if the number of studies on the neural underpinnings of aesthetic is growing, some issues have to be taken into account. First of all, the inconsistency of results between studies. Nadal et al. (2008) suggested that these discrepancies could be related to the different kinds of stimuli used, different number of male and female participants, different experimental procedures and different instructions and tasks used to measure aesthetic responses. A recent meta-analysis (Brown et al., 2011) with stimuli from different modalities found some regions that respond independently from the stimulus type, thus suggesting a modality-independent system for the judgment of beauty a topic that still need to be explored. Finally, neuroimaging studies are mostly correlational in nature the specific role of different brain regions involved in aesthetic appreciation is yet to be clarified.

1. Study 1: Hemispheric asymmetry of liking for paintings

1.1. Introduction

As mentioned in the general introduction, despite growing interest in the field of neuroaesthetics many issues regarding the mechanisms underlying art appreciation remain unsolved. One of them that merits further research is whether both hemispheres are involved to the same extent in the appreciation of visual art. It is well documented that neither hemisphere is solely responsible for art production or appreciation (Zaidel, 2013, 2015). However, the existence hemispheric asymmetries in low-level and high-level perceptual functions (Hellige, 1993; Hellige, Laeng, & Michimata, 2010), together with evidence from brain lesion studies (Bromberger et al., 2011), suggest the possibility that some processes underlying aesthetic appreciation are lateralized. In fact, experiments on hemispheric asymmetries in memory and liking for different styles of art suggest that this is the case.

Zaidel and Kasher (1989) showed that laypeople recall surrealist paintings with greater accuracy when presented in the right visual field than when presented in the left one. No such advantage was observed for realist paintings. This suggests an advantage of the left hemisphere in processing meaningful but incongruous images (Zaidel & Kasher, 1989; Zaidel, 1994). Such patterns of asymmetry in memory for artworks can change with acquired expertise, especially in relation to abstract artworks (Vogt & Magnussen, 2005).

A number of studies have used indirect methods to test for hemispheric asymmetries in preference for artworks. Early studies focused on the possible association between aesthetic preference and handedness and sex. For instance, Van Houten, Chemtob, and Hersh (1981), presented pairs of artworks tachistoscopically in the left or right visual field of participants whose task was to judge which artwork in each pair was aesthetically superior. Performance on the task was defined as the degree to which participants' judgments approached those made by art experts. Participants classified a -priori as "highly-lateralized", either on the basis of handedness or on the basis of sex, showed superior performance in one of the visual fields (there was no systematic evidence supporting one hemisphere advantage). In turn, judgments of participants classified a priori as "little-lateralized" were equally accurate—that is to say, in agreement with those of the experts—irrespective of the visual field in which the artworks were projected. These findings extended prior evidence showing that level of lateralization derived by handedness could predict subjective preference for paintings in which the important content was skewed to either the left or the right side of the image. In particular, Levy (1976) found that right-handers showed a preference for images in which the important content was skewed to the right, probably compensating for their pre-existing attentional bias to the left and resulting into a more "balanced" image (Ellis & Miller, 1981; McLaughlin, Dean, and Stanley, 1983, Beaumont, 1985; Valentino et al. 1988; Mead and McLaughlin 1992). More recently, using a divided visual field (DVF) paradigm, Coney and Bruce (2004) investigated possible lateral asymmetries in aesthetic evaluation of paintings and found that paintings (of all art styles) were in general liked more when presented in the right visual field (RVF).

Neuroimaging and electrophysiological evidence also suggests a degree of lateralization in aesthetic judgments, though not always consistent with behavioural data. For instance, in an ERP study, Jacobsen and Höfel (2003) found that evaluative aesthetic judgments of complex graphic patterns revealed a more pronounced right lateralization compared to descriptive judgments (i.e., judge with regard to symmetry) of the same patterns (see also Jacobsen & Hofel, 2001). The authors argued that the right lateralization they reported may reflect general processing characteristics of evaluative categorization, since a similar pattern was reported by prior studies investigating neural basis of evaluative decisions using a different task (e.g., Cacioppo, Crites, & Gardner, 1996). In a MEG study, Cela-Conde et al. (2009) found different activity between male and female observers' parietal regions when participants judged paintings and photographs as beautiful. In particular, aesthetic appreciation was mediated by significant bilateral parietal activity in female observes, whereas activity in parietal regions was lateralized to the right hemisphere in male observers (Cela-Conde et al., 2009).

Using brain stimulation, was found that modulating activity in the left prefrontal cortex affected aesthetic appreciation of paintings (Cattaneo, Lega, Flexas et al., 2014a; Cattaneo, Lega, Gardelli et al., 2014b), while modulating activity in the right prefrontal cortex influenced the apparent attractiveness of faces (Ferrari et al., 2015). Moreover, symmetry, an important cue in driving the aesthetic judgment, seems to be encoded preferentially in the right hemisphere (Bona et al., 2015).

In this study the aim was to investigate possible hemispheric lateralization in judging paintings, using a DVF paradigm as in Coney and Bruce (2004). In Coney and Bruce 40 participants were tested, but only four were males. Prior neuroimaging and behavioural evidences suggest gender differences in the way the two hemispheres are involved during aesthetic appreciation, 80 participants were recruited, 40 males and 40 females. Moreover, prior evidence has revealed that abstract and figurative paintings are mediated by different neural mechanisms, at least in laypeople (Cattaneo, Lega, Gardelli et al., 2014b; Cattaneo, Lega, Ferrari et al., 2015). Here participants are presented with many paintings, half representational, and half abstract. Coney and Bruce (2004) reported similar lateralization irrespective of art style, however, there is also evidence of sex differences in preference for abstract and figurative art (Bernard, 1972; Chamorro-Premuzic, Reimers, Hsu, & Ahmetoglu, 2009; Frumkin, 1963; Furnham & Walker, 2001; Savarese & Miller, 1979). Hence degree of lateralization in males and females may differ for abstract and representational stimuli.

1.2. Method

Participants

Eighty participants (40 females, mean age = 22.8 ys, SD = 2.6, range = 19–32) with no previous formal or informal training 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 colour perception.

Material and Procedure

Participants sat in front of a 15.5” PC (1280*800 pixels) screen at an approximate distance of 57 cm, in a normal-lightened and silent room, and were asked to perform a computerized evaluation task. Stimuli to be evaluated consisted of 104 paintings (52 representational, 52 abstract) belonging to a lager set of images used in previous work (Cattaneo et al., 2014b; Cela-Conde et al., 2004, 2009). Representational paintings comprised realist, impressionist and postimpressionist artworks. A divided visual field procedure was used (following strict criteria recommended by Bourne, 2006). The timeline of an experimental trial is presented in Figure 1.1. Each trial started with a central fixation cross appearing for 500 msec. Hence a painting (subtending approximately 6.5° x 7° degrees of visual angle) was presented for 150 ms located 3° to the left or 3° to the right of the fixation cross. Participants had to indicate as fast as possible whether they liked the painting or not. The central fixation cross remained visible until participants' response and participants were instructed to maintain fixation over the central fixation cross throughout the task. Participants responded with their right index and middle finger, response key assignment for yes/no responses was counterbalanced across participants.

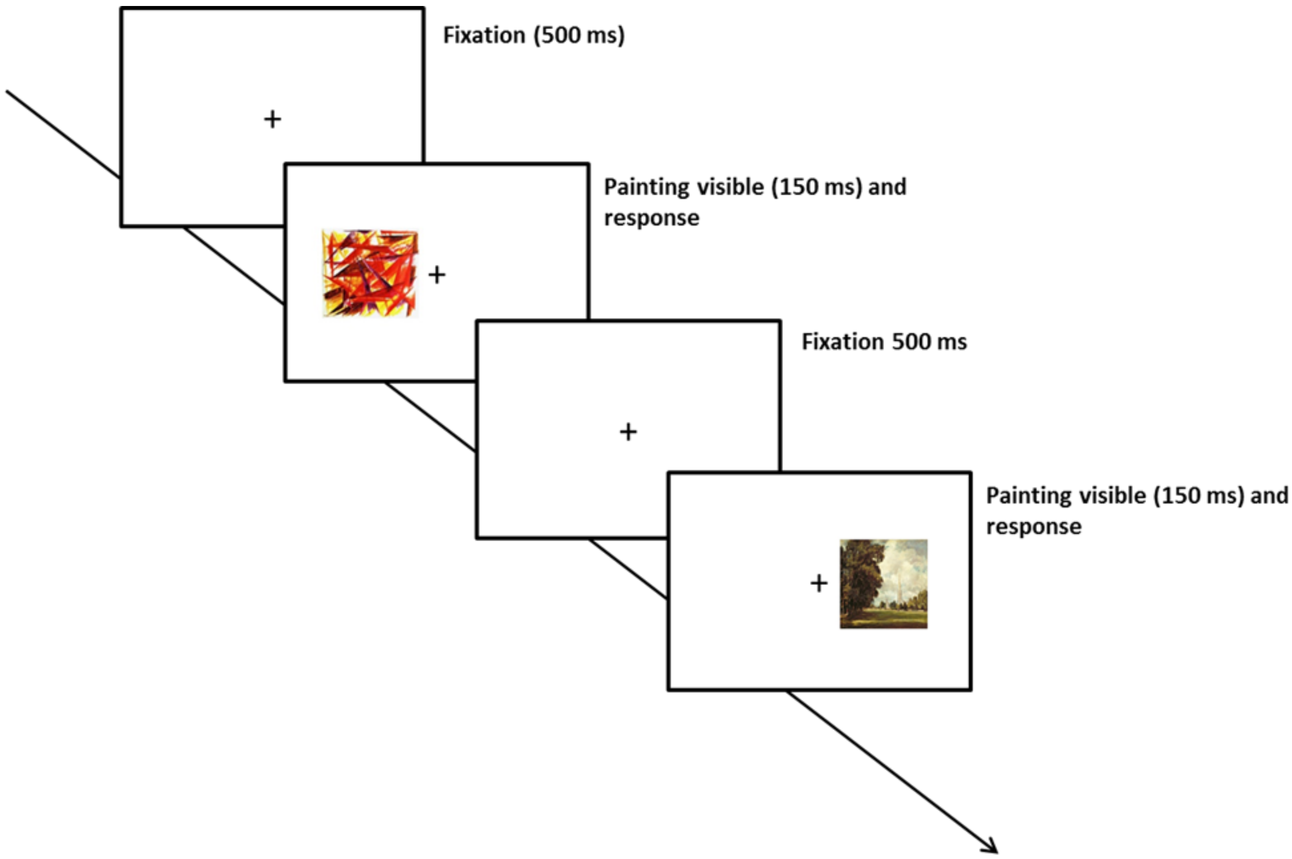


Figure 1.1 Timeline of an experimental trial. Participants were presented with a painting of either figurative or abstract category to the left or right of a central fixation cross and had to indicate whether they liked it as fast as possible.

Each painting appeared once to the left and once to the right of the central fixation, so that the experiment consisted of 208 trials. Four practice trials were presented before the experiment (using paintings not shown in the experiment) to familiarize participants with the task. Paintings were presented in random order with the exception that the same painting was never shown consecutively. A chinrest was used to ensure that the head was aligned with the middle of the screen and that the distance from the screen was kept constant. Percentages of "I like it" responses and mean response latencies (RT) were recorded. E-Prime 2 (Psychology Software Tools, Pittsburgh, PA) was used for stimuli presentation and data collection.

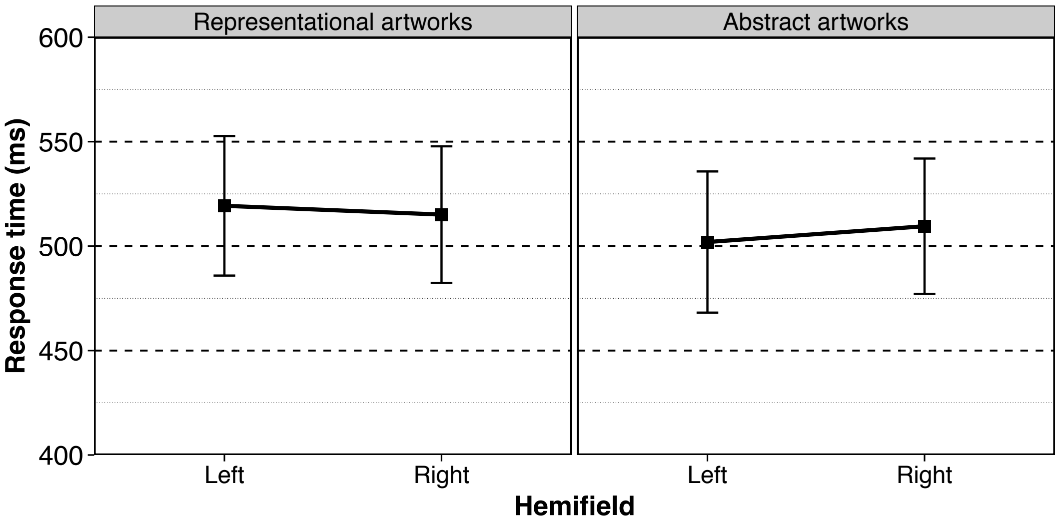
Analysis We analysed the effects of hemifield (left vs. right), artwork category (abstract vs. representational), and sex (men vs. women) on participants' liking responses and response times by means of generalized linear mixed effects models (Hox, 2010; Snijders & Bosker, 2012). This method accounts simultaneously for the between-subjects and within-subjects effects of the independent variables (Baayen, Davidson, & Bates, 2008). It is thus especially suitable to study aesthetic appreciation, where people differ considerably in their responses to different artworks (Silvia, 2007; Brieber, Nadal, Leder, & Rosenberg, 2014; Cattaneo et al., 2015). For this study, the linear mixed effects models were used to analyze the impact of hemifield, artwork category, and sex, as well as their interaction, on liking and response times. Additionally, in order to control for the effects of the response key used by participants to indicate they liked each stimuli or not (left for "I like" vs. right for "I like") we also included this variable in both models (liking and response time). All predictor variables were categorical, and the reference levels were *left* for hemifield, *abstract* for artwork category, *women* for sex, and *left* for response key. All predictor variables were successive difference coded. 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. Thus, both models included the triple interaction between hemifield, artwork category, and sex, as well as the control variable response key for liking, as fixed effects, and random intercepts and slope for the interaction between hemifield and artwork category within participants, and random intercepts and slope for hemifield 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 for liking and scale for response time). 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.

1.3 Results

Liking responses. We excluded extremely fast and slow trials from the analyses. These were defined based on the interquartile range (IQR) criterion. First we calculated participants' IQR for each hemifield. Thereafter, trials in which response times were over 1.5 times the IQR above the third quartile or below the first quartile were removed from the dataset (4.4% of trials). The results of the linear mixed effects model of liking responses revealed a main effect of artwork category z = 5.150, p < .001, indicating that participants liked representational artworks (58.8%) more than abstract artworks (37.1%). The main effects of hemifield z = 1.410 p = .159, sex z = 0.083, p = .934, and response key z = 0.702, p = .483 were non-significant. The interaction between hemifield and artwork category was significant z = 2.356, p = .018 (figure 1.2), indicating that whereas participants liked representational artworks more when presented in the right visual field (61.1%) than when presented in the left visual field (56.5%), liking for abstract artworks was unaffected by hemifield (37.2% when presented in the right, 36.9% when presented in the left). None of the remaining interactions reached significance, including hemifield by sex z = 1.562, p = .118, artwork category by sex z = 0.466, p = .642, and hemifield by art category by sex z = 0.684, p = .494.

Response times. As before, extremely fast and slow responses were excluded from the analysis (4.4% of trials). The linear mixed effects model revealed a main effect of artwork category $t_{(106.37)}$ = 2.034, p = .044, indicating that participants responded faster to abstract artworks (505.74 ms) than to representational artworks (517.20 ms). The main effects of visual field $t_{(78.03)}$ = 0.371, p = .712, sex $t_{(76.88)}$ = 1.113, p = .269 and response key $t_{(76.99)}$ = 0.070, p = .944 were non-significant.

A)



B)

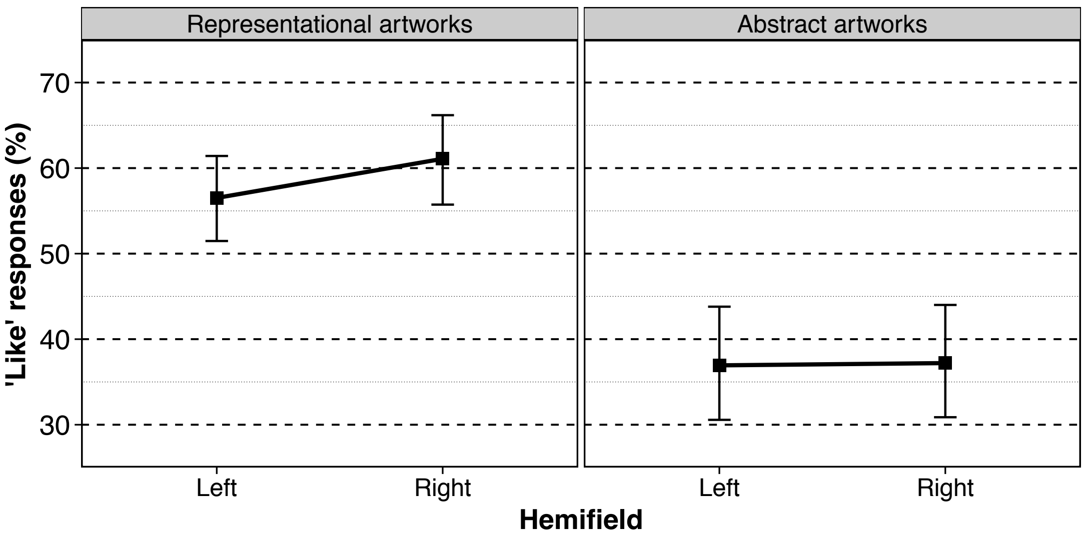


Figure 1.2. Frequency histograms for "I like it" responses **(A)** and mean response latencies in msec **(B)** as a function of art category and visual filed in which the painting appeared. Participants overall liked more and took more time to evaluate figurative than abstract artworks. Critically, figurative paintings were liked more when displayed in the RVF compared to the LVF. Error bars depict ± 1 SEM. Asterisks indicate a significant visual field difference.

The interaction between hemifield and artwork category was significant $t_{(77.82)} = 2.055$, $p = .043$ (figure 1.3), indicating that whereas participants gave faster responses to representational artworks when presented in the right hemifield (515.10 ms) than when presented in the left (519.31), they gave faster responses to abstract artworks when presented in the left hemifield (501.95 ms) than when presented in the right (509.53 ms). None of the remaining interactions reached significance, including hemifield by sex $t_{(77.95)} = 0.285$, $p = .776$, artwork category by sex $t_{(77.77)} = 1.426$, $p = .158$, and hemifield by art category by sex $t_{(77.92)} = 0.980$, $p = .330$.

1.4 Discussion

In this first study the addressed issue, relatively unexplored in experimental settings, is that of the hemispheric lateralization of the processing of features relevant to aesthetic preference (Coney & Bruce, 2004; Zaidel, 2015). We used a divided visual field paradigm to test for hemispheric asymmetries in men and women's preference for abstract and representational artworks.

We included abstract and representational artworks because studies have shown that people respond differently to them, and that their appreciation engages different neural processes (Cattaneo et al., 2014a, 2014b, 2015; Fairhall & Ishai, 2008). Indeed, in line with previous experiments, we found that participants liked representational artworks more than abstract artworks (Cattaneo et al., 2015; Furnham and Walker, 2001; Kettlewell et al., 1990; Knapp and Wulff, 1963; Pihko et al., 2011). This common finding is generally attributed to laypeople's approach to art, which can be conceived as an extension of general viewing and perceptual processes (Cupchik & Gebotys, 1988). Laypeople lack experts' knowledge and schemes that allow them to extract meaning from artworks' style, expressive use of the medium, allusions to other artworks, and so on. Thus, they base their viewing of art mainly on object schemas, and search for recognizable elements that can elicit pleasant associations. Given that, by definition, abstract art does not depict immediately identifiable objects, laypeople, such as our participants, usually find little that fit their object schemas, and therefore, little to elicit the pleasant feelings they expect from artworks. Representational artworks, conversely, offer laypeople the chance for understanding, if not the artwork itself, at least the depicted scene.

Our main finding showed that, independently of their sex, participants liked representational paintings more when presented in the right visual field, and that liking for abstract paintings was unaffected by presentation hemifield. These results suggest certain processes underlying laypeople's liking for representational art are hemispherically lateralized. But which processes? Two separate strands of research converge on a suggestive possibility. On the one hand, eye tracking experiments of art appreciation have shown that when laypeople look at representational paintings they adopt a local, rather than global, viewing strategy. That is to say, they fixate mostly on informative details of recognizable objects, rather than on background features or on the relations among objects (Nodine, Locher, & Krupinski, 1993; Vogt, 1999; Vogt & Magnussen, 2007; Zangemeister, Sherman, Stark, 1995). This strategy yields little for abstract art, where the foreground-background distinction is blurred, and where a local viewing strategy reveals nothing but meaningless and disjointed patches and brushstrokes of paint. On the other hand, behavioral, brain lesion and brain imaging studies have shown that both hemispheres differ in the extent to which they are involved in processing local and global features of visual stimuli. Specifically, the left hemisphere is relatively specialized in processing the local details of visual stimuli and in determining whether objects belong to given categories; the right hemisphere is relatively specialized in processing the global or configural properties (Fink et al., 1997; Hellige et al., 2010; Hübner, 1998; Van Kleeck, 1989).

Weaving these two strands together, we argue that certain processes involved in the performance of the liking task—specifically, participants' search for recognizable informative features—were facilitated when representational artworks were presented in the right visual field, given the left hemisphere's advantage in processing such local features. This interpretation is also congruent with participants' faster responses when representational artworks were presented in the right visual field. Conversely, processing of configural features could have been facilitated when abstract simuli were presented in the left visual field, given the right hemisphere's advantage in processing global features, a possibility that is supported by the faster response times in this condition. However, this potential facilitation did not translate into differences in liking, probably because, as aforementioned, laypeople lack the necessary knowledge to make sense of and use configural or relational features in their judgments.

Our results are in line with Coney and Bruce's (2005): Both studies report increased liking when artworks were presented in the right visual field. However, whereas Coney and Bruce (2005) found that presentation hemisphere mainly influenced liking for modern artworks (including abstract paintings) but not traditional artworks, we found that it influenced liking for representational but not abstract artworks. There are several reasons that might account for this discrepancy. First, the stimuli categories in both studies do not overlap. Our set of representational artworks includes styles that cluster as modern art (Cubism and Expressionism) and as traditional art (Renaissance and Impressionism) in Coney and Bruce's (2005) study. Second, whereas our set of stimuli includes works by renowned artists, an effort was made to exclude familiar pieces, especially those that are usually exhibited at museums (Cela-Conde et al., 2004, 2009), the images in Coney and Bruce's (2005) set "were selected from among those currently on display in museums and galleries around the world" (Coney & Bruce, 2005, p. 187). Thus, both stimuli sets might differ as to the familiarity of the works included. Third, whereas Coney and Bruce (2005) explicitly "invited participants to rate their *emotional* reaction to the stimuli" (Coney & Bruce, 2005, p. 194), no such indication was given to the participants, and in fact, the set used in the present study excluded works that could evoke strong emotional responses (Cela-Conde et al., 2004, 2009). Thus, it is possible that the materials and instructions in Coney and Bruce's (2005) study prompted participants to focus on the emotional aspect of their experience, whereas our materials and instructions prompted participants to focus on the more perceptual features of the images.

2. Study 2: The contribution of brain region V5/MT to the perception of implied motion in art and its appreciation

2.1. Introduction

After addressing a more general issue regarding hemispheric advantage in aesthetic appreciation, the next two studies presented aim to deepen our knowledge about the specific role of sensory areas into not only art perception, but also art appreciation. One interesting matter is the role of dynamism. Indeed, static images can contain cues conveying information about objects' direction and speed, such as dynamic balance, stroboscopic effects, forward lean, blurring, or action lines (Cutting, 2002). In such cases, motion is implied in form. These form cues contribute to enhance, or even create, the perception of motion (e.g., Krekelberg, Vatakis, & Kourtzi, 2005; Pavan, Cuturi, Maniglia, Casco, & Campana, 2011; Ross, Badcock, & Hayes, 2000). Deriving a sense of motion from form cues is the basis for understanding action photography, graphics, flow charts, and narrative illustrations (Cohn & Maher, 2015). It is in the visual arts, however, that form cues are used most often, systematically, and successfully to create a sense of motion. Artists have exploited visual form resources to convey a sense of motion from static depictions in painting and sculpture for centuries (Gombrich, 1964). The use of form to convey a sense of motion in art reached its peak in the early twentieth century, when some groups of artists developed novel means to reflect the remarkable dynamism and speed that characterized their time. The Futurist Manifesto explicitly declared that ". . . the splendor of the world has been enriched by a new beauty: the beauty of speed." (Martinetti, 1908, p. 286). The representational content of the images was still present, but only as an embodiment of motion, seeking to capture "the dynamic sensation itself" (Boccioni, Carrà, Russolo, Balla, & Severini, 50 1910, p. 289). Figure 2.1A illustrates the use of stroboscopic effects to convey the sensation of movement of a dog walking. Similarly, abstract action painting represents another paradigmatic example of the use of formal features in art to create a sense of motion in the viewer, even in the absence of recognizable objects (Figure 2.1B). Indeed, in abstract action painting, developed toward the mid-twentieth century by some of the American Abstract Expressionists, the canvas became “an arena in which to act” (Rosenberg, 1952), rather than a place to produce (or reproduce) an object. Over the last decade, researchers have sought to understand the brain mechanisms involved in the appreciation of art (Chatterjee & Vartanian, 2014; 65 Chatterjee, 2011, 2014a, 2014b; Freedberg & Gallese, 2007; Ishizu & Zeki, 2011, 2013; Nadal & Pearce, 2011; Nadal, 2013).

Figure 2.1. A) *Dynamism of a Dog on a Leash*. Giacomo Balla, 1912. Free from copyright at http://www.wikiart.org/ . B) *Untitled (Abstraction No. 3)*. Earle M. Pilgrim, 1964. Free from copyright at https://commons.wikimedia.org/

The picture emerging from this line of research is that of a complex interaction between neural systems involved in sensory, affective, and semantic processing (Chatterjee & Vartanian, 2014; Freedberg & Gallese, 2007; Nadal, 2013; Ticini, Rachman, Pelletier, & Dubal, 2014). Consistent neuroimaging results show an increased activity in sensory processing regions for artworks and other visual stimuli that people find more appealing.
For instance, Vartanian and Goel (2004) asked participants to evaluate their preference for representational and abstract paintings on a 0–4 scale. Their fMRI results showed that activity in bilateral occipital gyri, left cingulate sulcus, and bilateral fusiform gyri increased together with preference (see also Cupchik, Vartanian, Crawley, & Mikulis, 2009; Lacey et al., 2011). In another fMRI study, Zeki and Stutters (2012) asked participants to rate their preference for kinetic dot patterns. They observed that preferred configurations produced stronger activity in visual areas V5, V3A/B, and in the parietal cortex. The functional significance of this enhanced activity in sensory brain regions during aesthetic appreciation is probably related to an increased orientation toward the perceptual features people find appealing (Cupchik et al., 2009; Nadal, 2013). Similar findings have also been reported in studies on the appreciation of dance (Calvo-Merino, Jola, Glaser, & Haggard, 95 2008; Cross, Kirsch, Ticini, & Schütz-Bosbach, 2011) and music (Koelsch, Fritz, von Cramon, Müller, & Friederici, 2006). In line with these neuroimaging results, brain stimulation studies have shown that transcranial magnetic stimulation (TMS) reduces the appreciation of dance when applied over the extrastriate body area (Calvo-Merino, Urgesi, Orgs, Aglioti, & Haggard, 2010), and reduces the appreciation of representational paintings—though not abstract ones—when applied over the lateral occipital area (Cattaneo et al., 2015). Converging evidence from neuroimaging and brain stimulation studies shows that area V5 in the occipito-temporal cortex plays a key role in the computation and cognitive representation of the direction and speed of moving objects (e.g., Beckers & Zeki, 1995; Zeki et al., 1991; for reviews, see Born & Bradley, 2005; Zeki, 2015). The representation of implied motion also relies on neural activity in V5 (e.g., Fawcett, Hillerbrand, & Singh, 2007; Kourtzi & Kanwisher, 2000; Krekelberg et al., 2005; Lorteije et al., 2006; Proverbio, Riva, & Zani, 2009; Senior, Ward, & David, 2002). In particular, in implied motion processing V5 is thought to be involved in the integration of top-down object categorization and knowledge with low-level form cues

to provide a unified perception of the motion of objects (e.g., Kourtzi & Kanwisher, 2000; Lorteije et al., 2006). In this study we were interested in investigating the intriguing possibility that V5 activity is related not only to the generation of a sense of motion from visual cues used in artworks (Kim & Blake, 2007; Thakral, Moo, & Slotnick, 2012), but also to the appreciation of those artworks. To this aim, we presented art-naïve participants with a series of (unfamiliar) paintings and asked them to express whether or not the paintings conveyed a sense of motion, and whether or not they liked them, while TMS was simultaneously applied either over Vertex (control condition) or over V5. We expected TMS over V5 to cause a reduction in participants' perception of motion in the paintings. As noted above, aesthetic appreciation is accompanied by enhanced activity in sensory brain regions (Cupchik et al., 2009; Lacey et al., 2011; Vartanian & Goel, 2004; Zeki & Stutters, 2012). In line with such evidence, it is conceivable that, by encoding the sense of motion, V5 also contributes to the appreciation of art. Therefore, if the strength with which motion is perceived is related to art appreciation, then interfering with motion detection should also result in a reduction in the liking of artworks. However, in a prior fMRI study, Thakral et al. (2012) found that activity in V5 tracked motion but not pleasantness when participants viewed representational paintings. Hence, the extent to which sensory regions are involved in the aesthetic process seems to depend on the kind of stimuli. Indeed, we already pointed out in study 1 that different cognitive and neural mechanisms mediate laypeople's aesthetic appreciation of representational and abstract artworks. In particular, when viewing abstract art, more attention is allocated to the low-level features (i.e., motion, colors, or orientation; Cupchik et al., 2009; Nadal, 2013). Thus, the aesthetic appreciation of abstract art seems to be closely related to activity in sensory brain regions. If this is the case, TMS over V5 can be expected to reduce the experience of motion for both abstract and representational paintings, but reduce liking only—or mainly—for abstract paintings. Hence, although implied motion can be elicited by both figurative and abstract artworks, interfering with motion detection may affect appreciation of representational and abstract art to a different extent. To examine this possibility, in our experiment we used both representational and abstract paintings

2.2 Method

Participants

Thirty-six neurologically healthy Italian students (10 males, Mean age: 23.3 years, SD: 2.8 years) with no previous training or special interest in art, assessed with a brief screening questionnaire (Brieber, Leder, & Nadal, 2015; Brieber, Nadal, Leder, Rosenberg, & Martinez, 2014), participated in the study. All participants were right-handed (Oldfield, 1971), and were naïve to the purpose of the study. They all had normal or corrected-to-normal vision, and normal color vision. Prior to the experiment, each participant filled out a questionnaire (translated from Rossi, Hallett, Rossini, & Pascual-Leone, 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.

Material

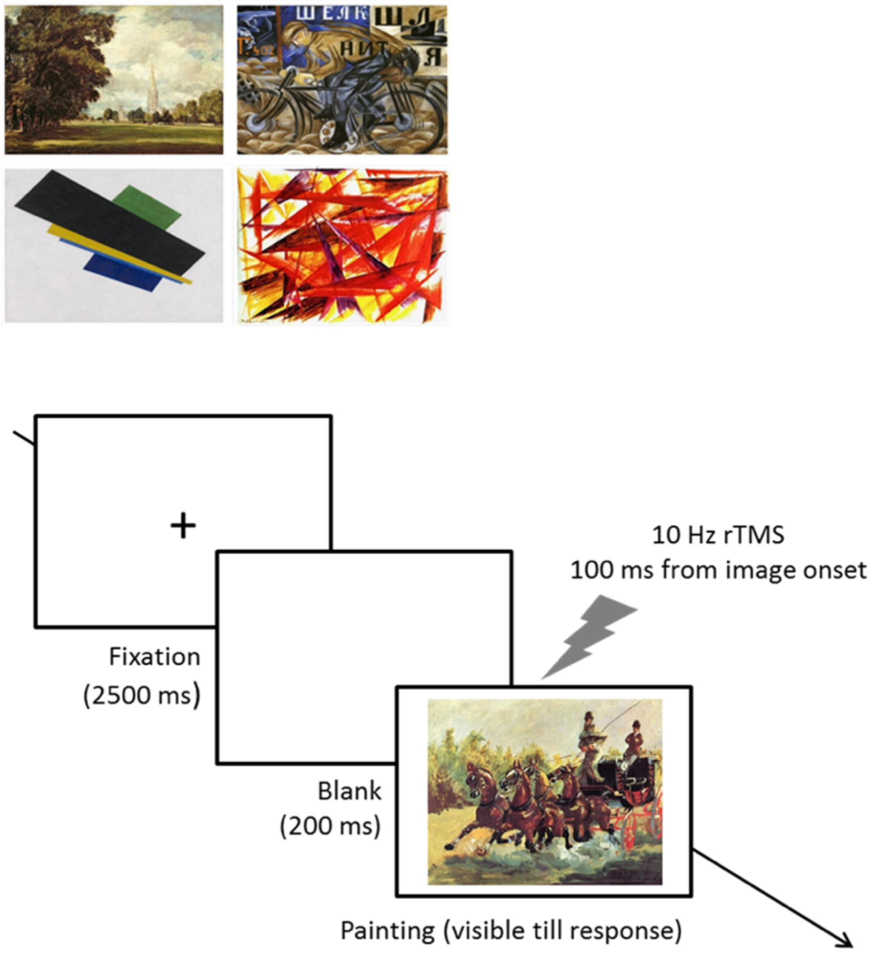
Stimuli consisted of 80 representational paintings and 80 abstract paintings taken from a large set of reproductions of paintings from the eighteenth to the twenty-first century, covering a wide range in the extent to which they conveyed a sense of motion (i.e., from quite stationary to very dynamic; see Figure 2 for examples). Representational paintings contained examples of varied representational content, such as still lives, landscapes, and genre painting, and from varied styles, including—but not limited to—classic and contemporary realism, impressionism, and futurism. Abstract artworks exemplified different manifestations of abstract painting, including geometrical abstraction, neoplasticism, lyrical abstraction, abstract expressionism, and action painting. Although they were the work of renowned artists, this set included only 210 relatively unknown pieces, in line with previous research (Cattaneo et al., 2014a, 2014b; Cela-Conde et al., 2004, 2009). In a pilot study, 18 right-handed participants (9 males, Mean age = 24.0 years, SD = 2.16), with no previous training or practice in art and not taking part in the TMS experiment, rated on a 1–7 Likert scale the sense of motion conveyed by each painting (1 = very stationary;7= very dynamic) and their liking for each painting (1 = I do not like it at all;7= I like it very much). The order of Motion and Liking task was counterbalanced across participants; abstract and representational paintings were presented blockwise, in random order and viewed at a self-paced rate. Pearson correlation (two-tailed) analysis indicated that the more a painting was perceived as dynamic, the more it was liked, this being the case for both representational paintings, $r(78) = .433$, $p < .001$, and abstract paintings, $r(78) = .829$, $p < .001$. 23

Procedure

The experiment was conducted in a normally lit and silent room. Participants were seated in front of a 17" PC screen (1280 × 800 pixels) at an approximate distance of 57 cm, and asked to perform a computerized rating task. The experiment consisted of two task conditions: A motion rating task and a liking rating task. Each task was consecutively performed twice, once for each TMS site (see below). Figure 2.2 shows the timeline of an experimental trial. Each trial started with a fixation cross presented for 2500 ms 240 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. In the sense of motion task, participants were instructed to indicate, as fast as possible, whether they got a sense of motion from the painting or not. In the liking task, they were asked to indicate whether they liked the painting or not. In both cases participants used left/ right key pressing with their right index and middle finger. Response key assignment for yes/no responses was counterbalanced across participants. After the response, a new trial started. In each TMS block, 80 paintings were presented (all representational or abstract, depending on the art condition group, see below). Within each TMS block, stimuli were presented in random order. There was a short break (2–3 mins) between blocks. Order of tasks (Motion and Liking) and order of TMS site stimulation (V5 and Vertex) was counterbalanced across participants. The order of TMS site stimulation was kept the same for each participant for the two experimental tasks. Participants were randomly assigned to two different groups: One group only viewed representational paintings, and one group only viewed abstract paintings. Transcranial magnetic stimulation 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 reporting disrupting effects of V5 TMS on motion perception at this stimulation intensity (e.g., Campana, Cowey, & Walsh, 2006; Cattaneo & Silvanto, 2008; Muggleton, Juan, Cowey, & Walsh, 2003; Silvanto, Lavie, & Walsh, 2005). V5 was localized as the point situated 3 cm dorsal and 5 cm lateral to the inion, as in previous studies (e.g., Beckers & Zeki, 1995; Ellison, Battelli, Walsh, & Cowey, 2003; Grossman, Battelli, & Pascual-Leone, 2005; Senior et al., 2002; Silvanto et al., 2005). The coil was held tangential to the skull with the handle oriented parallel to the horizontal plane and pointing toward the occiput, and hence adjusted for each participant in order to minimize discomfort. We stimulated the left hemisphere, as done by many other studies (Antal et al., 2003; Beckers & Homberg, 1992; Koivisto et al., 2010; Silvanto & Cattaneo, 2010; Silvanto et al., 2005; Stewart, Battelli, Walsh, & Cowey, 1999). 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 Vertex the coil was oriented tangentially to the scalp parallel to the nasion-inion line. Three TMS pulses were delivered at 10 Hz (pulse gap of 100 ms) 100 ms after the onset of each painting. This timing of stimulation was chosen on the basis of previous electrophysiological evidence showing that implied motion (i.e., motion in pictures) detection activates V5 100 ms later than real motion (see Lorteije et al., 2006). Short 10-Hz pulse trains are andard protocols for interfering with activity in the targeted brain regions, inducing virtual lesions (e.g., Bona, Cattaneo, & Silvanto, 2015; Cattaneo, Mattavelli, Papagno, Herbert, & Silvanto, 2011; Pitcher, Walsh, Yovel, & Duchaine, 2007). Moreover, triple-pulse 10-Hz TMS allows to cover an early time window in which a first aesthetic impression is likely to be formed, as evidenced by prior converging evidence (e.g., Cattaneo et al., 2014a, 2014b; CelaConde et al., 2009; De Tommaso, Sardaro, & Livrea, 2008; Jacobsen & Höfel, 2003; Sbriscia-Fioretti et. al, 2013; Wang et. al, 2012). Prior to the experiment, short practice blocks (with stimuli different 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 was used for stimuli presentation, data collection and TMS triggering. The whole experiment lasted approximately 75 minutes. None of the participants reported phosphene detection during the experiment.

A

B



A) Upper panel, from left to right: example of a representational painting mostly perceived as dynamic (*The Cyclist*. Natalia Goncharova, 1913) and of a representational painting conveying little sense of motion (*Salisbury Cathedral from Lower Marsh Close*. John Constable, 1820). Lower panel, from left to right: example of an abstract painting mostly perceived as dynamic (*Red Rayonism*. Mikhail Larionov, 1913) and of an abstract painting mostly perceived as static (*Suprematism, 18th Construction.* Kazimir Malevich, 1915). **B)** Example of an experimental trial. In each trial a painting was presented in the middle of the screen and participants had to indicate as fast as possible whether they perceived the image as dynamic or not (sense of motion task) or whether they liked it or not (liking task). The painting shown in this figure is *Le Comte Alphonse de Toulouse Lautrec Conduisant un Attelage à Quatre Chevaux*, by Henri de Toulouse-Lautrec, 1881. All paintings shown in this Figure are free from copyright at http://commons.wikimedia.org/ and/or http://www.wikiart.org/).

2.3 Results

Percentage of yes/no responses and Mean response times were recorded for both the Motion and Liking task. Figure 2.3 shows the Mean percentage of paintings judged as dynamic in the Motion task and the Mean percentage of paintings liked in the Liking task, for participants judging representational paintings and for those judging abstract artworks.

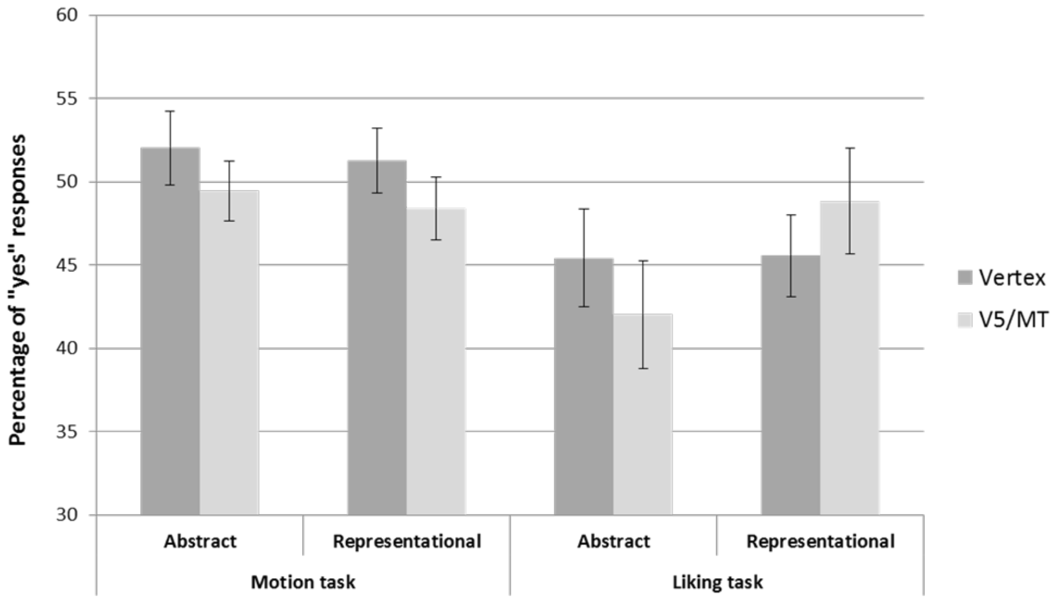


Figure 2.3 Frequency histograms for "I find this dynamic" (Motion task) and "I like it" (Liking task) responses as a function of Art-style (half participants viewed abstract paintings and half representational paintings). TMS over V5 reduced the number of paintings perceived as dynamic irrespective of art style. In turn, TMS over V5 selectively reduced appreciation for abstract artworks. Error bars depict ± 1 SEM.

A mixed repeated-measures ANOVA with TMS site (V5 vs. Vertex), Task (Motion vs. Liking) as within-subjects variables, and Art-Group (Representational vs. Abstract) as between-subjects variable was performed on the percentage of "yes" responses. The analysis revealed a significant TMS site × Task × ArtGroup three way-interaction, $F(1, 34) = 4.38$, $p = .044$, $\eta 2\ p = .11$. The significant three-way interaction was further investigated in each group by a repeated-measures ANOVA with Task and TMS site as within-subjects variable. For the Representational art group, the ANOVA showed no significant main effects of either Task, $F(1, 17) = 1.2$, $p = .33$ $\eta 2$ $p = .06$, or TMS site, $F(1, 17) < 1$, $p = .87$, $\eta 2$ $p = .002$. The TMS × Task interaction was significant, $F(1, 17) = 6.19$, $p = .024$, $\eta 2$ $p = .27$. Post-hoc comparisons showed that TMS over V5 reduced the number of paintings perceived as dynamic compared to the Vertex condition, $t(17) = 2.70$, $p = .030$ (Bonferroni-Holm correction applied). In turn, TMS did not affect the Liking task, $t(17) = 1.46$, $p = .32$. For the Abstract art group, a similar analysis revealed a significant main effect of Task, 360 $F(1, 17) = 6.61$, $p = .02$, $\eta 2$ $p = .28$, indicating that the number of paintings perceived as dynamic was higher than the number of paintings liked. The main effect of TMS was significant, $F(1, 17) = 17.86$, $p = .001$, $\eta 2$ $p = .51$, whereas the interaction Task × TMS was not, $F(1, 17) = 3.13$, $p = .71$, $\eta 2$ $p = .01$. Overall, for the Abstract art group, TMS over V5 reduced the number of "yes" responses irrespective of the task, that is to say, it reduced both the number of abstract paintings perceived as dynamic and the number of abstract paintings liked. Mean response times are shown in Figure 2.4.

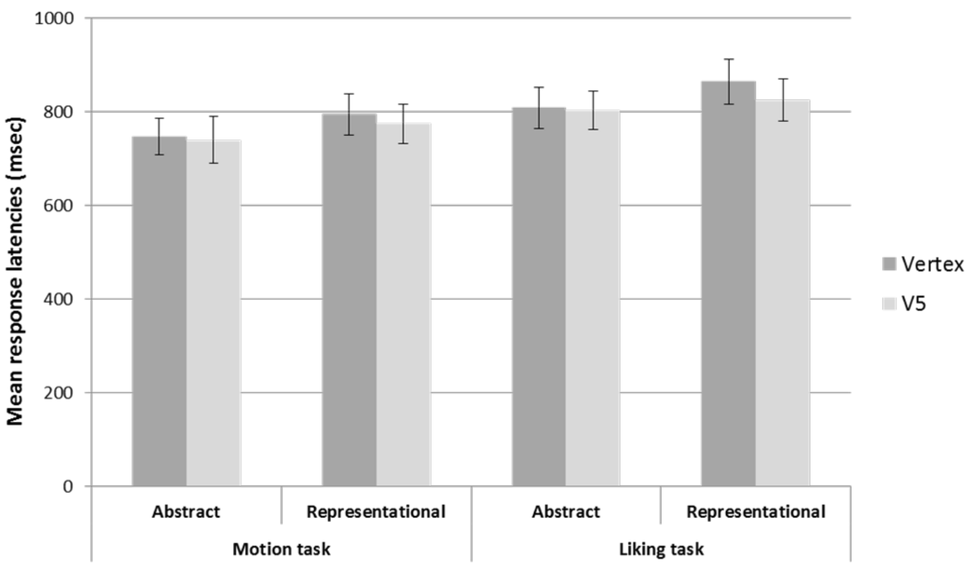


Figure 2.4 Participants' mean response latencies (msec) in deciding whether they found a painting dynamic (Motion task) and whether they liked a painting or not (Liking task) as a function of art style (representational vs. abstract). Participants were overall slower in deciding whether they liked a painting rather than deciding whether the painting was dynamic or not. TMS did not affect response latencies. Error bars depict ± 1 SEM.

A mixed repeated-measures ANOVA with TMS site (V5 vs. Vertex), Task (Motion vs. Liking) as within subjects variables, and Group (Representational vs. Abstract) as between-subjects variable performed on the Mean response times revealed a significant main effect of Task, $F(1, 34) = 10.34$, $p = .002$, η2 p = .24, indicating that it took overall longer for participants to decide whether they liked a painting (Mean response time = 824 ms) rather than deciding whether the painting was dynamic or not (Mean = 764 ms). The main effect of TMS was not significant, $F(1, 34) = 1.16$, $p = .29$, η2 p = .03, nor was the main effect of Art-Group, $F(1, 34)<1$, $p = .485$, η 385 2 p = .01. None of the interactions reached significance: Task × Art-Group (p = .97), TMS × Art-Group (p = .49), Task × TMS (p = .57), Task × TMS by Art-Group (p = .52).

2.4 Discussion

We presented participants with a series of abstract and representational paintings varying in the range of the dynamism they express and we asked them to indicate whether they found the image dynamic or not and whether they liked it or not, while interfering with activity in motion-sensitive region V5 via triple pulse TMS. V5 TMS caused a significant reduction in the sense of motion participants perceived in artworks, both representational and abstract. Moreover, V5 TMS significantly reduced liking of abstract paintings, but it did not affect liking of representational paintings, even though a pilot experiment showed that liking of both representational and abstract paintings positively correlated with the extent to which paintings were perceived as dynamic, in line with prior evidence (Massaro et al., 2012; Valentine, 1962). Overall, participants took longer to decide whether they liked a painting or not than do decide about whether they found the painting dynamic. TMS did not affect response latencies. The selective effect of V5 stimulation on liking for abstract paintings discourages an interpretation of our results in terms of TMS affecting response bias (i.e., TMS did not make participants less willing to respond “yes” regardless of task requirements). In turn, our results fit well with previous TMS evidence showing that the same cortical regions mediating perception of physical motion also mediate processing of implied motion (e.g., Urgesi, Moro, Candidi, & Aglioti, 2006; Senior et al., 2002; but see Alford, van Donkelaar, Dassonville, & Marrocco, 2007). In particular, our data add to prior (correlational) neuroimaging evidence (e.g., Kim &

Blake, 2007; Thakral et al., 2012) demonstrating that V5 is causally involved in the representation of movement based on form features depicted in paintings. Moreover, given that the abstract paintings we used lack any representation of discernable objects and are constituted solely of formal features, such as color, line, stroke, composition, and texture, our results suggest that V5 activity is causally related to the perception of motion even in the absence of real objects, that is to say, based solely on formal cues. The TMS effects we observed on liking of abstract art are in accordance with Zeki and Stutters' (2012) finding that patterns of moving dots that were preferred by participants elicited greater activity in V5 than those patterns that were least preferred (but see Thakral et al., 2012). Indeed, as abstract art is devoid of any physical form, it is likely closely related to sensory neural processes (i.e., motion perception). Prior studies showed increased activity in sensory brain regions also when viewing representational paintings liked by the viewer (e.g., Lacey et al., 2011; Vartanian & Goel, 2004) as well as other figurative stimuli, such as dance movements (e.g., Calvo-Merino et al., 2008). However, representational art is defined by the physical form/content and therefore the aesthetic experience (i.e., pleasantness) is likely tied (Figure 2.4). Participants' mean response latencies (ms) in deciding whether they found a painting dynamic (motion task) and whether they liked a painting or not (liking task) as a function of art style (representational vs. abstract). Participants were overall slower in deciding whether they liked a painting rather than deciding whether the painting was dynamic or not. TMS did not affect response latencies. Accordingly, modulating activity in prefrontal cortices, tied to more conceptual processing, affected aesthetic appreciation of representational artworks in prior studies (Cattaneo et al., 2014a, 2014b), whereas it would be unlikely to affect sensory judgments, such as motion detection. The increase in sensory activity in aesthetic appreciation is believed to reflect an orientation toward the perceptual features people find appealing in the stimuli (Cupchik et al., 2009; Nadal, 2013), as also suggested by brain stimulation studies demonstrating that interfering with activity in these regions modulates aesthetic appreciation (Calvo-Merino et al., 2010; Cazzato, Mele, & Urgesi, 2014). Indeed, naïve viewers tend to look at art searching for recognizable objects they can associate with stored knowledge, under the (naïve) belief that understanding the artwork equates to understanding the depicted scene (Cupchik & Gebotys, 1988). Content-related features, such as familiarity or affective valence, therefore, take precedence over the artwork's formal features, and the way the medium heightens its expressiveness, and other aspects that are central to art experts' approach of art (Cupchik & Gebotys, 1988; Nodine, Locher, & Krupinski, 1993; Winston & Cupchik, 1992). Abstract art, by definition, represents no recognizable objects, so liking can only be based on formal features, some of which constitute cues for motion. Because in abstract art the contribution of form to liking is not overshadowed by the contribution of content, it stands to reason that the effects of interfering with formal features should be larger than for representational art. This notwithstanding the importance that the dynamism perceived in a representational painting has in driving its aesthetic appreciation, as demonstrated by our pilot study and by prior evidence (Massaro et al., 2012; Valentine, 1962). Finally, in considering our results, it is important to acknowledge that V5 was localized in our participants relying on craniometric coordinates, without further adjusting the coil position on the basis of phosphenes appearance (Pavan et al., 2011) and without relying on neuronavigation. However, the finding that TMS over V5 reduced motion perception indicates that V5 was successfully targeted.

3. Study 3: The role of expression recognition in aesthetic evaluation of portraits

3.1 Introduction

Following study 2 where a role of a sensory area was shown in abstract but not representational art we decided to further investigate the issue of dynamism in representational painting, focusing on dynamic aspects of faces, namely expressivity.

Expressivity in the visual arts is the quality of showing, through gestures and facial expressions, feelings, emotions and intentions. Despite also hand movements, gestures, body postures can convey information, faces are one of the most informative stimuli human can encounter (Bruce & Young, 2012).

As a matter of fact, human figures and faces play a central role in Western art (Kandel, 2012). Studies have shown that laypeople usually prefer representational over abstract painting (Cattaneo et al., 2015; Furnham & Walker, 2001; Kettlewell, Lipscomb, Evans, & Rosston, 1995; Knapp & Wulff, 1963; Pihko et al., 2011). In the previous discussions was already mentioned that laypeople's appreciation of art is intrinsically related to recognition of the depicted elements and abstract art, by definition, represents no recognizable objects. Moreover, objects depicted in representational paintings are often more familiar and familiarity is known to increase appreciation (Flexas, Rosselló, de Miguel, Nadal, & Munar, 2014).

Human faces and bodies are the most familiar stimuli we can consider. They carry emotional information, and can induce empathetic engagement in the viewers (Kirsch, Urgesi, & Cross, 2016). Freedberg and Gallese (2007) in their review suggest that an important component of aesthetic response could be the activation of embodied mechanisms. Among the different brain processes involved in positive aesthetic experiences some studies found an enhancement of somatosensory cortical processing (Azañón et al., 2014; Calvo-Merino, Jola, Glaser, & Haggard, 2008; Calvo-Merino, Urgesi, Orgs, Aglioti, & Haggard, 2010). However, the role of expression recognition and embodiment have been overlooked in the study of paintings appreciation.

Artworks containing faces and people have been widely studied in behavioral experiments (Graham, Meng, Pallett, & Leder, 2014; Leder, Ring, & Dressler, 2013; Massaro et al., 2012). Graham et al. (2014) explored the relation between the aesthetics of portraits and the aesthetics of real faces, showing that a series of differences in aesthetics for the two kind of stimuli exist. Leder et al. (2013) used artistic portraits to examine how different variables could affect aesthetic responses of portraits, showing that emotional valence is strongly related to aesthetic liking and interestingness. However, none of the aforementioned studies on portraits investigated their relation with expressivity.

Consistent neuroimaging results show an increased activity in sensory processing regions for artworks and other visual stimuli that people find more appealing. We argue that, if aesthetic appreciation of portraits is correlated with their expressivity, then liking may rely on the specific activity from superior temporal sulcus and somatosensory regions involved respectively in the analysis of expressions and empathetic engagement.

Neuroimaging studies show that STS plays an important role in processing eye gaze, emotional expression and dynamic information about faces (Calvert & Campbell, 2003; Engell & Haxby, 2007; Haxby, Hoffman, & Gobbini, 2000). Moreover, TMS studies have demonstrated that the STS is causally engaged in eye gaze discrimination (Pourtois et al., 2004), in judgments of facial trustworthiness (Dzhelyova, Ellison, & Atkinson, 2011) and facial expression recognition (Pitcher, 2014). Lesion and functional studies suggest that the right somatosensory cortex (SC) contributes to facial expression processing regardless emotion type (Adolphs et al., 2002; Winston et al., 2003). In line with this, Pitcher et al. (2008) showed that repetitive TMS over SC disrupted accuracy in discriminating faces on the basis of emotional expressions. However, two studies (Redies, 2007; Schweinhart & Essock, 2013) found that painted portraits have statistical properties that are closer to those of natural landscapes than to those of natural faces and consistently Hayn-Leichsenring et al. (2013) showed that perceptual adaptation effects for faces and portraits do not transfer between domains. Therefore, we cannot assume that portraits and faces have the same properties and recruit the same neural networks.

The purpose of this study is thus to find out whether areas involved in expression recognition of faces are also involved in perceiving expressivity of portraits and whether they play a role in aesthetic judgment. To this aim, we stimulated two areas involved respectively in the analysis of expressions and empathetic engagement, the posterior STS and the SC of the right hemisphere. Specifically, triple-pulse TMS was applied on the targeted areas to induce transient disruption in the underlying neural activity (e.g., Kadosh et al., 2007) while participants evaluated whether they found expressive and liked a series of paintings representing either portraits or non-portraits humane figures.

3.2 Method

Participants

Thirty-two neurologically healthy Italian students (8 males, Mean age: 23.0 years, SD: 1.8 years) with no previous training or special interest in art, assessed with a brief screening questionnaire (Brieber, Leder, & Nadal, 2015; Brieber, Nadal, Leder, Rosenberg, & Martinez, 2014) participated in the study. Participants were randomly assigned to two different groups: one group (16 participants) only did the Expressivity task and one group (16 participants) only did the Liking task. All participants were right-handed (Oldfield, 1971), and were naïve to the purpose of the study. They all had normal or corrected-to-normal vision, and normal color vision. 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.

Material

Stimuli consisted of 120 reproductions of artistic representational paintings organized into two sets of 60 images, one set with paintings categorized as portraits and the other set with representative paintings categorized as non-portraits, but still containing human figures. Although they were the work of renowned artists, this set included only relatively unknown pieces, in line with previous research (Cattaneo et al., 2014a; Cela-Conde et al., 2004, 2009). In a pilot study, 30 right-handed participants (11 males, Mean age = 22.17 years, SD = 1.46), with no previous training or practice in art and not taking part in the TMS experiment, rated on a 1–9 Likert scale the amount of expressivity conveyed by each painting (1 = not expressive; 9 = very expressive) and their liking for each painting (1 = I do not like it at all; 9 = I like it very much). For the TMS experiment we selected paintings with intermediate values of expressivity (that is to say with a mean rating score of expressivity between 3 and 6).

Procedure

The experiment was conducted in a normal-lightened and silent room. Participants were seated in front of a 17'' PC (1280*800 pixels) screen at an approximate distance of 57 cm, 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 x 10 degrees of visual angle) was presented in the central field of view. Participants were instructed to indicate as fast as possible whether they found the painting very expressive or little expressive (Expressivity taks) or whether the liked or not the painting (Liking Task) by left/right key pressing with their right index and middle finger. After the response, a new trial started. Within each TMS block, stimuli were presented in random order. There was a short break (2–3 mins) between TMS blocks. The order of the TMS site stimulation was counterbalanced across participants.

Transcranial Magnetic Stimulation

TMS was delivered using a Magstim Rapid2 stimulator (Magstim Co Ltd, Whitland, UK) connected to a 70mm butterfly coil at a fixed intensity of 60% of the maximum stimulator output. A fixed intensity was used in accordance with previous studies reporting disrupting effects of SC and STS stimulation on facial expression perception (Grossman, Battelli, & Pascual-Leone, 2005; 2014; David Pitcher et al., 2008). The stimulated areas were the STS, SC and the Vertex (control site). Both SC and STS were localized using the SofTaxic Evolution Navigator System (E.M.S., Bologna, Italy). This system allows the co-registration of the coil and subject's head positions and the localization on the scalp of the position corresponding to the cortex area of interest on the basis of the subject's estimated magnetic resonance image (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). This procedure has been proven to ensure a global localization accuracy of roughly 5 mm, a level of precision closer to that obtained using individual MRIs than to what can be achieved using other localization methods (Carducci & Brusco, 2012). Talairach's coordinates for rSC ($x = 44$, $y = -12$, $z = 48$) were the same of Pitcher et al. (2008) and are the average from 12 neurologically normal participants in an fMRI study of facial expression (Winston, O'Doherty, & Dolan, 2003). The center of the coil was positioned over the cortical site to be stimulated in a parasaggital line with the handle pointing posteriorly.

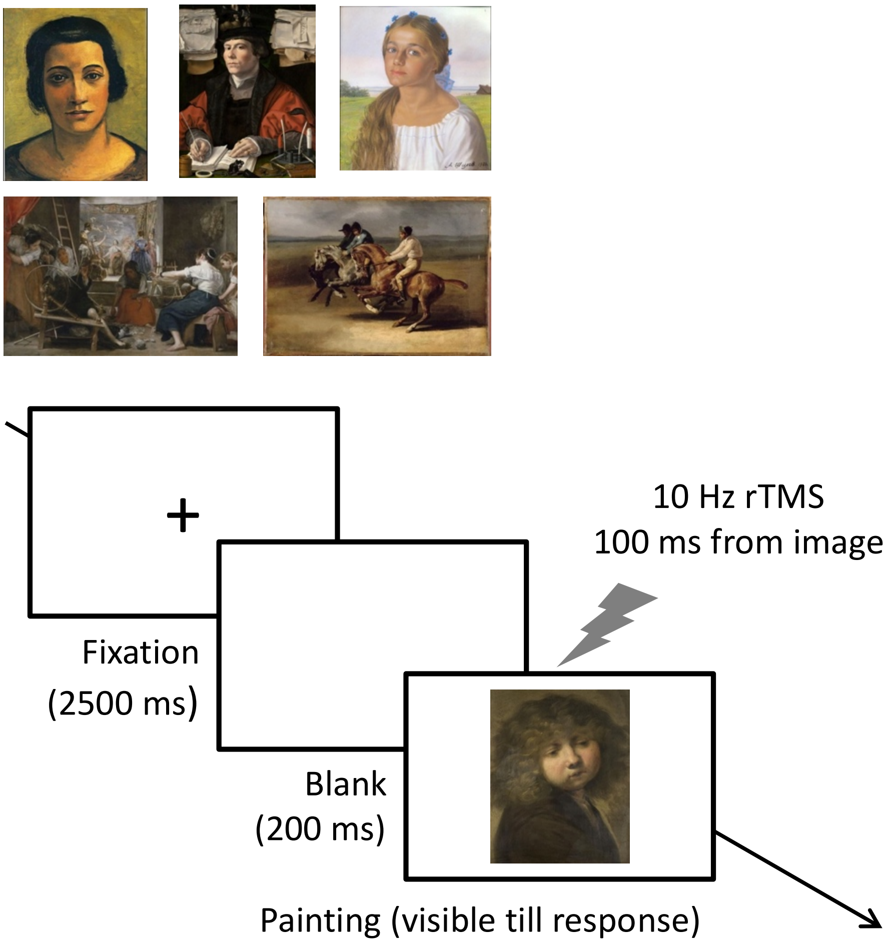


Figure 3.1 A) Upper panel, example of a portraits from left to right : *Portrait of a merchant*, Jan Gossaert, 1530; *Portrait of Madame Carco,* André Derain, 1923; *Portrait Of Olenka*, Alexander Shilov, 1981. Lower panel, example of non-portrait representational paintings, from left to right: *Las Hilanderas*, Diego Velázquez, 1657; *The Horse Race*, Theodore Gericault, 1820). **B)** Example of an experimental trial. In each trial a painting was presented in the middle of the screen and participants had to indicate as fast as possible whether they perceived the image as expressive or not (expressivity task) or whether they liked it or not (liking task). The painting shown in this figure is *Head of a Boy*, Rembrandt, 1643.

The STS was targeted in its posterior aspect (x = 52, y = −48, z = 8), on the base of previous studies (Candidi, Stienen, Aglioti, & de Gelder, 2011; Engell & Haxby, 2007)During stimulation, the coil was held tangential to the scalp, with the handle pointing backward and medially at a 45° angle from the middle sagittal axis of the participant's head. Vertex was used as a control site for nonspecific effects of TMS caused by noise and tactile sensations and was localized as a 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. Three TMS pulses were delivered at 10 Hz, 100 ms after the onset of each painting.The timing of stimulation was chosen on the basis of previous electrophysiological evidence showing that emotional face processing happened in a range from 120 to 180 ms (Eimer & Holmes, 2007) and on the basis of prior TMS studies (Dzhelyova et al., 2011; Pitcher, 2014; Pourtois et al., 2004). Prior to the experiment, short practice blocks (with different stimuli 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.

3.3. Results

Percentage of yes/no responses and mean response times were recorded for both the Expressivity and Liking task. Figure 3.2 shows the Mean percentage of paintings judged as expressive in the Expressivity task and the Mean percentage of paintings liked in the Liking task. A mixed repeated-measures ANOVA with TMS site (STS vs. SC vs. Vertex) and Content (Portrait vs. Non-Portrait) as within subjects variables, and Task (Expressivity vs. Liking) as between-subjects variable was performed on the percentage of "yes" responses. The analysis revealed a significant TMS site × Content × Task three way-interaction, $F(2, 29)=4.87$, $p=.011$, $\eta^2_p=.14$. The significant three-way interaction was further investigated in each group by a repeated-measures ANOVA with TMS site and Content as within-subjects variable. For the Expressivity group, the ANOVA showed no significant main effects of either Content $F(1, 15)=.268$, $p=.612$ $\eta^2_p=.018$, or TMS site, $F(1, 15)=1.114$, $p=.341$, $\eta^2_p=.069$. The TMS × Content interaction was significant, F(1, 15)=6.12, p=.006, η^2_p=.29. A pairwise t-test comparison shows that the TMS over STS significantly reduced the number of "I find it expressive" responses for portraits compared to the vertex condition, t(15)=3.481, p=.003 (Bonferroni-Holm applied), but left the expressivity perception for whole bodies artworks unaffected. For the Liking group the ANOVA showed no significant main effects of either TMS site F(1, 15)=.038, p=.96, η^2_p=.003, or Content, F(1, 15)=1.15, p=.30, η^2_p=.071. The TMS × Content interaction was also not significant, F(1, 15)=0.39, p=.68, η^2_p=.025. These results indicate that none of the stimulated areas affected the liking of a painting whereas TMS over STS affected the expressivity perceived in portraits.

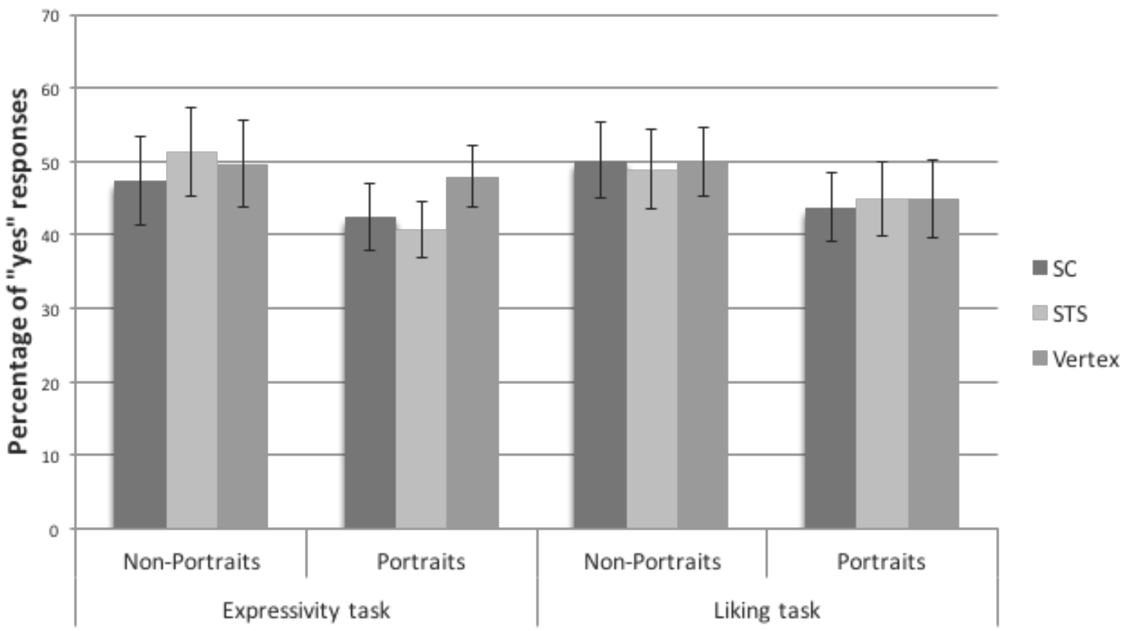


Figure 3.2 Frequency histograms for "I find this expressive" (Expressivity task) and "I like it" (Liking task) responses as a function of Content. TMS over STS reduced the number of portraits perceived as expressive. In turn, TMS did not affect appreciation for artworks. Error bars depict ± 1 SEM.

Mean response latencies (for all responses) for participants in each TMS condition and for each painting category are reported in Figure 3.3.

A mixed repeated-measures ANOVA with TMS site (STS vs. SC vs. Vertex) and Content (Portrait vs. Non-Portrait) as within subjects variables, and Task (Expressivity vs. Liking) as between-subjects variable was performed on the mean response times.

This analysis revealed a main effect of Content $F(1, 30)=21.98$, $p < .001$, $\eta^2_p=.42$ showing that participants were faster in evaluating portraits. The main effect of TMS site was not significant, $F(1, 30)=.013$, $p=.98$, $\eta^2_p=.00$. None of the interactions reached significance: TMS site× Task (p=.22), TMS site× Content (p=.23), Task × Content (p=.14), TMS site × Content × Task (p=.32).

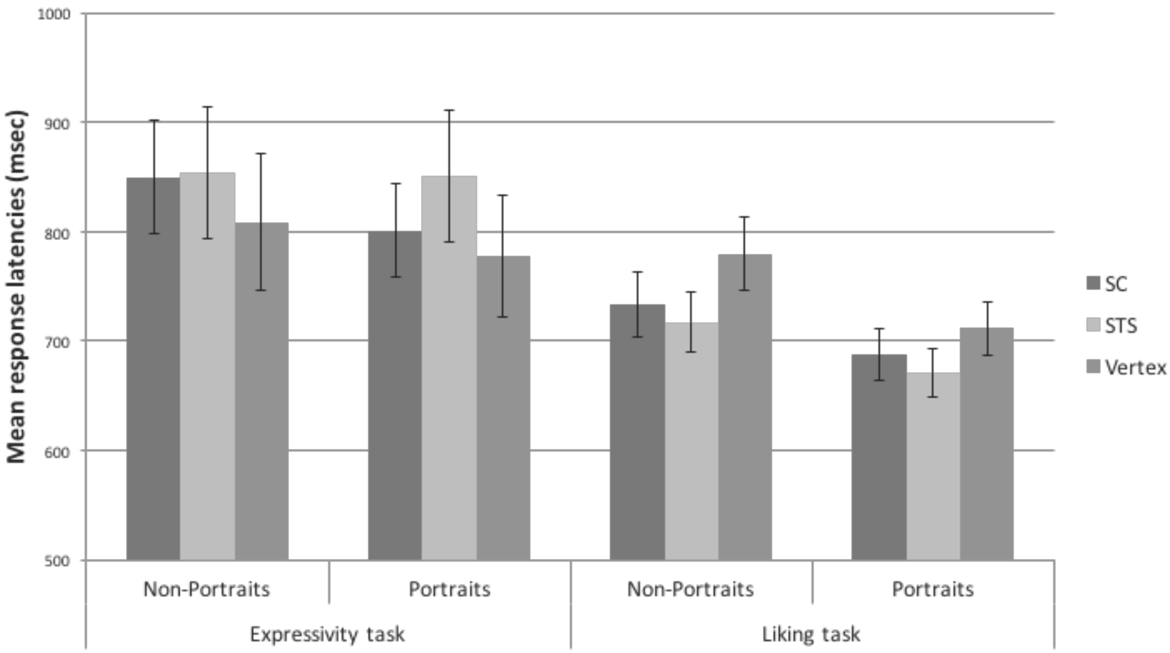


Figure 3.3 Participants' mean response latencies (msec) in deciding whether they found a painting expressive (Expressivity task) and whether they liked a painting or not (Liking task) as a function of Content (potraits vs. non-portraits). Participants were overall faster in deciding whether they found expressive and liked portraits rather than non-portraits. TMS did not affect response latencies. Error bars depict ± 1 SEM.

3.4. Discussion

We presented participants with a series of representational paintings, varying in the range of the expressivity they convey and in the type of content, either portraits or non-portraits. We asked them to indicate whether they found the image expressive or not and whether they liked it or not, while interfering with activity in the STS and SC via triple pulse TMS.

TMS over STS caused a significant reduction in the expressivity participants perceived in portraits, but not in non-portrait paintings while TMS over SC had no effect on expressivity judgment. TMS did not affect liking of paintings, even though a pilot experiment showed that liking was positively correlated with the extent to which paintings were perceived as expressive. Overall, participants took longer to judge paintings depicting entire humane figures than to judge portrait, showing that faces are a special stimulus for humans. TMS did not affect response latencies.

Our results fit well with previous evidence demonstrating that the STS is involved in expression recognition (Adolphs, 2002; 2011; Pitcher, 2014; Srinivasan, Golomb, & Martinez, 2016). Our data extend prior knowledge demonstrating that STS is causally involved in the expressivity perceived in portraits, thus suggesting that expression recognition in portraits and in faces relies on the same neural areas. Moreover, this result provides evidence that expression recognition in portrait play a role in expressivity judgment.

Stimulation of the somatosensory cortex did not affect expressivity judgment although previous studies indicate its involvement in expression recognition (Experience, Kragel, & Labar, 2016; David Pitcher et al., 2008; Pourtois et al., 2004). In order to explain this we should remember that portraits differ from natural faces (Graham et al. 2014). SC plays an essential role in the simulation processes necessary for expression recognition (Pitcher et al., 2008) and the activation of embodied mechanisms is a critical component of aesthetic response (Freedberg & Gallese, 2007). However, this mechanism may not be essential for portraits' expressivity judgment. Indeed, even if portraits depict a face, they are primarily artworks and as such could induce less embodiment that real faces. Moreover, the role of sensorimotor embodiment in aesthetic experience was mainly investigated for actions, gestures and body postures that for facial expressions (Kirsch et al., 2016, for a review).

With respect to the Liking Task we found that neither STS nor SC seem to be involved in the beauty judgment. Previous imaging studies investigating facial attractiveness found an increase in activity of the STS when judging attractiveness rather that age of a face (Winston, O'Doherty, Kilner, Perrett, & Dolan, 2007) or during implicit, but not explicit judgment (Iaria, Fox, Waite, Aharon, & Barton, 2008). However facial attractiveness and formal beauty of an artwork are not the same (Hayn-Leichsenring et al., 2013; Redies, 2015). We could argue that the activation of STS when people watch representational paintings (Fairhall & Ishai, 2008) could be only correlational.

In the pilot study we found a correlation between liking and expressivity judgment, meaning that laypeople apparently like more expressive paintings. Why then the reduction of perceived expressivity through STS stimulation did not affect liking?

Expressivity seems indeed to be an important component of beauty and to some extent, at least in portraits, relies on expression recognition. Nonetheless beauty is the result of a complex interplay of sensation, emotion and cognition (Chatterjee & Vartanian, 2014; Pearce et al., 2016). Due to its multicomponent nature interfering with one aspect does not lead to a change of judgment. Even in study 3, V5 stimulation did affect only liking for abstract paintings although the same area is activated in watching dynamic bodies, showing that for representational painting a single attribute modulation is not enough to affect beauty judgment.

It is interesting to notice that judgements regarding portraits are made faster in both expressivity and liking task. Even if no study in literature compared reaction time in evaluation of portraits in comparison to other representational painting the result is not surprising. Many studies on face processing suggest that emotional faces processing is extremely fast, with latencies between 100 and 360 ms (e.g. Streit et al., 2003). Another possible explanation is that in the non-portrait paintings more element have to be evaluated and processing is not holistic as with faces hence takes longer.

Finally, some possible limitations to these findings must be taken into account. A recent study (Perruchoud, Michels, Piccirelli, Gassert, & Ionta, 2016) discovered that sensorimotor regions are activated for local components (hands) whereas the visual regions for global components (body). This could be a reason for the absence of effect for SC stimulation. Here the focus was mainly on portraits and an interesting issue for future research would be the study of local part of the painting such as gestures, however has to be notice that by isolating components of a painting, the very nature of the artwork could be lost.

4. Study 4: The role of the ventromedial prefrontal cortex in aesthetic liking of representational paintings.

4.1. Introduction

In study 2 and 3 the focus was on sensory and somatosensory areas thus not encompassing other important regions essential to aesthetic experience. Many neuroimaging studies have found the involvement of reward-related areas, like medial prefrontal cortex (mPFC), orbitofrontal cortex (OFC), and ventromedial prefrontal cortex (vmPFC) when stimuli are judged as beautiful (Tomohiro Ishizu & Zeki, 2011; Jacobsen et al., 2006; Kawabata & Zeki, 2004; Pegors, Kable, Chatterjee, & Epstein, 2015). Moreover, a recent meta-analysis (Kühn & Gallinat, 2012) on fMRI studies trying to uncover the biological basis of pleasure found positive correlation of subjective pleasantness in these areas across a wide range of different modalities and domains.

Among the reward-related areas a critical role is played by the vmPFC. Beyond the above-mentioned engagement in aesthetic appreciation, this area is involved in encoding subjective and emotional value (Grabenhorst & Rolls, 2011; Levy & Glimcher, 2011; Winecoff et al., 2013) and in value-based decision making (Grabenhorst & Rolls, 2011). More in general the vmPFC seems to be implicated in the process the generation of affective meaning (Roy, Shohamy, & Wager, 2012). Since beautiful paintings are considered rewarding stimuli (Lacey et al., 2011; Vartanian & Skov, 2014), we will investigate the causal role of vmPFC in their appreciation using non-invasive brain stimulation.

Consistent evidence suggests that anodal tDCS causes an increase of cortical excitability which lasts several minutes after the end of the stimulation, and usually elicit an enhancement in cognitive performance (e.g. Batsikadze, Moliadze, Paulus, Kuo, & Nitsche, 2013; for a review see Jacobson, Koslowsky, & Lavidor, 2012) The observable behavioral changes that tDCS can induce, allow to extend neuroimaging and electrophysiological studies by establishing the causal role of a specific brain region in mediating a certain function/task (e.g. Miniussi, Harris, & Ruzzoli, 2013)

A recent tDCS study (Nakamura & Kawabata, 2015) applied anodal and cathodal stimulation to the medial prefrontal cortex (mPFC) and the left primary motor cortex (lPMC) to examine whether it was possible to modulate the subjective evaluation of beauty and ugliness. They found that inhibition of mPFC led to a decrease in beauty ratings, however enhancing neural excitability in the mPFC did not significantly influence the perception of beauty. Their study however considers beauty and ugliness as two independent dimensions differently from the imaging studies addressing the same issue (T. Ishizu & Zeki, 2013; Kawabata & Zeki, 2004). Moreover, their stimuli consist only in abstract paintings that by definition lack of meaningful content thus inducing less affective reaction (Flexas et al., 2014) who play and important role in the reward system. Consistently Cattaneo et al. (2014a) found that anodal stimulation on the left DLPFC increased the appreciation for representational images, but did not affect appreciation for abstract paintings. The aim of the present study was to clarify the involvement of the vmPFC in the appreciation representational paintings. Participants had to indicate how much they like a series of painting on a Likert scale, both before and after receiving anodal tDCS over the vmPFC. They underwent two stimulation session: in one session, the stimulation was real, while in the other session the stimulation was sham.

4.2 Method

Participants

24 participants (6 males, mean age=22,70 years, s.d.=1,9 years, range: 20-28) with no previous training or special interest in art, volunteered to participate in this study. They were all right handed (Oldifield, 1971) and all had normal or corrected to normal vision and normal color vision. Written informed consent was obtained from all participants. The experiment was approved by the local ethical committee of the University of Milano-Bicocca and subjects were treated in accordance with the Declaration of Helsinki.

Stimuli

Stimuli consisted of reproduction of representational paintings. Two sub-sets of pictures were created: each set contained 80 images. The images of the two sets were matched painting by painting: if in set A there is a painting by one painter, in set B there is a similar painting by the same painter (see Figure 4.1 for an example). Eight additional pictures were used in a first practice session that preceded the experiment itself.

Figure 4.1 Example of pictures used in the experiments. Upper panel paintings belonging to set A, from left to right: *Romantic Landscape with a Temple,* Thomas Doughty, 1834 and *La merienda a orillas del Manzanares*, Francisco Goya, 1776. Lower panel paintings belonging to set B, from left to right: *On the Hudson*, Thomas Doughty, 1835 and *El baile a orillas del Manzanares*, Francisco Goya, 1776. Paintings in the two set are matched by painter and content.

Transcranial direct current stimulation

tDCS was delivered by a battery driven, constant current stimulator (Eldith, Neuroconn, Ilmenau, Germany) through a pair of saline soaked sponge electrodes (7x5 cm: 35 cm^2) kept firm by elastic bands. The excitability-enhancing anodal electrode was placed horizontally over FpZ (between Fp1 and Fp2 and over the glabella) according to the 10–20 EEG system. The return electrode was placed over the vertex, Cz of the 10–20 EEG system. This electrode arrangement (anodal electrode over FpZ with the cathodal electrode over the vertex) is thought to induce modulation of the vmPFC and has been shown effective in a computational model (Figure 4.2). Each participant underwent two stimulation sessions: a real one and sham one.

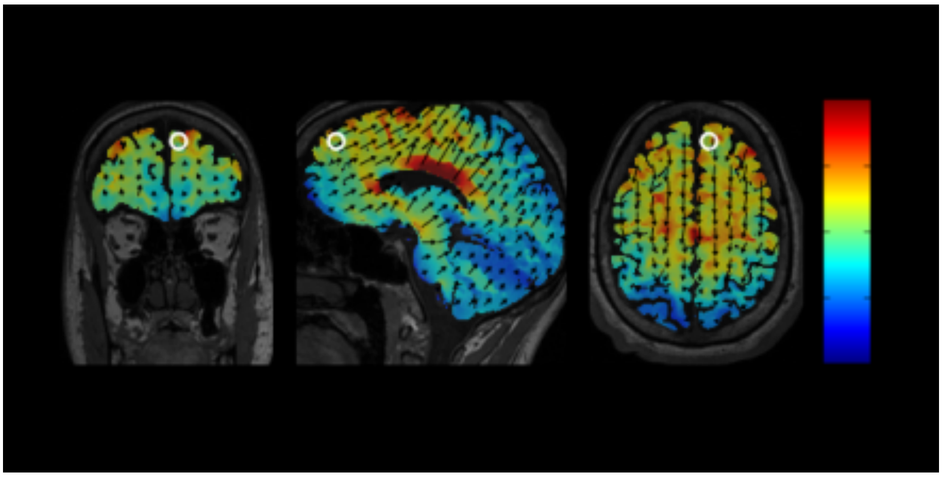


Figure 4.2 Modeling of current flow corresponding to our montage (anodal electrode placed horizontally over FpZ (between Fp1 and Fp2 and over the glabella), according to the 10–20 EEG system. The return electrode was placed over the vertex, Cz of the 10–20 EEG system. Field strength is color-coded from 0 to 0.4 mV/mm, coordinates of the reference point (white circle) is x 5, y 55, z 26 in MNI.

In each session, participants performed the task twice: once before stimulation, and once after stimulation. The images they evaluated were the same in the real and sham tDCS stimulation, but different in the pre and post sessions. Sessions were separated by an average of 4 days (range: 2 -7 days). The order of stimulation session was counterbalanced across participants, so that half started with the sham session and the other half with the real session. In the real tDCS session, stimulation intensity was set at 2mA and the duration of stimulation was 20 min. Previous studies have shown that this intensity of stimulation is safe and can be more effective than a 1mA stimulation (Moos et al., 2012). Moreover, 20 min of 2mA anodal stimulation results in an excitability enhancement that is still observable 90 min after the end of the stimulation (e.g. Batsikadze et al., 2013). Current densities for the two session were maintained below the safety limit of 0.052 mA/cm2 (Nitsche et al., 2008; Iyer et al., 2005). The impedance was controlled by the device and kept low for all stimulation sessions. For the sham stimulation, the electrodes were placed at the same positions as for active stimulation, but the stimulator was turned on only for 30s. Thus, participants felt the initial itching sensation associated with tDCS, but received no active current for the rest of the stimulation period. This procedure ensured that participants felt the initial itching sensation at the beginning of the sham stimulation, but prevented any effective modulation of cortical excitability by sham tDCS, thus allowing for a successful blinding of participants for the real vs sham stimulation condition (Russo et al., 2013). The study was a single-blind experiment: participants were not aware of the type of stimulation they received, whereas the experimenter was fully informed (see Cattaneo et al., 2011; Pisoni et al., 2012 for a similar procedure).

Procedure

Participants were seated in front of a 15.5 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. The participants were instructed to indicate how much they find the paintings beautiful on a 1-7 Likert scale (1= not at all; 7= very very beautiful), similarly to previous studies (Ishizu and Zeki, 2013). The painting remained visible till response was given. There was no time limit but participants were encouraged to respond within 1 min after the appearance of each stimulus. After responding, the screen was cleared-out for 1s, after which a new image was presented. A timeline of the experiment is shown in Figure 4.3. Images in each set were presented in random order. In each experimental session (sham and real), participants were first informed about the task and the FpZ and the vertex were localized. Set A (or set B) was hence presented. After completion of the ratings for Set A, electrodes were placed over the participants' head and the stimulation was started. Concurrently with the beginning of the stimulation, a cartoon movie was projected on the computer screen. This was done to reduce inter-subject's variability by exposing participants to the same visual experience during the stimulation period (see Cattaneo et al., 2011; Pisoni et al., 2012 for a similar procedure). After 18 min since the beginning of the stimulation, the cartoon movie was stopped and subjects were told that in 2 min they would have to perform the rating task for to perform the rating task for a new set of images, Set B (or set A). The rating task was administered within 1 min from the end of the tDCS stimulation. In all participants, the task was completed within 10 min from the end of the tDCS stimulation. The order of the Set presentation was counterbalanced across participants. Each experimental session lasted approximately 45 min. The software E-prime 2.0 (Psychology Software Tools, Inc., Pittsburgh, PA, USA) was used for stimuli presentation and data recording.

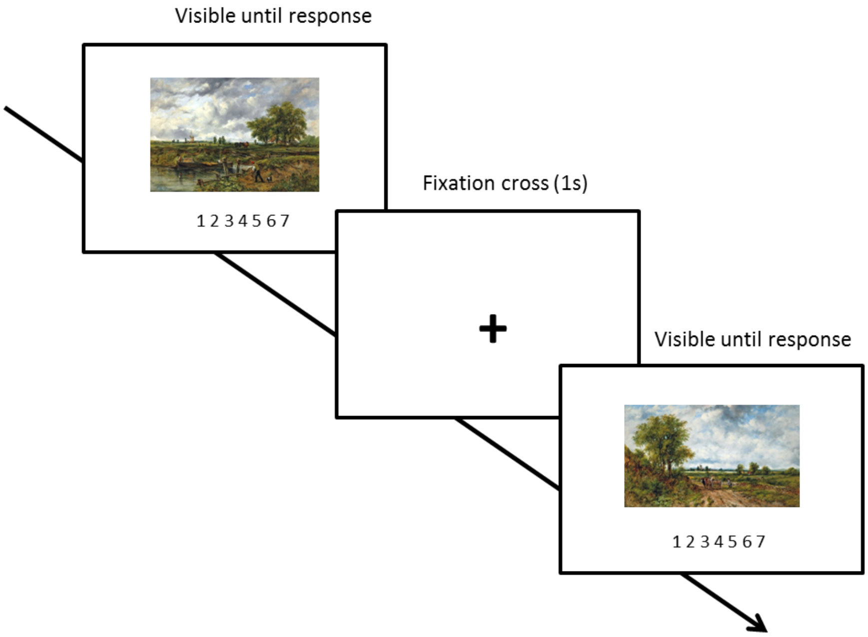


Figure 4.3 Example of an experimental trial. In each trial, a picture was presented in the middle of the screen and participants had to indicate, by pressing the number on the keyboard, how much they liked the image.

4.3 Results

Analyses were performed on rating scores and median RTs. A repeated-measures ANOVA with tDCS (real vs. sham) and session (pre vs. post) as within-subjects variables was performed on mean participants' liking scores and median RTs.

Rating scores Figure 4.4 shows the mean rating scores for the aesthetic evaluation in the different experimental conditions. The main effect of tDCS and of Session were not significant, $F(1,23)=1.902$, $p=.181$, $\eta_p^2=.076$ and $F(1,23)=.206$, $p=.654$, $\eta_p^2=.009$. Also the interaction tDCS*Session $F(1,23)=2.219$, $p=.150$ $\eta_p^2=.088$ was not significant. Although the interaction term failed in reaching the significance level, we explored the effect on the two groups for exploratory reasons. Pairwise t-tests showed that liking scores were higher after real than after sham stimulation t(23)=2.289, p=.032 whereas the scores before real and sham tDCS were not significantly different, t(23)=.522, p=.61, indicating that there was an increase of rating scores after real but not sham stimulation. The difference between pre-post tDCS was not significant neither for sham, t(23)=.581, p=.567, nor for real stimulation t(23)=1.33, p=.197.

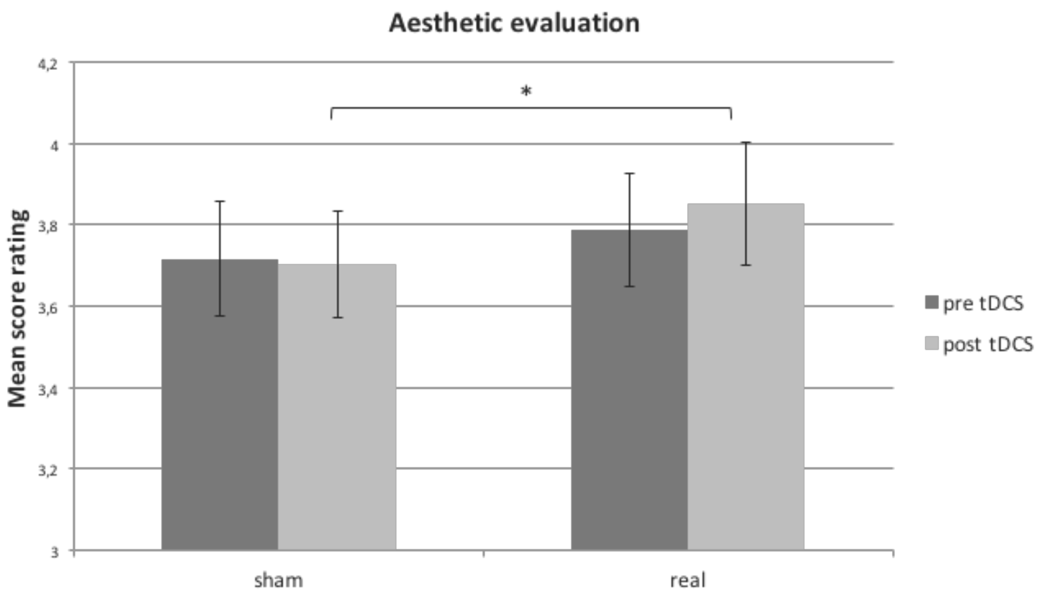


Figure 4.4 Participants' mean rating scores in the aesthetic evaluation for the paintings in the different stimulation conditions (i.e. prior to/following real vs sham tDCS). Error bars represent ±1 s.e.m

Response latencies The main effect of tDCS was not significant F(1,23)=.092, p=.764 η_p^2=.004, while the main effect of session was significant F(1,23)=13.109, p=.001 η_p^2=.363, with evaluation being faster in the post-tDCS than in the pre-tDCS session (regardless of stimulation type, i.e. real vs sham), likely reflecting stabilization of criterion used/task familiarization effects resulting in faster responses. The interaction tDCS*session approached significance F(1,23)=4.166, p=.053, η_p^2=0.153, indicating that the difference in median reaction times between the two sessions was slightly greater for the real than for the sham stimulation. Figure 4.4 shows the median RTs for the aesthetic evaluation in the different experimental conditions.

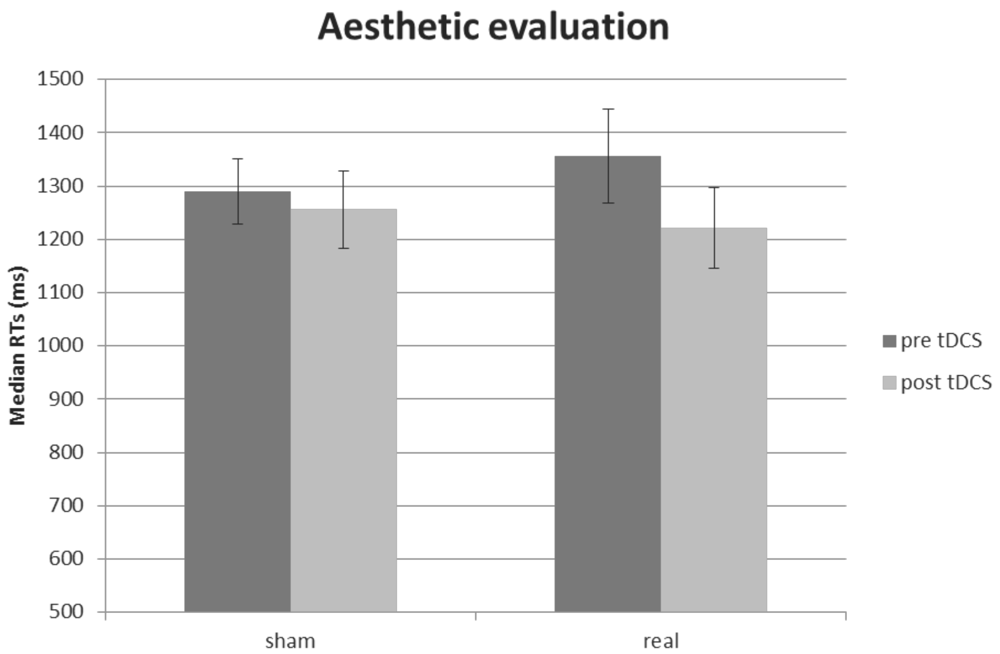


Figure 4.4 Participants' median RT in the aesthetic evaluation for the paintings in the different stimulation conditions (i.e. prior to/following real vs sham tDCS). Error bars represent ±1 s.e.m

4.4 Discussion

The aim of this experiment was to explore the role of the vmPFC in the evaluation of beauty in representational paintings using tDCS. In the comparison of post-tDCS sessions emerged that after real stimulation, liking scores were significantly higher than the ratings given after sham stimulation. Although pairwise comparisons alone cannot support a differential effect of real and sham tdcs in the post- but not in the pre-intervention session, we consider this study as explorative and suggest that anodal stimulation over the vmPFC does, to a certain extent, modulate aesthetic evaluation, in line with previous neuroimaging studies showing an enhanced activity of this region when subjects were presented with paintings they found beautiful (Tomohiro Ishizu & Zeki, 2011; Kawabata & Zeki, 2004). Differently from Nakamura and Kawabata (2015) who only showed a reduction in the experience of beauty inhibiting it by applying cathodal tDCS over mPFC, we were able to find a minor enhancement in beauty appreciation stimulating the vmPFC. Our results, rather than being in contrast with their findings, integrate them. In fact, while they use abstract paintings as stimuli, we focus our study on representational paintings.

Laypeople, as was already pointed out in all the previous studies, usually like representational artworks more than abstract artworks (Cattaneo et al., 2015; Furnham & Walker, 2001; Pihko et al., 2011). This happens mainly because laypeople find representational art to be more familiar and familiarity tends to increase the preference (Flexas et al., 2014). In the model proposed by Leder et al. (2004), familiarity contributes to the affective evaluation that takes place during the entire aesthetic experience, likely increasing a positive affective state. vmPFC is known to play a key role in evaluation of subjective value of a stimulus (Bartra, McGuire, & Kable, 2013) in generation of affective meaning (Roy et al., 2012). An enhancement of the activation of this area could induce a greater affective response in the viewer thus resulting in an increase of liking for the stimuli.

Liking however is only one of aspect of reward. Reward system can be dissociated in the two component, namely liking and wanting (Berridge, Robinson, & Aldridge, 2010). Liking is related to the pleasurable aspect of rewarding stimulus, while wanting to the motivational one, that is to say the desire to possess the stimulus. They are mediated by different neurochemical systems and they are associated respectively with vmPFC and Ventral Striatum. Thus the involvement of the vmPFC in aesthetic appreciation reported here support the view that paintings are a stimulus category that engage the liking system more than the wanting system (Chatterjee, 2014a, 2014b).

When considering the presented results, we should however be aware of some possible limitations. Differently from TMS used in study 2 and 3, tDCS has a low spatial resolution. Despite a computational modelling showing that the affected area is mainly vmPFC (Figure 4.2), given the dimension of the sponge pads and their position on the scalp, we cannot rule out that the stimulation also spread to neighbouring areas (Datta et al., 2009; Bikson et al., 2013; Bestmann et al., 2015; Shin et al. 2015), thus resulting in a widespread frontal modulation.

One issue that could serve as a starting point for a future research is the implication of vmPFC in self-referential processing (Kelley et al., 2002; Northoff et al., 2006; Wicker et al., 2003) that means that this area is active the content of the judgements given is self-relevant. This could be the case for art-expert rather than laypeople.

5. Study 5: The role of the dorsomedial prefrontal cortex in mediating the Beauty-is-Good stereotype

5.1 Introduction

In evaluating other individuals, we typically consider their conduct and behaviors (from which we infer their personality traits), but we also look at the way they appear. Indeed, when little information is available about another agent, guesses about personality traits are mainly based on the way that person looks like. One of the features that is most salient when forming a first impression about another individual on the basis of her/his appearance is attractiveness, whose evaluation occurs quite automatically (Locher et al., 1993; Olson & Marshuetz, 2005; Sui & Liu, 2009). Converging evidence suggests that in first impression formation, more attractive persons are also judged to possess more positive qualities (such as trust, intelligence and competence) compared to less attractive ones (Dion et al., 1972; Eagly, Ashmore, Makhijani, & Longo, 1991; Langlois et al., 2000), even though inferring positive traits from an attractive face does not necessarily lead to a correct estimate of the person (Jussim, 1991, 1993; Olivola & Todorov, 2010). This short-cut in evaluation, also known as the *Beautiful-is-Good* stereotype (e.g., Eagly et al., 1991), is intriguing because it reveals a recurrent parallel in the history of Western philosophy (and language) between the aesthetic and the ethical dimensions. In fact, the link between beauty and good has been present in Western thinking at least since Classical Greece, where "'Beautiful' meant […] good and pleasant." (Tatarkiewicz, 1970a, p. 47). In the perspective of contemporary neuroscience, the intersection between ethics and aesthetics suggests the possibility that the apprehension of physical and moral beauty may indeed engage similar neuro-cognitive mechanisms (see Zaidel & Nadal, 2011, for a review). Does beauty appreciation of a painting for instance elicit similar brain responses than admiration of a heroic altruistic gesture? The range of natural and artificial beautiful things is likely infinite, and "goodness" is also difficult to define, including human actions and creations, but also possibly extending to the non-human domain. It is though in the human person that the aesthetic and the ethical dimensions are easier to define and compare. Indeed, Cicero in the *Tusculan Disputations* highlighted the parallels between the features of physical and moral beauty in humans: "And as in the body a certain symmetrical shape of the limbs combined with a certain charm of colouring is described as beauty; so, in the soul the name of beauty is given to an equipoise and consistency of beliefs and judgments, combined with a certain steadiness and stability following upon virtue or comprising the true essence of virtue." (cited in Tatarkiewicz 1970b, p. 206). Accordingly, to shed light on the neural underpinning of the intersection between ethical and aesthetic values, we decided to circumscribe our investigation to "human" beauty and goodness, i.e., to individuals' physical attractiveness and personality traits. In this regards, the *Beauty-is-Good* association is interesting for our purposes not as a case of social stereotype (such as racial and gender stereotypes), but inasmuch this association represents a "window" into the intersection between ethics and esthetics' systems of value.

The *Beauty-is-Good* association emerges quite early in development (Griffin & Langlois, 2006; Langlois et al., 2000) and is extremely pervasive impacting on many social aspects, such as success in school, job opportunities, and even jury-ruled court sentences (e.g., Hamermesh & Parker, 2005; Frevert & Walker, 2014). But what do we know about the neural correlates behind this phenomenon? Although most research has selectively focused on one or the other aspect (e.g., facial attractiveness judgment, inference on personality traits, evaluation of social behaviors), a few neuroimaging studies have directly investigated the connection between moral and aesthetic dimensions in social evaluation (Zaidel & Nadal, 2011, for review). These studies have revealed an extended cortical and subcortical network mediating the evaluation of both aesthetic and moral value including the amygdala, insula, nucleus accumbens, and also the orbitofrontal cortex (OFC) and medial and lateral sectors of the prefrontal cortex (Avram et al., 2013; Bzdok et al., 2012a; Mende-Siedlecki, Said, & Todorov, 2013; Tsukiura & Cabeza, 2011; Wang et al., 2014). For instance, Bzdok et al. (2012a) found that explicit face trustworthiness judgments and face attractiveness judgments both induced activation in the dorsomedial prefrontal cortex (dmPFC) and in the inferior frontal gyrus. Common responses in the insula and in the medial OFC were also reported in the fMRI study by Tsukiura & Cabeza (2011) when participants evaluated attractiveness of faces and when they decided about the morality of behavioral statements. Similarly, evaluating beauty in faces and morality in vignettes representing positively-valenced or neutral behaviors resulted in the activation of a common network comprising the OFC, the inferior temporal gyrus and the medial superior frontal gyrus (Wang et al., 2014). Interestingly, a similar neural circuit (encompassing the OFC and mPFC) was observed when participants judged morality and aesthetics in poems (Avram et al., 2013).

The evidence reviewed above shows that medial sectors of the prefrontal cortex are recruited by both aesthetic and moral evaluations. Indeed, the mPFC is a core region of the "social brain" (Amodio & Frith, 2006; Van Overwalle, 2009): neuroimaging evidence suggests that it is involved in several aspects of social cognition, mediating self-representation (e.g., D'Argembeau et al., 2007; Gusnard, Akbudak, Shulman, & Raichle, 2001; Jenkins & Mitchell, 2011), first impression formation (e.g., Baron, Gobbini, Engell, & Todorov, 2011; Mitchell, Macrae, & Banaji, 2005a), personality traits inference (e.g., Ma et al., 2013a; Ma, Vandekerckhove, Van Overwalle, Seurinck, & Fias, 2011), attribution of mental states (Mitchell, Banaji, & Macrae, 2005b), and social categorization, including stereotyping (Gilbert, Swencionis, & Amodio, 2012; Knutson, Mah, Manly, & Grafman, 2007; Quadflieg et al., 2009). Studies in the aesthetic domain found also consistent activation in the mPFC in response to preferred stimuli, whether faces or artworks (Chatterjee, Thomas, Smith, & Aguirre, 2009; Chatterjee & Vartanian, 2016; Jacobsen, Schubotz, Höfel, & Cramon, 2006). Lesion studies confirm the central role of the mPFC in social cognition. Indeed, damage to the ventromedial prefrontal cortex may lead to impaired theory of mind abilities (Jenkins et al., 2014), abnormal social functioning and limited attention to moral rules (e.g. Anderson, Bechara, Damasio, Tranel, & Damasio, 1999). Furthermore, patients with lesions in mPFC not only are more inclined to approve moral violations compared to control participants (Ciaramelli, Muccioli, Ladavas, & Di Pellegrino, 2007), but also show less or more pronounced stereotypical attitudes depending on the damaged portion of the mPFC (Gozzi, Raymont, Solomon, Koenigs, & Grafman, 2009), and abnormal trustworthiness perception in trust-games (Krajbich, Adolphs, Tranel, Denburg, & Camerer, 2009). However, whether damage to medial sectors of the prefrontal cortex also biases aesthetic evaluations (of faces), or whether it impacts on how face attractiveness affects social (moral) evaluation, is not known.

Another region that deserves attention when investigating the link between ethical and aesthetic evaluation is the dorsolateral prefrontal cortex (dlPFC). The dlPFC is involved in face attractiveness decisions (Chatterjee et al., 2009; Ferrari, Lega, Tamietto, Nadal, & Cattaneo, 2015; Nakamura et al., 1998; Winston, O'Doherty, Kilner, Perrett, & Dolan, 2007) and moral reasoning (Greene, Sommerville, Nystrom, Darley, & Cohen, 2001; Greene, Nystrom, Engell, Darley, & Cohen, 2004; Jeurissen, Sack, Roebroeck, Russ, & Pascual-Leone, 2014; Tassy et al., 2011), and it has been found to respond to both moral and aesthetic evaluation within the same participants (Bzdok et al., 2012a). However, the dlPFC is not part of the core social brain (Van Overwalle, 2009), and its involvement in social decisions may reflect a general role of this structure in decision making and conflict regulation beyond the social domain (e.g., Fleck, Daselaar, Dobbins, & Cabeza, 2006; Kim, Johnson, & Gold, 2014). Nonetheless, we were interested in studying whether the dlPFC regulates flow of information from one system of value (i.e., aesthetics) towards another system of value (i.e., ethics), as it does for instance when controlling emotional responses in social evaluation (Cattaneo, Mattavelli, Platania, & Papagno, 2011; Ito & Bartholow, 2009; Knutson et al., 2007; Kubota, Banaji, & Phelps, 2012; Quadflieg et al., 2011).

In this study, we combined a paradigm designed to assess the *Beauty-is-Good* stereotype with transcranial magnetic stimulation (TMS) to investigate the causal role of the mPFC and of the dlPFC in bridging ethical and aesthetic evaluations (note here that the OFC would also be an interesting area to study in this context, but unfortunately it cannot be effectively reached by TMS). Brain stimulation allows interfering with the neural activity in a targeted region in a controlled and reversible manner. It is thus able to shed light on the *causal* role of different brain areas in mediating a particular function/behavior, adding to the correlation evidence provided by neuroimaging studies. Importantly, participants in TMS experiments act as their own controls, overcoming some of the limitations intrinsic in patients' studies, such as potential differences in pre-morbid ability, and variability depending on high heterogeneity of lesions' extents and severity. We used a prime paradigm to elicit the *Beauty-is-Good* stereotype, priming/adaptation effects being particularly susceptible to the effects of TMS (e.g., Cattaneo, Rota, Vecchi, & Silvanto, 2008; Cattaneo & Silvanto, 2008). Participants were asked to judge the trustworthiness of faces that were preceded by an adjective conveying desirable aesthetic qualities (e.g., *attractive*), undesirable aesthetic qualities (e.g., *ugly*) or neutral qualities (e.g. *horizontal)*. In two behavioral studies we showed that faces appeared more trustworthy when preceded by aesthetically positive adjectives, in line with the *Beauty-is-Good* stereotype, and suggesting that prime and target stimuli were somehow tapping on a related evaluative scale. In fact, other prime cues unrelated to physical appearance but still evoking a negative/positive continuum (e.g. *less*/*more*; *little/a lot*) did not affect trustworthiness evaluation, ruling out unspecific *halo* effects.

If the mPFC mediates the link between moral and aesthetic valuation, as suggested by prior fMRI evidence (Avram et al., 2013; Bzdok et al., 2012a; Wang et al., 2014), interfering with its activity should interfere with the effect of the aesthetic prime over the trustworthiness evaluation, possibly attenuating the behavioral expression of the *Beauty-is-Good* stereotype. Predictions about the effects of stimulation of the dlPFC are less straightforward. Although this region exerts a role in controlling inappropriate emotional responses in social contexts (i.e., stereotyping) (Gilbert et al., 2012; Knutson et al., 2007; Quadflieg et al., 2009), in our task participants are unlikely to be aware of the priming effect and/or to consider it as socially "inappropriate" and hence as a response to inhibit. Nonetheless, it may be that TMS over the dlPFC interferes with the way a general evaluative system allows information coming from different domains (aesthetics, moral) to interact, thus affecting priming effects.

5.2.1 Experiment 1

5.2.2 Method

Participants

Twenty participants (5 males, mean age=22.4 years, *SD*=2.0) volunteered to participate in the study. They were all right handed as assessed by a standard questionnaire (Oldfield, 1971) and all had normal or corrected to normal vision. Prior to the TMS experiment, each participant filled in a questionnaire (translated from Rossi, Hallett, Rossini, & Pascual-Leone, 2011) to evaluate TMS safety. An additional 34 participants were tested in two pilot behavioral experiments. The experiment was approved by the local ethical committee and participants were treated in accordance with the Declaration of Helsinki.

Stimuli

Experimental stimuli consisted of 32 young Caucasian faces displayed in frontal pose and with a neutral expression and of 6 adjectives. Face stimuli (7 × 7 deg of visual angle) were selected from a larger set of computer-generated faces (cf. http://tlab.princeton.edu/databases/randomfaces/) for which rating scores (on a 9-point Likert scale) on different trait dimensions (including trustworthiness) are available (for details, see Oosterhof & Todorov, 2008). From this set, we selected 16 unambiguously males and 16 unambiguously females of medium trustworthiness (within +/- 1 *SD* from the mean of the whole sample, mean= 4.8, *SD*= .7). Medium trustworthiness faces were intentionally chosen, allowing for the possible influence of the prime-adjective on participants' evaluations. All the adjectives were selected from the Corpus CODIS of written Italian (http://corpora.dslo.unibo.it/coris_ita.html) and referred either to desirable human aesthetic attributes (we used 2 adjectives: *attractive* and *beautiful*), or to undesirable aesthetic features (we used 2 adjectives: *horrid* and *ugly*), or described neutral traits not related to human qualities (we used 2 adjectives: *horizontal* and *diagonal*).

Procedure

Participants were seated in front of a 15.5" PC (1280 × 800 pixels) screen at an approximate distance of 57 cm, in a normally lightened and silent room, and performed a computerized task. Before starting the experiment, participants were informed that they would be viewing a set of faces and that their task was to indicate whether each face appeared trustworthy to them or not. Figure 5.1 shows the timeline of an experimental trial. Each trial started with a central black fixation point (1200 ms). Next, the adjective-prime appeared for 300 ms, followed by a blank screen (150 ms) and by the target face stimulus immediately after, which remained on the screen until participants responded. Participants were instructed to (silently) read the prime adjective and to judge the face as trustworthy or not by left/right key pressing using their right hand (response key assignment was counterbalanced across participants). Participants were instructed to be as accurate and fast as possible. TMS was delivered between the appearance of the adjective-prime and the face to be judged (see below for TMS details). Each participant performed 3 experimental blocks, one for each TMS targeted site. In each block, each face was presented three times, once for each prime-adjective type (*beauty*-prime, *ugliness*-prime, or *neutral*-prime), for a total of 96 trials in each block. Faces were presented in random order within each block, with the only constraint that the same face never appeared in two consecutive trials. The tree experimental blocks were performed within the same session (participants were given a few minutes break after the first and second block); the order of the TMS targeted sites was counterbalanced across subjects. Participants performed six practice trials at the beginning of the experimental session to familiarize with the task. The software E-prime 2.0 (Psychology Software Tools, Inc., Pittsburgh, PA, USA) was used for stimuli presentation, TMS triggering and data recording.

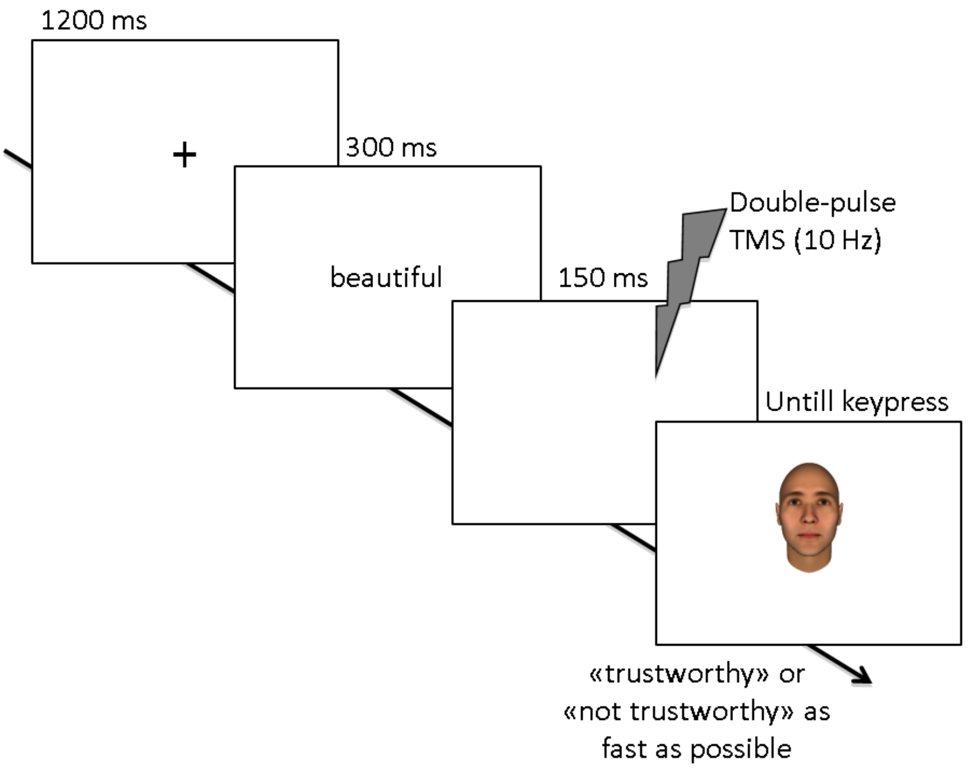


Figure 5.1 The timeline of an experimental trial. Participants had to classify a face as trustworthy or not trustworthy. Each face was preceded by an adjective-prime that was either neutral; related to beauty (e.g., *beautiful*, *attractive*) or related to ugliness (e.g., *ugly, horrid*). 10 Hz double-pulse TMS was applied over the dmPFC (Tal x=-4, y=40, z=50), the right dlPFC (Tal x=29, y=16, z=40) or over the vertex (control site) between the presentation of the prime and the target face.

Transcranial Magnetic Stimulation (TMS)

Online neuronavigated TMS was performed with 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 (e.g., Campana, Cowey, Casco, Ousen, & Walsh, 2007; Cattaneo et al., 2014a; Cattaneo et al., 2015). Double-pulse TMS (10 *Hz*) was delivered 50 ms after the offset of the adjective-prime. Accordingly, the first TMS pulse was given 100 msec before the onset of the face, and the second pulse upon onset of the face. Targeted sites were the dmPFC, the right dlPFC, and the vertex (control site). We targeted the dlPFC in the right hemisphere in light of converging evidence indicating that the right more than the left dlPFC is involved in social decisions, including face attractiveness evaluation (e.g., Ferrari et al., 2015), social categorization (e.g., Mitchell, Ames, Jenkins, & Banaji, 2009; for a review, Amodio, 2014), implementation of fairness-related behaviours (Knoch, Pascual-Leone, Meyer, Treyer, & Fehr, 2006), and moral reasoning (Green et al., 2004; Tassy et al., 2011). The vertex was localized as the point falling half the distance between the nasion and the inion on the same midline. The dmPFC and the right dlPFC were localized by means of stereotaxic navigation (see study 3 for details). Anatomical MNI coordinates were obtained from previous neuroimaging studies on traits perception and stereotypes (Mitchell, Cloutier, Banaji, & Macrae, 2006; Mitchell et al., 2009) and were x=-3, y=48, z=48 for the dmPFC, and x=32, y=22, z=38 for the right dlPFC. MNI coordinates were then converted in the Talairach space (Talairach & Tournoux, 1988) to be suitable for the stereotaxic navigation (see Figure 5.2). The coil was placed tangentially to the scalp with the handle pointing backward and held parallel to the midsagittal line in the vertex and mPFC stimulation conditions, and pointing backward and rightward at a 45° angle from the mid-sagittal line in the right dlPFC condition.

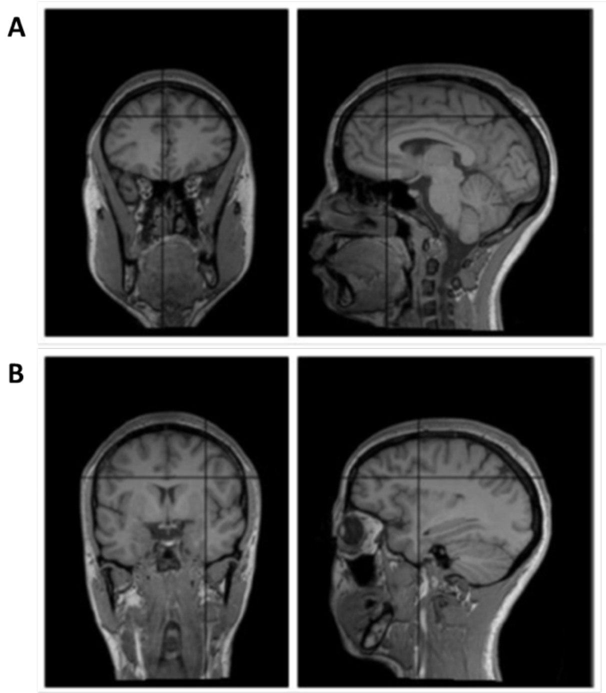


Figure 5.2 The coronal (left) and sagittal (right) sections of the estimated MRI of a representative participant showing the targeted site in the **A**) dorsomedial prefrontal cortex (dmPFC, MNI x=-3, y=48, z=58); and **B**) dorsolateral prefrontal cortex (dlPFC, MNI x=32, y=22, z=38).

5.2.3 Results

The number of positive (i.e., "this face is trustworthy") responses was calculated for each participant in each block and converted into a percentage score. Similarly, mean response latencies (RT) were calculated for each participant in each TMS condition. Trials in which participants' RT were ±3SD above or below their own average response time were excluded from the analyses (.99 % of trials were excluded following this criterion). The dependent variables were analysed via repeated-measures ANOVAs with prime (*beauty*, *ugliness*, neutral) and TMS (dlPFC, dmPFC, and vertex) as within-subjects factors. The Bonferroni-Holm correction was applied to all post-hoc comparisons.

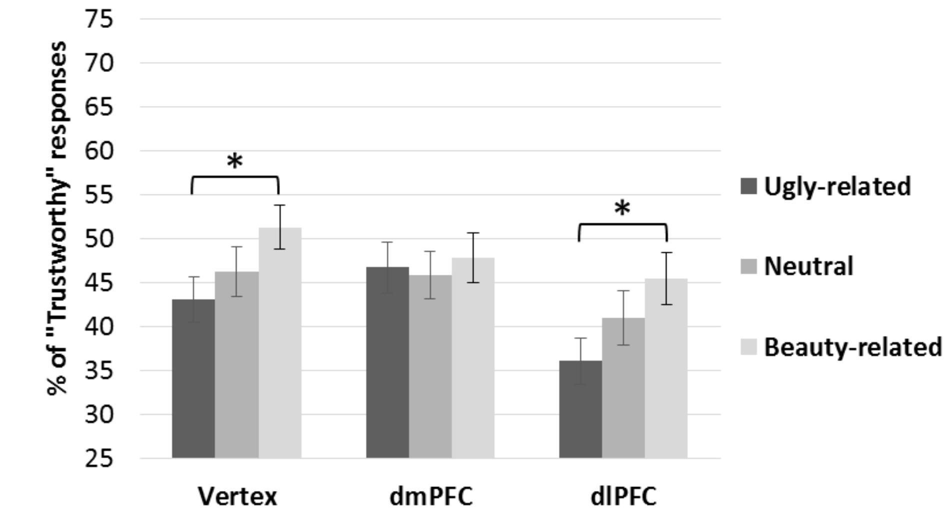


Figure 5.3. Percentage of positive responses (i.e., *The face is trustworthy*) as a function of prime (ugliness, neutral, beauty) and TMS condition (vertex, dmPFC, dlPFC). In the baseline (vertex) and in the dlPFC TMS conditions, faces were classified as trustworthy significantly more frequently following *beaut*y primes than *ugliness* primes. Although participants evaluated faces as overall less trustworthy when TMS was applied over the dlPFC, stimulation over this region did not impact on the *Beauty-is-Good* stereotype. In turn, TMS over the dmPFC abolished the effect of priming. Error bars indicate ± 1 SEM. Asterisks indicate significant differences in priming effects within each TMS condition.

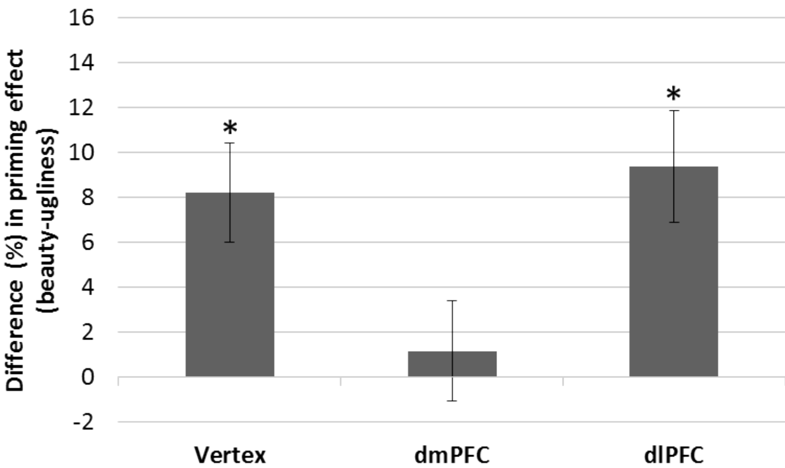


Figure 5.4 Difference in the percentage of faces classified as trustworthy when faces were preceded by *beauty*-primes vs. *ugliness*-primes (i.e., *beauty* minus *ugliness*). Asterisks indicate a significant difference compared to zero (i.e., no priming effect). Error bars indicate ± 1 SEM.

The analysis revealed a significant main effect of TMS on the percentage of faces judged as trustworthy (Figure 5.3) $F(2,38)=5.15$, $p=.010$, $\eta_p^2=.21$, a significant effect of prime $F(2,38)=8.39$, $p=.001$, $\eta_p^2=.31$, and a significant interaction TMS by prime $F(4,76)=2.67$, $p=.039$, $\eta_p^2=.12$. TMS over dlPFC lowered the percentage of faces judged as trustworthy, compared to both vertex $t(19)=3.18$, $p=.015$ and dmPFC stimulation $t(19)=2.99$, $p=.014$. In turn, the percentage of "trustworthy" responses did not differ significantly in the dmPFC and vertex TMS conditions $t(19)<1$, $p=.98$. The effect of prime was modulated by the TMS condition. In the baseline (vertex) condition, the effect of prime was significant $F(2,38)=7.78$, $p=.001$, $\eta_p^2=.29$. Specifically, faces were judged as trustworthy significantly more frequently when preceded by *beauty*-related primes than when preceded by *ugliness*-related primes $t(19)=3.73$, $p=.003$ (Figure 5.4). A similar trend emerged also for the *beauty*-related vs. neutral comparison $t(19)=2.07$, $p=.11$ (without correction, $p=.53$). Also, faces tended to be judged as trustworthy less frequently when preceded by the *ugliness*-related than neutral primes $t(19)=2.03$, $p=.057$. Overall, this pattern resembled the one found in the pilot behavioral experiment.

In the dlPFC condition, similar priming effects were observed $F(2,38)= 6.86$, $p=.003$, $\eta_p^2=.27$. In particular, faces preceded by *ugliness*-related primes were judged as trustworthy significantly less frequently than faces preceded by *beauty*-related primes $t(19)=3.77$, $p=.003$ and neutral primes $t(19)=2.49$, $p=.044$. The priming effect for beauty vs. neutral failed to reach statistical significance $t(19)=1.47$, $p=.16$, although the pattern was similar to the one observed in the baseline Vertex condition (Figure 5.3). In the dmPFC condition, critically, the main effect of prime was not significant $F(2,38)<1$, $p=.60$. It seems, thus, that TMS over this region prevented the emergence of the *Beauty-is-Good* stereotype.

Mean RT for positive and negative responses are reported in Figure 5.5. The ANOVA on the mean RT for positive responses revealed a significant main effect of prime $F(2,38)=9.07$, $p=.001$, indicating that responses were faster overall when following *beauty*-related primes than when following *ugliness*-related primes $t(19)=4.20$, $p<.001$, and neutral primes $t(19)=2.27$, $p=.070$. Furthermore, RT were slightly slower following *ugliness*-related primes than neutral primes $t(19)=2.05$, $p=.06$. Neither the main effect of TMS

$F(2,38)<1$, $p=.63$, nor the interaction prime by TMS $F(4,76)=1.18$, $p=.33$, reached significance. The ANOVA on the mean RT for negative responses revealed neither a significant effect of prime $F(2,38)<1$, $p=.42$, TMS $F(2,38)<1$, $p=.40$, or their interaction $F(4,76)=2.18$, $p=.08$.

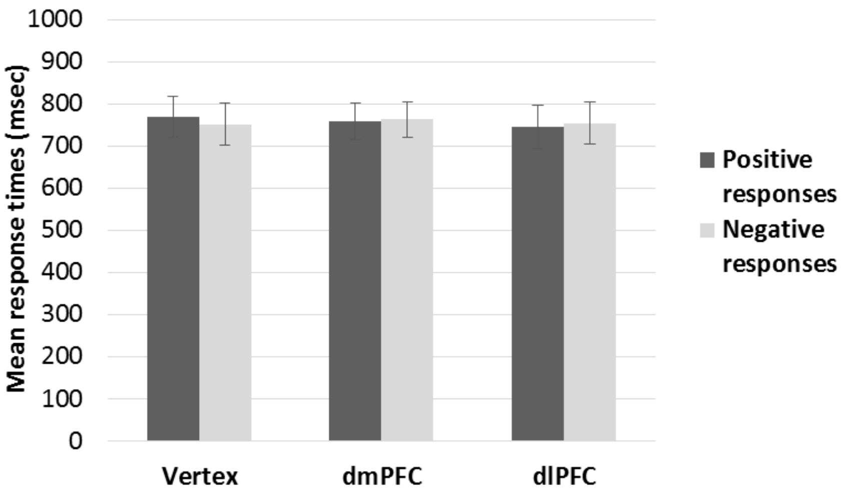


Figure 5.5 Mean reaction times as a function of participants' positive (i.e., *The face is trustworthy*) or negative (i.e., *The face is not trustworthy*) responses and TMS condition in Experiment 1. TMS did not affect response times. Error bars indicate ± 1 SEM.

5.3.1 Experiment 2

Experiment 1 shows that interfering with dmPFC activity abolishes the effect of aesthetic primes over face trustworthiness decisions. However, the effects (also at baseline) were overall of small size. In order to rule out the possibility that our findings possibly reflected a false positive, we decided to carry out a second experiment to verify whether the pattern of results obtained in Experiment 1 could be replicated in a new sample of participants. The experimental procedure was identical to that of Experiment 1 except for the fact that only positive and negative aesthetic primes were used. Neutral primes were not used in this second Experiment given that our interest was mainly in the differential effect of the two poles of the aesthetic dimension (ugliness vs. beauty) over trustworthiness valuation.

5.3.2 Methods

Participants

Twenty participants (3 males, mean age=22.6 years, *SD*=1.4) volunteered to participate in the study. None of them had participated in Experiment 1. Inclusion criteria were the same as for Experiment 1.

Stimuli and Procedure

The experimental paradigm was identical to Experiment 1, with the exception that the neutral adjectives were not included. TMS sites, parameters and timing were the same as those of Experiment 1.

5.3.3 Results

Analyses were carried out as in Experiment 1. Trials in which participants' RT were ±3SD above or below their own average response time were excluded from the analyses (.87% of trials were excluded following this criterion). A repeated-measures ANOVAs with prime (*beauty* vs. *ugliness*) and TMS (dlPFC, dmPFC, and vertex) as within-subjects factors was carried out on percentage scores and mean RT. The analysis on the percentage of faces judged as trustworthy revealed a significant main effect of TMS $F(2,38)=3.80$, $p=.031$, $\eta_p^2=.17$. As shown in Figure 5.6, TMS over the dlPFC lowered the percentage of faces judged as trustworthy, compared to vertex stimulation $t(19)=2.97$, $p=.024$ (Bonferroni-Holm correction applied), whereas there were no main differences between dlPFC and dmPFC stimulation $t(19)=1.22$, $p=.24$, and between dmPFC and vertex stimulation $t(19)=1.44$, $p=.17$. The main effect of prime $F(1,19)=7.30$, $p=.014$, $\eta_p^2=.28$, and the interaction TMS by prime $F(2,38)=3.26$, $p=.049$, $\eta_p^2=.15$ were also significant. In the baseline (vertex) condition, faces were judged as trustworthy significantly more frequently when preceded by *beauty*-related primes than when preceded by *ugliness*-related primes $t(19)=3.20$, $p=.005$ (Figure 5.7). In the dlPFC TMS condition, a similar priming effect was observed $t(19)= 2.30$, $p=.033$ (Figure 5.7). In turn, when TMS was delivered over the dmPFC condition, no difference was observed between positive and negative primes in biasing "trustworthy" responses $t(19)=1.14$, $p=.27$.

Mean RT for positive and negative responses are reported in Figure 5.8. The ANOVA on mean RT for positive responses revealed no significant effect of either TMS $F(2,38)<1$, $p=.84$, or prime $F(1,19)=1.46$, $p=.24$. The interaction prime by TMS was not significant $F(2,38)=2.02$, $p=.15$. The ANOVA on mean RT for negative responses did not reveal any significant effect: TMS $F(2,38)<1$, $p=.41$, prime $F(1,19)=2.42$, $p=.14$, prime by TMS interaction $F(2,38)<1$, $p=.73$.

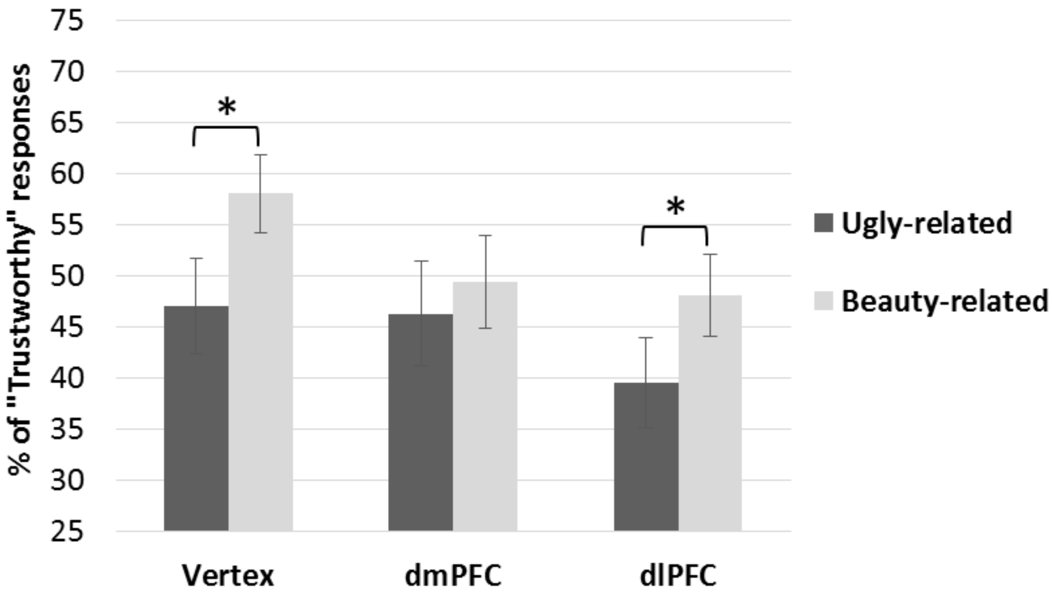


Figure 5.6 Percentage of positive responses (i.e., *The face is trustworthy*) of Experiment 2 as a function of prime (ugliness vs. beauty) and TMS condition (vertex, dmPFC, dlPFC). Similarly to Experiment 1 the *Beauty-is-Good* stereotype was observed when TMS was delivered over the vertex and over the dlPFC, but not when TMS was delivered over the dmPFC. TMS stimulation of the dlPFC decreased the overall number of positive responses. Error bars indicate ± 1 SEM. Asterisks indicate significant differences in priming effects within each TMS condition.

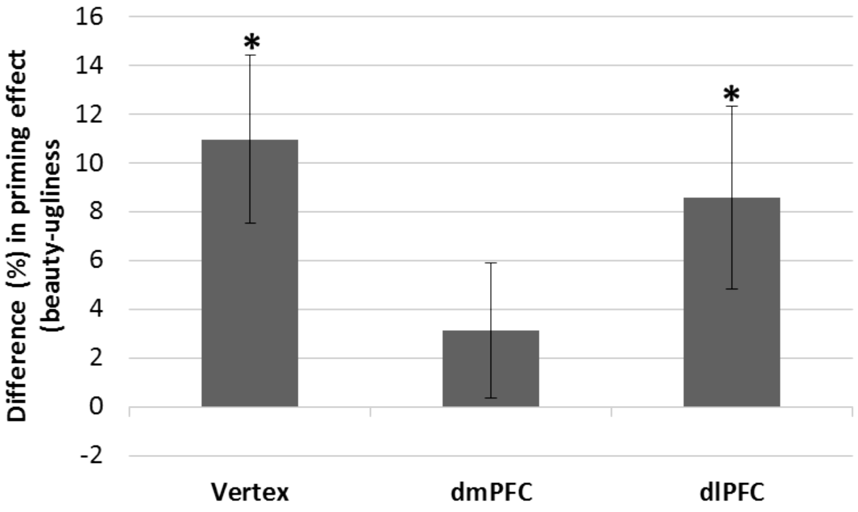


Figure 5.7 Difference in the percentage of faces classified as trustworthy when faces were preceded by *beauty*-primes vs. *ugliness*-primes (i.e., *beauty* minus *ugliness*) in Experiment 2. Asterisks indicate a significant difference compared to zero (i.e., no priming effect). Error bars indicate ± 1 SEM.

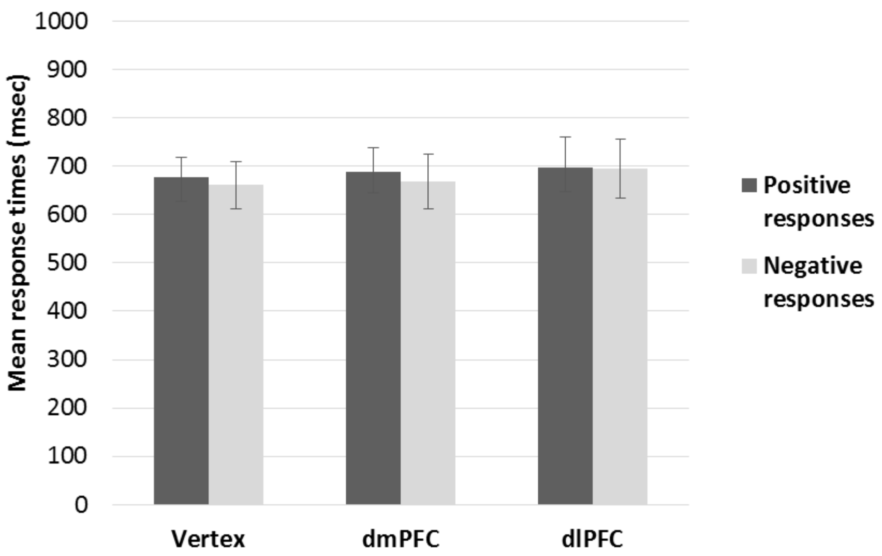


Figure 5.8 Mean reaction times as a function of participants' positive (i.e., *The face is trustworthy*) or negative (i.e., *The face is not trustworthy*) responses and TMS condition in Experiment 2. Response times were not affected by TMS. Error bars indicate ± 1 SEM.

5.4 Discussion

In two different experiments, participants had to evaluate trustworthiness of a series of computer-generated faces that were preceded by prime adjectives denoting desirable (beauty), undesirable (ugliness), or neutral aesthetic qualities (in Experiment 2, neutral primes were not used). In the baseline control condition (Vertex stimulation) of both experiments, faces were rated as more trustworthy when preceded by *beauty*-related primes than when preceded by *ugliness*-related primes. Results in this condition replicated the same pattern obtained in a pilot behavioral study, and revealed the *Beauty-is-Good* stereotype (Eagly et al., 1991; Langlois et al., 2000). Critically, when TMS was applied over the dmPFC, the stereotypical association between attractiveness and trustworthiness disappeared. In turn, following dlPFC stimulation faces tended to appear overall as less trustworthy, but the *Beauty-is-Good* stereotype was still observed. Overall, thus, our data suggest that the dmPFC (but not the dlPFC) plays a key role in linking aesthetic and moral evaluation.

Interfering with neural activity in the dmPFC did not affect face trustworthiness evaluation *per se*: when faces were preceded by neutral primes (Experiment 1), participants' responses did not differ between the dmPFC and the control condition. This is in line with prior TMS evidence showing that interfering with dmPFC activity did not impact perceived face trustworthiness when the judgment was exclusively based upon face appearance (Ferrari et al., 2016), and with prior neuroimaging evidence indicating that evaluations uniquely based on face appearance are likely to elicit responses in subcortical (e.g., amygdala) more than in cortical regions (Baron et al., 2011; Fouragnaet al., 2013; Mende-Siedlecki et al., 2013; Said, Baron, & Todorov, 2009; but see Bzdock et al, 2012a). In turn, TMS over the dmPFC reduced the effect of priming (more consistently so across the two experiments for the positive primes), such that trustworthiness responses in this TMS condition were similar regardless the prime type (Experiment 1 and 2). This is in line with reports of (anterior) mPFC critical involvement in social priming in prior fMRI research (Wang & Hamilton, 2015).

The lack of priming effects following dmPFC TMS is unlikely to reflect a general role of this region in mediating semantic priming *per se*. Indeed, semantic priming tasks unrelated to a social dimension do not recruit the dmPFC (e.g., Copland, de Zubicaray, McMahon, & Eastburn, 2007; Kircher, Sass, Sachs, & Krach, 2009). Accordingly, neuroimaging evidence suggests that person knowledge is functionally dissociable within the brain from other classes of semantic knowledge (for instance, related to objects features) (Mitchell, Heatherton, & Macrae, 2002; see also Ma, Baetens, Vandekerckhove, Van der Cruyssen, & Van Overwalle, 2013b). In line with this, damage to medial sectors of the PFC tends to elicit specific deficits in social reasoning and cognition (e.g., Anderson et al., 1999; Gozzi et al., 2009; Jenkins et al., 2014), but does not typically affect semantic knowledge in general that is mainly mediated by temporal regions (e.g., Campanella, D'Agostini, Skrap, & Shallice, 2010; Gainotti, 2000; Piretti et al., 2015). Moreover, it is unlikely that TMS over the dmPFC acted by disrupting maintenance of the verbal cue in memory. Indeed, interfering with dmPFC activity with TMS in prior studies did not affect maintenance of verbal primes (e.g., Ferrari et al., 2016; Mattavelli, Cattaneo, & Papagno, 2011). In turn, short–term memory for visually presented words is usually affected by stimulation of visual (e.g., Amassian et al., 1989; van de Ven, Jacobs, & Sack, 2012) or language-related areas (e.g., Deschamps, Baum, & Gracco, 2014).

If on one hand our results are unlikely to depend on an unspecific role of the dmPFC in semantic priming or short term memory (see above), on the other hand we do not argue for a selective role of the dmPFC in mediating aesthetic-to-ethical (priming) associations. In fact, although in our study we focused on the *Beauty-is-Good* stereotype as a "window" onto the intersection of moral and aesthetic evaluation, previous neuroimaging studies have shown preferential activation in the medial PFC when responses matched other stereotypical social beliefs, as those concerning gender or race (Gilbert et al., 2012; Ito & Bartholow, 2009; Knutson et al., 2007; Mitchell et al., 2006; Quadflieg et al., 2009). Accordingly, interfering with mPFC activity via brain stimulation was found to affect implicit measures of stereotypical beliefs about gender and in-group/out-group (positive vs. negative) attributes (Cattaneo et al., 2011; Sellaro et al., 2015). Brain-lesion evidence also supports the involvement of the (ventro-) medial PFC in stereotypical beliefs (see Gozzi et al., 2009). Still, although activity in the dmPFC is certainly modulated by the stereotypicality of the information available about another agent (Van der Cruyssen, Heleven, Ma, Vandekerckhove, & Van Overwalle, 2015), the dmPFC is also involved in social evaluation beyond stereotypical categorizing. Indeed, converging evidence points to an involvement of the mPFC in different aspects of social evaluation such as first impression formation, personality traits inference, and attribution of mental states (Baron et al., 2011; Contreras, Banaji, & Mitchell 2012; Fouragnan et al., 2013; Ma et al., 2013a,b; Mitchell et al., 2005; Van den Stock et al., 2014; for a review, Van Overwalle, 2009). Our study critically adds to this prior evidence by showing that the mPFC is also a key region in mediating the "transfer" from the domain of aesthetics to the domain of ethics (in the form of a stereotypical *Beauty-is-Good* association). This is also in agreement with prior evidence pointing to a critical role of the mPFC not just in selectively mediating moral judgments (e.g., Beer & Ochsner, 2006; Bzdok et al., 2012b; Englander, Haidt, & Morris, 2012; Greene & Haidt, 2002; Yoder & Decety, 2014) and aesthetic judgments (Jacobsen et al., 2006; Kirsch, Urgesi, & Cross, 2015; Pegors, Kable, Chatterjee, & Epstein, 2015; Vessel, Stahl, Purton, & Starr, 2015), but also in linking aesthetic and moral valuations (Avram et al., 2013; Bzdok et al., 2012a; Wang et al., 2014).

Following dlPFC stimulation, faces tended to be generally judged as less trustworthy, but the effect of *beauty*-related primes on trustworthiness decisions was still observed. We were interested in verifying whether the dlPFC plays a role in regulating flow of information between the aesthetic and ethical dimensions in impression formation, in light of its regulatory role in controlling emotional responses in tasks tapping on social categorization (e.g., Cattaneo et al., 2011; Ito & Bartholow, 2009; Knutson et al., 2007; Kubota et al., 2012; Quadflieg et al., 2011). Our data suggest that this was not the case. However, it is important to note that the dlPFC typically responds in social decision making when a conflict is detected, for instance when a stereotypical representation is violated (e.g., a woman depicted in a male-stereotypical occupation, such as a "chef", Quadflieg et al., 2011). In our paradigm, there was no "conflict" between the aesthetic cues and the faces, because faces were all of average-trustworthy. It may be that using other paradigms eliciting a conflict between the aesthetic and ethical dimension (for instance, a very beautiful male face associated with the description of a very bad act) may then recruit the dlPFC. Future research may address this issue.

In turn, the overall decrease in the number of faces perceived as trustworthy following dlPFC stimulation (irrespective of the prime) compared to the control condition is in line with neuroimaging evidence on the role of this region in the evaluation of trustworthiness in faces (Bzodck et al., 2012a) and behaviors (Watabe, Ban, & Yamamoto, 2011), in addition to evaluations of moral appropriateness and moral reasoning (Greene et al., 2001; 2004; Jeurissen et al., 2014; Tassy et al., 2011). Furthermore, the dlPFC may regulate subjective evaluations of positive traits in general: for instance, increasing excitability in the dlPFC resulted into higher attractiveness judgments for faces (Ferrari et al., 2015), and interfering with its activity also affected appreciation of visual artworks (Cattaneo et al., 2014a; 2015; Chatterjee & Vartanian, 2016; Cupchik, Vartanian, Crawley, & Mikulis, 2009).

The priming effect we reported in our baseline condition did not depend on unspecific halo effects, since other verbal cues unrelated to physical appearance but still evoking a negative/positive continuum (e.g. *less*/*more*; *little/a lot*) did not affect trustworthiness evaluation. Hence, one may question whether priming occurred because faces were perceived as less/more beautiful and hence less/more trustworthy following *ugliness*- vs. *beauty*-related primes. We think that this possibility is unlikely, and that the aesthetic adjectives directly biased trustworthiness decisions (possibly by activating a common evaluative scale), without going through an intermediate visual step in which faces also appeared less/more attractive. In fact, deciding about attractiveness of computer-generated faces as the ones we used (that were specifically created to vary along the trustworthiness dimension, Oosterhof & Todorov, 2008), especially if a yes/no decision response is required, feels unnatural because these faces lack important features that are typically used to determine attractiveness (e.g., hair, skin texture, eye colour, variation in symmetry, masculine/feminine traits). Accordingly, several studies focusing on mechanisms implied in face attractiveness evaluation employed real faces (e.g., Jones et al., 2004; Mitrovic, Tinio, & Leder, 2016; Little, Jones, & DeBruine, 2008), whether the use of computer generated-faces may be supobtimal for this purpose (e.g., Komori, Kawamura, & Ishihara, 2009; Sutherland et al., 2013).

In our study, TMS affected the decision output but not response latencies. Dissociation of TMS effects on responses bias/accuracy and reaction times are not uncommon (Devlin & Watkins, 2007; Robertson, Theoret, & Pascual-Leone, 2003), and largely depend on the specific paradigm used. As we mentioned above, we used average trustworthy faces so that decisions were uncertain and could be modulated by the primes we used: TMS is more effective in affecting responses when uncertainty is higher (Robertson et al., 2003). In turn, when there are clear correct vs. incorrect responses (with accuracy being high), behavioral effects induced by TMS tend to manifest more in terms of differences in reaction times (Devlin & Watkins, 2007). In case of our paradigm priming effects manifested essentially in the type of response given and only marginally so in the response latencies (with no priming effects on RT in the purely behavioral studies and in the baseline condition of Experiment 2); it is thus less surprising that TMS mainly modulated the bias induced by the prime cues rather than RT.

The effects of TMS over the dmPFC were overall of small size. In this regard, it is important to consider that other cortical and subcortical regions have been found to respond to both moral and aesthetic evaluation, such as the orbitofrontal cortex (involved in reward processing, common to both aesthetic and ethical evaluation, see Tsukiura & Cabeza, 2011), the insular cortex (critical in mediatingnegative emotions and social negative signals, see Tsukiura & Cabeza, 2011). Other structures might also contribute to this phenomenon, such asa the temporal pole (important for emotional memoriesand for social knowlegde), (see Zaidel & Nadal, 2011, for a review). The relative small size of the effect of TMS over the dmPFC may also partially reflect the work of these other regions in mediating the association between ethical and aesthetic value. Nonetheless, it is worth noting that TMS can modulate activity not only in the neurons under the coil but also in interconnected regions (e.g., Avenanti, Annella, Candidi, Urgesi, & Aglioti, 2013; Siebner, Hartwigsen, Kassuba, & Rothwell, 2009). For instance, the OFC and the mPFC are known to be inherently connected (Öngür & Price, 2000); it is thus possible that the TMS effects we reported did not solely reflect direct interference with the mPFC activity but also indirect modulation of a larger network including the OFC.

In our study we did not consider whether positive personality traits would also prime a face to appear more attractive, and whether this would in case rely on similar neural mechanisms. Accordingly, literature has mainly focused on the “what is beautiful is good” rather than the reverse inference, possibly reflecting the precedence of the aesthetic attribute over other personal attributes in first impression formation (see Eagly et al., 1991). Nonetheless, available evidence suggests that attractiveness judgments can also be permeable to the influence of “goodness” evaluation. In particular, Little and colleagues

(Little, Burt, & Perrett, 2006) found that individuals positively valuing particular personality traits found faces displaying those traits to be more attractive. Similarly, Zhang et al. (2014, see also Eagly, Gross & Crofton, 1977) reported that faces presented simultaneously with positive personality traits were rated as more attractive than faces presented with negative personality traits or no-information. Although we are not aware of any study that directly looked at the neural underpinning of the influence of perceived goodness of a person over her/his face attractiveness, it is reasonable to speculate that the dmPFC would be involved, given its role in encoding personality traits (Ma et al., 2013a,b; Van Overwalle, Ma, & Baetens, 2015). Future neuroimaging and brain stimulation research may shed light on this interesting issue.

6. Conclusions

Humans have produced and enjoyed art for centuries and they still do. Recently neuroscience has begun to investigate the nature of such aesthetic experience. Neuroimaging experiments have provided new insights into the cognitive and neural correlates of aesthetic appreciation. One basic finding in this field is that the aesthetic appreciation emerges from a complex interplay of perceptual, affective and cognitive processes (Leder & Nadal, 2014), related to activity in neural networks encompassing sensory-areas, cortical and subcortical regions involved in reward processing and prediction, and high-level processing regions, such as the prefrontal cortex (Brown et al., 2011; Chatterjee & Vartanian, 2014; Nadal, 2013). The studies presented here extend previous findings shedding light on some unresolved issues and providing starting points for future experiments.

Study 1 aimed to clarify the issue of hemispheric lateralization in painting appreciation. The results showed that both men and women liked representational artworks more when they were presented in the right visual field than when they were presented in the left visual field, and that liking for abstract artworks was unaffected by presentation hemifield. One possible explanation is that the effect owes to the facilitation of the sort of visual processes relevant to laypeople's liking for art, specifically, local processing of highly informative object features, when artworks are presented in the right visual field, given the left hemisphere's advantage in processing such features. Further studies are required to clarify the mediating role of particular artistic style, familiarity, and emotional investment. While study 1 focused on hemispheric influence on artworks perception studies 2 and 3 examined artworks perception more in detail, investigating the role of specific sensory areas in perception of certain features that are meant to play a role in artworks appreciation and aesthetic judgment. Both studies used a TMS technique, aiming to overcome the correlational nature of neuroimaging.

Study 2 demonstrated that the motion-sensitive region V5 is causally involved in the use of form cues to represent motion information even when the objects in motion are not real, but pictorial representations (as opposed to photographs or film frames), and even in the absence of any representation, as in the case of abstract art, where only formal features are present. Moreover, the study showed that TMS over V5 causes a decrease in liking for abstract painting in laypeople, suggesting that the aesthetic experience of art (at least, for the abstract art we considered) is directly related with activity in sensory regions.

Study 3 demonstrated that the superior temporal sulcus (STS), but not the somatosensory cortex (SC), is causally involved in expressivity judgment of portraits, suggesting that expression recognition plays a critical role in the expressivity conveyed by this kind of stimuli. Moreover, study 3 showed that TMS over STS and SC does not affect liking for paintings. This can be explained considering the complex nature of aesthetic experience. Since different components contribute to the experience of beauty (Chatterjee & Vartanian, 2014), interfering with just one of them seem to be not enough to modulate the aesthetic experience, especially in representational paintings (see also Study 2). Finally, this study indicated that portraits are processed faster than other representational paintings, adding further evidence to the special status of faces for humans.

In order to extend the investigation beyond perceptual aspects of artworks, thus addressing also their rewarding nature, in study 4 the role vmPFC was investigated. This area belongs to the reward system, that seems to respond to aesthetic stimuli of various nature. The results point towards an involvement of vmPFC in aesthetic evaluation in line with previous neuroimaging studies (Tomohiro Ishizu & Zeki, 2011; Kawabata & Zeki, 2004), which showed an enhanced activity of this region when subjects were presented with paintings they found beautiful. Moreover, the suggested involvement of this region in appreciation supports the idea of paintings as a stimulus category that engage the liking system more than the wanting system (Chatterjee, 2014a, 2014b).

Study 5 partially differed from the previous ones, inasmuch as it does not use paintings as stimuli. This study was designed to address the interdisciplinary nature of aesthetic experience, specifically the influence of beauty in other kind of evaluation. The study provided evidence for a causal role of the dmPFC in mediating the link between aesthetic and ethical evaluation. Critically, it went beyond prior correlational evidence supporting the existence of a common brain network mediating aesthetic and moral evaluation (e.g., Avram et al., 2013; Bzdok et al., 2012a; Mende-Siedlecki et al., 2013; Tsukiura & Cabeza, 2011; Wang et al., 2014). This network is believed to encode value in terms of a common neural currency and assign value and motivational relevance to social and non-social stimuli alike (Ruff, Ugazio, & Fehr, 2013; Zaki, López, & Mitchell, 2014).

From this perspective, aesthetics and ethics are linked in terms of a common valuation neural system that assigns congruent values to beauty and goodness, and common motivational dispositions to attraction and trustworthiness. Morality and aesthetics are likely to be distinct human traits, and have been systematically associated in the history of Western philosophy. These results add to prior neuroimaging findings (e.g., Tsukiura & Cabeza, 2011) and suggest the possibility that the experienced association between aesthetics and ethics may actually be due to the two systems of value exploiting a common neural network, at least in as much they apply to evaluation of other individuals (see Zaidel & Nadal, 2011, for a review).

In summary, this dissartation examined the neural correlates of beauty appreciation of paintings and faces considering the role of the two hemispheres, sensory and somatosensory areas and the prefrontal cortices. Because of the fact that aesthetic appreciation is a highly complex phenomenon and consists of different neural networks interacting each other, it appears complex to draw conclusions and connections between the results presented here. However, when looking at all the gathered evidence both here and in previous literature, a partial framework can be designed.

First of all, it was shown that left hemisphere could have an advantage in processing representational paintings. This integrates previous findings supporting the view that neither hemisphere is dominant in general aesthetic appreciation, but each hemisphere is recruited during perceptual analysis of specific features.

Second, results from study 2 and 3, taken together show that the neural network involved in low-level and high-level processing of non-artistic stimuli is also active when subjects see paintings. This supports the idea that there is no specialized system for art processing, but rather an overlapped system for artistic and non-artistic stimuli perception and evaluation. Neural network for beauty appreciation shares not only the same network of sensory processing but also the same network of other cognitive processes as suggested by the role of dmPFC in mediating both aesthetic and ethical evaluation showed in study 5.

Finally, study 4 attempted to unravel the rewarding nature of beautiful paintings through that stimulation of the vmPFC, a key hub in the reward system. The stimulation led to a slight enhancement of the aesthetic experience, hence suggesting a role of this region in paintings appreciation. This study presented a series of limitations already discussed in the specific chapter, and by itself is not enough to provide evidence for a causal involvement of the reward system in paintings appreciation. However, it paves the way for further investigations that are still needed to better understand this issue.

The experiments presented here raised a variety of new questions that need to be investigated, among others how context, expertise, and personality could affect the neural network underlying appreciation.

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