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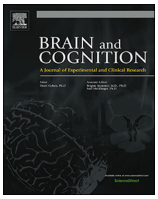

Perception of direct vs. averted gaze in portrait paintings: An fMRI and eye-tracking study

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ABSTRACT

In this study, we use separate eye-tracking measurements and functional magnetic resonance imaging to investigate the neuronal and behavioral response to painted portraits with direct versus averted gaze. We further explored modulatory effects of several painting characteristics (premodern vs modern period, influence of style and pictorial context). In the fMRI experiment, we show that the direct versus averted gaze elicited increased activation in lingual and inferior occipital and the fusiform face area, as well as in several areas involved in attentional and social cognitive processes, especially the theory of mind: angular gyrus/temporo-parietal junction, inferior frontal gyrus and dorsolateral prefrontal cortex. The additional eye-tracking experiment showed that participants spent more time viewing the portrait's eyes and mouth when the portrait's gaze was directed towards the observer. These results suggest that static and, in some cases, highly stylized depictions of human beings in artistic portraits elicit brain activation commensurate with the experience of being observed by a watchful intelligent being. They thus involve observers in implicit inferences of the painted subject's mental states and emotions. We further confirm the substantial influence of representational medium on brain activity.

1. Introduction

1.1. Gaze in art theory and cognitive neuroscience

Gaze represents an important topic in both art history/visual studies and cognitive neuroscience. Art historians and art critics have written extensively on both various forms of gaze depicted in figural representations in paintings, photography and videoart, as well as on practices of gazing at works of art (e.g. Bryson, 1983; Wollheim, 1987; Belting, 2009). They distinguish various dimensions of depicted gazes (e.g. duration of the gaze, its "power", or sexual allure) but most of these qualities cannot be easily objectified or studied by empirical methods. One aspect of gaze, however, which features prominently in both art historical accounts and scientific examination is the direction of the gaze.

It is well-established that gaze direction is a critical facial cue, essential for social interaction and cognition (Argyle & Cook, 1976; Frischen, Bayliss, & Tipper, 2007; George & Conty, 2008; Gibson & Pick, 1963; Hamilton, 2016). As an instrument of social communication, it modifies the perception of emotions and enables decoding of mental states, related to the process of theory-of-mind or mentalizing. Gaze direction is a key element of socially relevant signaling encoded in and decoded from faces. Eye contact, modulates cognitive processing, particularly enabling to read or to see the minds of others in direct mutual interaction (Baron-Cohen, 1995; Nummenmaa & Calder, 2009; Senju & Johnson, 2009; Stawarska, 2006). Depending on the context, it can have various meaning, ranging from an expression of intimacy to that of dominance or hierarchy (George & Conty, 2008). In terms of Bayesian theories of the human brain, humans have prior expectation (priors) that other's gaze is directed toward them (Mareschal, Calder, & Clifford, 2013). Contemporary research thus sheds some light on the practice of visual artists who for centuries intuitively manipulated the direction of the gaze of depicted persons to imbue their works with distinct psychological effects. Eye contact was given prominence in Roman portrait busts, which often express an awareness of the viewer's gaze and initiate – probably for the first time in history of art – direct scopic and thus potentially psychic interaction with beholder

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(Nodelman, 1975). This potential has then been further explored in some of the arguably best Renaissance and modern portraits, where the gaze of the depicted subject returns the gaze of the viewer, or – on the other hand – avoids it in various ways. In summary, artists have been exploring the potential of a painted gaze for centuries, deploying it in specific ways and in conjunction with facial expression, to imbue portraits with distinct meanings and effects and they continue to do so (Kesner, 2011).

Several neuroimaging experiments have explored the neural correlates of direct versus averted gaze. The brain areas that respond differently to eye contact and averted gaze include the posterior superior temporal sulcus (STS) linked to processing of gaze shifts, the amygdala engaged in processing of threatening and ambiguous stimuli, the fusiform gyrus, the orbitofrontal cortex, as well as regions involved in self-related and complex social-cognitive processing and theory of mind/mentalizing (the paracingulate part of medial prefrontal cortex and temporo-parietal junction, TPJ) (for a review see Senju & Johnson, 2009; Nummenmaa & Calder, 2009; Hamilton, 2016). However, many inconsistencies among the findings prompt further research in this area. One of the specific problems concerns the role of specific visual modality, which conveys the face and gaze stimulus.

1.2. Aims and hypotheses

Neuroimaging studies on gaze direction conducted so far have used naturalistic photographs of isolated eyes and eyes in a face, in which the gaze direction is sometimes digitally manipulated (e.g. Kampe, Frith, & Frith, 2003; Mason, Tatkow, & Macrae, 2005; Straube, 2010; Berchio et al., 2016), symbolic line drawings (Friesen & Kingstone, 1998), video clips (Kuzmanovic et al., 2009; Pelphrey, Morris, & McCarthy, 2004), computer-generated agents (Schilbach et al., 2006; Wilms et al., 2010) and, most recently, also live people (Cavallo et al., 2015; Debruille, Brodeur, & Franco Porras, 2012; Myllyneva & Hietanen, 2015a, 2015b; Pönkänen et al., 2011). Different types of stimuli have different levels of ecological validity, social richness and potential to engage an audience effect (Hamilton, 2016; Risko, Laidlaw, Freeth, Foulsham, & Kingstone, 2012). So far, there is only scant evidence of the effect of representational medium in the perception of gaze direction. Several studies using event-related potential (ERP) N170 showed that the physical and structural characteristics (photographs or impoverished line-drawn faces) of the stimulus drive and modulate the response in favor of the photographs (Puce, Smith, & Allison, 2000; Rossi, Parada, Kolchinsky, & Puce, 2014; Rossi, Parada, Latinus, & Puce, 2015). Congruently, a comparison of responses to a directly gazing live person, photograph and dummy showed that ERPs in early windows (125–170 and 170–230 ms) depended on the nature of the stimulus and in N300 were significantly more negative in the case of the dummy (Debruille et al., 2012). However, it is not clear if the findings from these studies are generalizable to brain processing of artistic portraits. Clearly, the problem if (how) the representational medium modifies the neurobiological response to human faces and gazes prompts further investigation.

Our study, consisting of a separate fMRI and eye-tracking experiment, was designed to explore the neuronal and behavioral response to painted portraits with direct versus averted gaze. This study addressed two questions. First, we aimed to identify how the neural and behavioral response to emotional expressive faces in paintings is modulated by the direction of gaze. In other words, we asked if direct (vs. averted) gaze in painterly portraits affects the saliency of the social cognition brain areas. To identify the behavioral influence of the gaze direction in artistic portraits on the beholder's eye movements and visual scanning, we complemented the fMRI study by performing separate eye-tracking measurements. Second, to identify the modulatory effects of painting characteristics on brain activation, we further resampled our artistic portraits series according to three contrasting factors: (i) *period of the painting* (pre-modernist vs. modernist paintings); (ii) *influence of style* (painterly vs. linear),[1] and (iii) *pictorial context of the portrait* (face only vs. face and torso vs. face, torso and hand gesture).

We hypothesized that firstly; direct vs averted gaze will exert different brain activation similar to previous studies with photographs and videos. Specifically, direct gaze will be linked to activity in the fusiform gyrus and in brain areas processing mentalizing (paracingulate cortex, MPFC and TPJ). The separate eye-tracking experiment addressed the question of the behavioral effect of portrait characteristics. We expected that (i) beholders will spend more time viewing the eyes of the depicted person with direct gaze, than under an averted gaze condition; (ii) the representational medium characterized by the modern and painterly styles (i.e. less realistic) will engage cortical regions responsible for higher level of visual processing more intensively than realistic pictures (typically a linear style of painting). We assumed that this effect stems from the fact that more formalized or stylized/less realistic pictures need more effort (with larger hemodynamic response) to be recognized and processed properly. We further assumed that the specific face-processing brain areas (e.g. the fusiform gyrus) would be activated more intensively when viewing portraits depicting only faces versus portraits also depicting body and hand gestures.

2. Materials and methods

2.1. fMRI experiment

2.1.1. Stimuli

A set of artistic portraits was used as stimuli for the fMRI experiment. The portraits were organized in duplets – each duplet contains two portraits from the same artist, the first portrait being classified as "direct gaze" (the portrayed person gazes directly at the observer), the second one as "averted gaze" (the portrayed person gazes to the side or behind the observer). The direct gaze (or eye contact) group included both images with the face directed forward and faces averted at various degrees. The original set of 110 portraits from 32 artists was first assessed by 11 volunteers in a pilot study validating the set of stimuli. The evaluators were to decide whether the portrayed person was looking directly at them (direct gaze) or not (averted gaze). The portraits with a consensus of a minority of less than seven evaluators were excluded from the final stimuli set together with the paired stimulus (from the same artist). The final set of 72 portraits (36 duplets, 72% with a consensus of at least 10 evaluators) is from 27 artists from various periods and provenances, beginning with Flemish Early Renaissance (Jan van Eyck, Hans Memling, Dieric Bouts, Petrus Christus, anonymous), Italian Renaissance and Mannerism (Domenico Ghirlandaio, Agnolo Bronzino), German Renaissance (Albrecht Dürer, Matthias Grünewald), followed by Baroque paintings (Christian Seybold, Pietro Antonio Rotari), modernism (Paul Cézanne, Oskar Kokoschka, Egon Schiele, Max Beckmann, Christian Schad, Charley Toorop, Paula Modersohn-Becker, Kathe Kollwitz, Vilma Vrbová-Kotrbová, Jan Preisler, Josef Šíma), and postmodern art: pop art with its typical comic book style (Roy Lichtenstein), or new figuration with distorted or

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[1] Here we adopted the historical categories of *linear* (or *tactile*) versus *painterly style*, introduced by art historians Heinrich Wölfflin and Alois Riegl. The *linear* style is characterized by sharp definition of the form (e.g. Albrecht Dürer's portraits): the style emphasizes contours, it radically differentiates the figure from the background or each individual shapes between each other. The figure is clearly shaped into a precisely "graspable" plastic shape, which can even induce "the feeling of touch", according to Wölfflin, such as we somehow touch the precisely sculptured figures with our eyes (Wölfflin, 1950: 21). Conversely, the element of physical touch or grasp is missing in painterly style, which does not differentiate shapes and the figure from the background so clearly, as it is organically interconnected, having its origin in the same material. Instead of precise lines and smooth surfaces, the painterly style makes the medium visible and thus the way the painting has been made (perceptible brushstrokes, blotches etc.; e.g. Oskar Kokoschka). Although it could invoke an intensive effect of plasticity or depth, it disrupts the "graspable feeling" of figures, as Wölfflin suggested (Wölfflin, 1950: 21), therefore paintings rendered in a painterly style engage only vision and lack the intention to grasp the figure.

blurred faces (Francis Bacon, Chuck Close, Marlene Dumas, Jenny Saville – see Supplementary Material). The pictures were gathered from various public websites and online databases. The size of the pictures varied, therefore we used Adobe Photoshop CS5 for the adjustment of all the stimuli to the resolution of the MRI projector and of the monitor screen used in the eye-tracking experiment (1024 × 768 pixels).

The portraits were divided into twelve blocks per six portraits (either “direct gaze” or “averted gaze”). Both sets of portraits were carefully matched by artist (duplets of direct and averted gaze portraits by the same artist). The blocks were balanced by average luminance and RGB color components assessed with ZONER photo studio software (the performed ANOVA showed no block × luminance/color interaction: $p > 0.05$; Luminance: $F(1, 11) = 0.389$; Red: $F(1, 11) = 0.466$; Green: $F(1, 11) = 0.496$; Blue: $F(1, 11) = 0.241$). In addition, the size of the face, eyes and mouth areas of individual portraits was compared between direct and averted gaze stimuli using Mann-Whitney/Wilcoxon test, showing no significant differences (eyes: Wilcoxon $W = 665$, $p = 0.854$; mouth: $W = 697$, $p = 0.585$; face: $W = 665$, $p = 0.8534$). Aside from these characteristics, all of the blocks were also counterbalanced by two experimenters for the following parameters (meaning each block contains the same amount of portraits with specific characteristics): artistic techniques (painting vs. drawing) and pictorial context of the portraits (detailed face/face only; face and torso without hands; face and torso with hand gestures) in order to suppress the possible effect of these characteristics on the measured brain activity. Notice that the *pictorial context* characteristic was later applied as a contrasting factor in the fMRI analysis together with two other characteristics: *period of the painting* (pre-modernist vs. modernist paintings) and *influence of style* (painterly vs. linear). All of the three mentioned characteristics were evaluated ad hoc by 19 art experts and students of art history in order to classify the portrait categories.

2.1.2. Participants

The fMRI group (**Experiment 1**) consisted of twenty-four healthy adult volunteers (11 females, 13 males, all right-handed, with a mean age of 30 years old (SD = 6), education years 17 (SD = 2.5), and with no previous expertise in art history.

The eye-tracking sample **(Experiment 2)** consisted of a different twenty-five healthy volunteers (mean age of 26 years, range 20–48; 11 women) again naive in art history. Due to inaccurate drift correction in one of the subjects, only data from 24 participants were analyzed.

All participants had normal or corrected-to-normal vision. The investigation was carried out in accordance with the latest version of the Declaration of Helsinki. We obtained written informed consent from all of the participants, and the local ethics committee approved the study.

2.1.3. fMRI data acquisition

The fMRI experiment was performed using a 3 T Siemens Trio MRI scanner (Erlangen, Germany). All of the participants had their heads firmly immobilized in a 12-channel head coil using foam inserts positioned on either side of the head. For stimulation by the artistic portraits, we applied the fMRI paradigm with contrasting fixation versus direct and averted gaze, and both gaze series between each other. During the fixation blocks, the subjects looked at a black screen with a white cross in the middle. The reproductions of 72 portraits (36 duplets) were displayed in a block design. The participants were instructed to passively view the portraits displayed by the LCD projector. The direct and averted gaze portraits were presented in 12 alternating 36-second blocks, 6 with “direct gaze” and 6 with “averted gaze”. Each portrait was presented for 6 s, with a 3-second inter-scan interval (ISI; 2 scans per portrait). An additional control condition was six fixation blocks lasting 36 s. All of the three conditions were presented in a pseudorandom order. In total, 216 brain volumes were acquired. The total acquisition time of each fMRI was 10 min, 48 s.

The fMRI images ($T2^*$-weighted gradient echo-planar imaging sequence) of 45 axial slices (3 mm thickness, no gap) parallel to the anterior and posterior commissure covering the whole brain were taken under the following conditions: echo time (TE) 30 ms, repetition time (TR) 3000 ms, matrix 64 × 64, bandwidth 1594 Hz/pixel, flip angle 90°. The field of view (FOV) was 192 mm and the in-plane spatial resolution was $3 \times 3\ \text{mm}^2$. For the fMRI data preprocessing, the participants were scanned using a $T1$-weighted 3D-MPRAGE sequence.

2.1.4. fMRI data analysis

The fMRI data were first analyzed using Statistical Parametric Mapping software version 8 (SPM8; www.fil.ion.ucl.ac.uk/spm/software/spm8) implemented in MATLAB version 7.3 (MathWorks). Statistical analysis of the data across all of the participants proceeded by entering each participant’s preprocessed functional data (realigned to correct for movement, normalized and smoothed using a Gaussian kernel of 8 mm FWHM) into a generalized linear model. Low-frequency noise was removed using a highpass filter (128 s). The first-level design matrix contained factors modelling regressors (in blocs) for the fixation, direct and averted gaze conditions convolved with a canonical hemodynamic response function. For the secondary objectives, we estimated by event-related design approach the effects of painting techniques and characteristics (one-way ANOVAs) for a) old and modern style of painting, b) linear and painting style, and c) depicted details of portraits presented during scanning. For this purpose, the portraits were sorted into three groups: face only (F), face and torso (FT) and face, torso and hand gesture (FTG).

The contrast images (linear combinations of β images) were then subjected to a second-level analysis to determine stimulus-specific regional responses at a group level (one sample T- test). For control type I error, we accepted as significant only conservative family-wise error (FWE) corrected findings ($p \le 0.05$) with the extent threshold consisting of 50 voxels per cluster for second level comparisons between portraits and fixation as a control condition. The coordinates for local maxima using the MNI (Montreal Neurological Institute) template were converted to stereotactic Talairach x, y, z coordinates (Lancaster et al., 2007). The results were displayed using MRIcro V1.4 (www.mricro.com) and its template.

2.2. Eye-tracking experiment

The set of artistic portrait stimuli used in the previous fMRI study was extended by an additional 22 stimuli (11 for each category of gaze direction) which we were specifically interested in obtaining eye-tracking data for. These consisted of expressionist and cubist portraits from the period between 1900 and 1960, by European artists (Pablo Picasso, Umberto Boccioni, Bohumil Kubišta, Emil Filla, Antonín Procházka, Jan Zrzavý, Francis Bacon) and applied in the eye-tracking experiment. After showing four additional portraits as training, the completed set of 94 stimuli was presented in randomized order in two blocks. The portraits were each displayed on a 19″ computer screen for 6 s. As previously, the volunteers were asked to look at the portraits the same as they would in a gallery, while their gaze-direction was recorded.

The eye movements were measured with the EyeLinkII eye-tracker (SR Research Ltd) with a head-mounted camera. The participants viewed portraits from approximately 60 cm (to achieve as natural viewing conditions as possible, no chinrest was used to enforce constant distance). We used a 9-dot grid calibration prior to each block and drift correction prior to each trial. The gaze samples were collected at 250 Hz. We collected data from one eye only (selected based on the results of the calibration). After filtering the data for blinks, we removed the trials where a participant spent less than 3 s (50% of time) looking at the portrait due to blinks or looking beyond the portrait boundaries. The total dataset for the analysis consisted of 2210 trials (88–94 per participant, representing 94–100%). We defined three areas of interest (AOI) manually for each portrait: area of the eyes, mouth, face (excluding the other two areas, see Fig. 3). We decided to create eyes and mouth AOI, unlike other local face features such as nose or forehead, because eyes and mouth are considered not only the core face features, but also the main cues for detecting emotions in other people and for communication (e.g. Morris, Pelphrey, & McCarthy, 2007; Wegrzyn, Vogt, Kireclioglu, Schneider, & Kissler, 2017). The eyes AOI covered the area for both eyes and the area around and between them. We calculated the corresponding dwell times for each AOI. The size of AOI varied across individual paintings, however the differences in AOI size between direct and averted gaze portraits were not significant. We examined whether the extent of AOIs differs between portraits with direct vs. averted gaze (measured in pixels). The eyes AOI subtended on average 23,580 pixels (SD = 27,231, median = 11,372, range 2160–154,069), the mouth AOI subtended on average 8560 pixels (SD = 10,746, median = 4243, range 616–55,759). The face AOI subtended on average 50,877 pixels (SD = 52,970, median = 28,063, range 3940–243,599). We compared the areas in portraits with direct vs. averted gaze and we found no difference in their extent (eyes: Wilcoxon W = 1019, $p = 0.522$; mouth: W = 1018, $p = 0.516$; face: W = 1071, $p = 0.804$; all p values are uncorrected).

2.3. Behavioral measurements and psychometrics (Experiment 1 and 2)

Participants in both the fMRI and eye-tracking experiments were asked about the characteristics of the individual portraits presented during the fMRI/eye-tracking paradigm in a debriefing questionnaire (stimuli were presented on the computer screen). The participants evaluated the gaze direction of the portrayed persons on a scale from −5 (averted gaze) to +5 (direct gaze). The subjects were also required to evaluate the following characteristics of individual stimuli (on a scales from −5 to +5): (1) Emotional valence (unpleasant/pleasant), (2) Arousal (calmness/tension). In addition, (3) the Familiarity of the individual pictures was rated (Yes/Maybe/No). In the fMRI experiment, this evaluation was done after the scanning using a paper-pencil debriefing questionnaire (stimuli were presented on the computer screen, in the same order as during the fMRI measurement), in the eye-tracking experiment using a computerized debriefing prepared in the PsychoPy software (pictures presented in a pseudorandomized order). Statistical analysis of the behavioral results was performed using STATISTICA 11 software (StatSoft). The non-parametric Mann-Whitney *U* test was used to analyze the differences of direct and averted gaze portraits in terms of the individual characteristics (Gaze direction, Emotional valence, Arousal, Familiarity). The Spearman Rank Order Correlation analysis was applied in order to calculate a possible relationship between gaze direction and/or the individual characteristics.

3. Results

3.1. fMRI experiment

3.1.1. The effect of direct and averted gaze portraits

Both direct and averted gaze portraits (compared to fixation) showed bilateral activation in occipital lobes including lingual and fusiform gyrus and the hippocampus. The main difference in the averted gaze portraits was the absence of activation in the left superior, inferior and medial frontal gyri, and the right angular and superior frontal gyri (FWE corrected $p \leq 0.05$, Fig. 1, Table S1). Deactivation by both types of portraits was found in default mode network regions areas covering posterior midline structures (precuneus and posterior cingulate), and bilateral temporo-parietal regions (angular, superior and middle temporal gyri). The main difference between the two kinds of gaze was identified in the anterior cingulate, which was deactivated for the direct gaze portraits but not for the averted gaze portraits (FWE corrected $p \leq 0.05$, Fig. 1, Table S1).

Direct gaze portraits contrasted to the averted gaze portraits elicited an increased BOLD signal in the occipital surfaces covering the calcarine fissure and surrounding the cortex bilaterally with the local maxima in the right lingual gyrus and cuneus and this cluster reached temporal lobe including fusiform gyrus (FWE corrected $p \leq 0.05$). Interestingly, the direct gaze portraits exerted higher activation in the fusiform gyrus, right angular gyrus and in prefrontal regions (left middle and the inferior frontal gyrus) but these results did not survive conservative FWE correction (Fig. 1, Table 1). We did not find any region with higher activity for the averted gaze portraits.

3.1.2. The effect of painting techniques and characteristics on brain activity (fMRI)

Modernist style contrasted against pre-modern style showed a greater activation in the occipital lobe bilaterally, notably in the lingual gyri and in the right fusiform gyrus. The opposite contrast showed no differences in neural processing of pre-modern paintings compared to new ones (Fig. 2, Table 2). Painterly style contrasted against linear style showed higher activation in the medial and inferior surfaces of the occipital lobe (calcarine fissure, cuneus, lingual and fusiform gyri) and the effect was more pronounced on the right side. The opposite contrast showed no increase in linear compared to painterly style (Fig. 2, Table 2).

3.1.3. The effect of the pictorial context of paintings

Comparing portraits with faces only (F) and faces with torso (FT), we found that faces activate more than the FT bilateral occipital cortex with the local maxima in the right cuneus, the inferior occipital gyrus and the left middle occipital gyrus (FWE $p \leq 0.05$).

Portraits with faces only compared to those showing also torso with hands (FTG) showed a higher BOLD signal in the lateral occipital cortex including the fusiform, middle and inferior occipital gyri. The opposite contrasts (FT > F, and FTG > F) showed no significant results. FTG exerted higher activation then FT bilaterally in the calcarine fissure and the surrounding cortex (with local maxima in the lingual gyrus) and in the right thalamus. FT compared to FTG did not show any significant increase in the BOLD signal (Fig. 2, Table 2).

3.2. Eye-tracking experiment

We analyzed the differences in dwell time with 2 × 2 ANOVA (two within-subject factors, gaze direction (direct, averted) and area of interest (eyes, mouth)). The participants preferred looking at eyes rather than at mouth ($F(1, 23) = 131.97$, $p < 0.001$, $\eta_g^2 = 0.763$)). When the portrait's gaze was directed towards the observer, participants spent more time viewing its eyes and mouth ($F(1, 23) = 149.76$, $p < 0.001$, $\eta_g^2 = 0.042$). The AOI × gaze interaction was significant ($F(1, 23) = 14.98$, $p < 0.001$, $\eta_g^2 = 0.012$), which is caused by a larger effect of portrait's gaze on eyes (mean difference = 212 ms, paired *t*-test, $t(23) = 8.025$, $p < 0.001$) compared to mouth area (mean difference = 68 ms, paired *t*-test, $t(23) = 4.250$, $p < 0.001$) (Fig. 3).

3.3. Behavioral effect and psychometric measurements (Experiment 1 and 2)

The debriefing of tested individuals showed that the subjective evaluation of the direct and averted gaze directions of the portrayed persons (scaled from −5 to +5) was in agreement with the two proposed categories (showing significant differences in the evaluated gaze direction between the proposed categories averted/direct gaze) in both the fMRI in Experiment 1 and the eye-tracking sample in Experiment 2 (for the detailed results see Supplementary Table S2). In the post-fMRI debriefing, no significant differences were observed between the two gaze direction categories in the two evaluated psychological characteristics ('Emotional valence' and 'Arousal') (for the results see Supplementary Table S2). However, 'Arousal' was significantly higher for the direct gaze portraits in the eye-tracking in Experiment 2 ($p < 0.001$), while no difference was observed in the 'Emotional valence' of the stimuli. Moderate negative correlations were also observed between the evaluated Emotional valence and Arousal characteristics in both experiments (1. fMRI: $r = -0.45$, $p < 0.05$; 2. Eye-tracking:

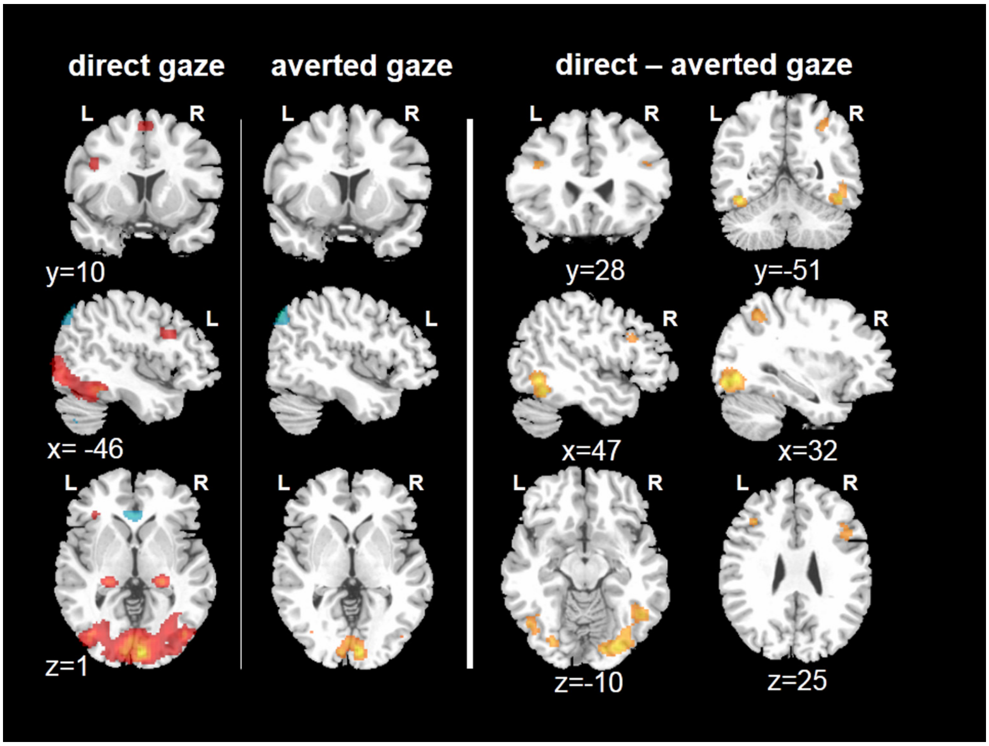

Fig. 1. The effect of direct and averted gaze on brain activity. Brain response to portraits of direct and averted gaze are compared to fixation cross viewing (two left columns). Increase (yellow-red) and decrease (blue) induced by portraits are displayed on corresponding MRI slices (FWE corrected $p \le 0.05$, exact statistical results are in Supplementary Table S1). Two right columns show the regions in which direct gaze activated more than averted gaze portraits. These results are displayed at uncorr. p-value $p \le 0.001$. For exact anatomical localization and description, see Table 1. *Legend*: L or R, left or right hemisphere; x, y, z, Talairach coordinates of the displayed slices of MRIcro V1.4 (www.mricro.com) template. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1

Activation of direct compared to averted gaze portraits.

Cluster vx	p(FWE)	T	Z	x	y	z	R or L	Local maximum
Activation of direct compared to averted gaze portraits								
2926	0.013	6.68	4.97	14	−91	−4	R	Lingual Gyrus
	0.015	6.62	4.94	6	−93	10	R	Cuneus
	0.079	5.75	4.51	15	−90	7	R	Cuneus
670	0.052	5.96	4.62	−20	−91	−6	L	Inferior Occipital Gyrus
	0.248	5.12	4.17	−25	−77	−12	L	Fusiform Gyrus
325	0.219	5.19	4.21	−40	−48	−17	L	Fusiform Gyrus
	0.772	4.27	3.64	−44	−62	−13	L	Fusiform Gyrus
	0.848	4.14	3.56	−49	−53	−7	L	Inferior Temporal Gyrus
227	0.450	4.74	3.94	−33	26	24	L	Middle Frontal Gyrus
	0.608	4.51	3.8	−40	28	24	L	Middle Frontal Gyrus
110	0.814	4.2	3.6	38	16	28	R	Middle Frontal Gyrus
	0.941	3.91	3.41	38	9	29	R	Inferior Frontal Gyrus
171	0.854	4.12	3.55	30	−60	42	R	Angular gyrus

Significant results at uncorrected $p \le 0.001$ for clusters consisting of ≥ 50 voxels are displayed. Legend: cluster vx, size in voxels; p(FWE), family-wise error corrected p-value; T, T-value; Z, Z-value equivalent; *x*, *y*, *z*, Talairach coordinates of voxel of maximum significance; R or L, right or left hemisphere.

$r = -0.55$, $p < 0.05$). Participants rated the portraits as unknown in 70% of all familiarity evaluations (cumulative for all participants and all stimuli) and only in 11% as known (the remaining 19% of the evaluations were undecided). Most of the stimuli were rated as known by less than 2 participants. The familiarity parameter did not differ between the direct and averted gaze portrait categories in any of the two experiments ($p > 0.05$).

4. Discussion

4.1. Direct vs. averted gaze

4.1.1. fMRI experiment

The present work was designed to explore the neuronal and behavioral responses to painted portraits with a direct versus averted gaze. We identified brain areas, which were selectively activated by a direct versus averted gaze in artistic (painted) portraits. We further identified brain areas functionally related to the distinct painting characteristics such as the period, general style (“linear” vs. “painterly”) and pictorial context. Not surprisingly, we found that both direct and averted gaze portraits (compared to fixation) showed bilateral activation in occipital lobes with local maxima in lingual and fusiform gyrus. This is fully in accord with influential models of face perception, which propose that FFA is involved in expression of invariant processing of faces (Calder & Young, 2005; Haxby, Hoffman, & Gobbini, 2000), as well as with more recent integrative models of face perception, which argue that the FFA contributes to the perception of changeable aspects of faces, through a broad sensitivity to shape information (Bernstein, Erez, & Yovel, 2018; Duchaine & Yovel, 2015).

Enhanced activity in the fusiform gyrus during direct gaze perception corresponds to several studies using photographic stimuli (George, Driver, & Dolan, 2001; Pageler et al., 2003). It has been suggested that a higher activation of the fusiform gyrus in these studies, which - much like our own study - involved presentation of many different faces, may reflect the need for a “deeper” processing and encoding of novel faces indicating that the interaction between a beholder and the direct gaze of the subjects in the painted portraits could be associated with the increasing feeling of novelty (Boyarskaya, Sebastian, Bauermann, Hecht, & Tuscher, 2015). However, at present, it is not possible to determine if differences in gaze direction have lesser impact on FG activity compared to the processing of whole face, as some have argued (Madipakkam, Rothkirch, Guggenmos, Heinz, & Sterzer, 2015), as these aspects cannot be reliably disentangled.

There are two possible explanations for our finding of enhanced FG activity to direct gaze portraits. First, it has been established that face

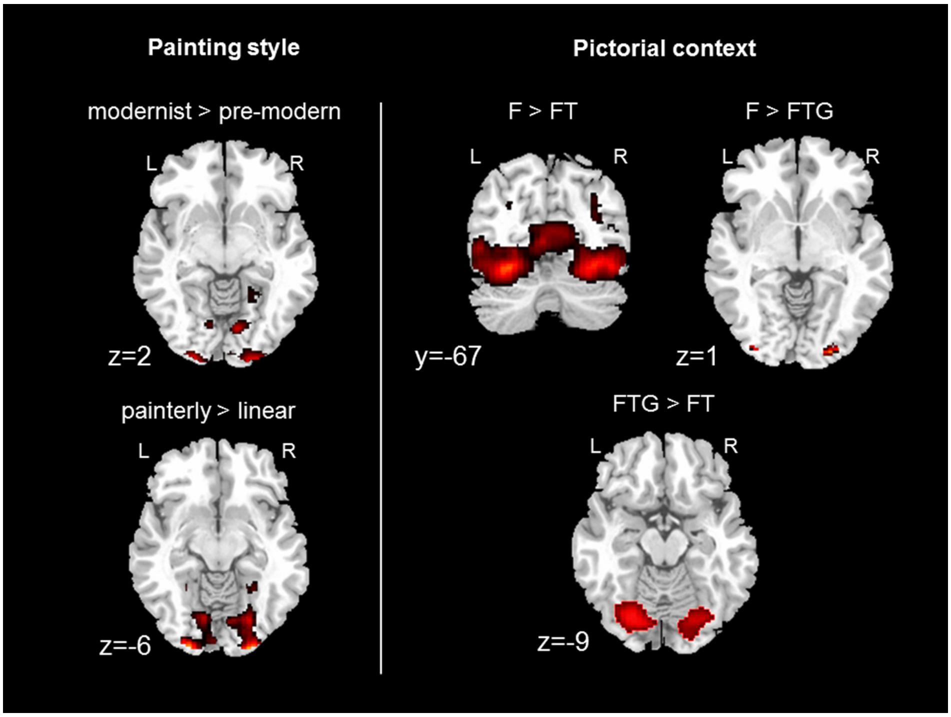

Fig. 2. The effect of painting style (left) and pictorial context on brain activity (right). The left part shows regions where modernist painting style portraits activated more than the pre-modern ones (upper left), and where painterly style activated more than the linear one (lower left). The right part displays the differences between portraits of different *pictorial context of the portrait.* Results are displayed at uncorr. p-value $p \leq 0.001$ for clusters located within the mask of all portraits effect vs fixation (FWE, $p \leq 0.05$). Anatomical localization and exact statistical results are in Table 2. *Legend*: L or R, left or right hemisphere; x, y, z, Talairach coordinates of the displayed slices of MRIcro V1.4 (www.mricro.com) template; F, face only; FT, face and torso; FTG, torso and hand gesture. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

processing in this region depends on voluntary attention. Several studies of face processing in ventral occipitotemporal cortex proved that FG activation as indexed by BOLD signal or N170 is amplified by attention (Pessoa et al., 2002; Srinivasan, Srivastava, Lohani, & Baijal, 2009; Vuilleumier, Armony, Driver, & Dolan, 2001; Wojciulik, Kanwisher, & Driver, 1998). Morris and colleagues, who examined the relationship between scanpath variations and FG activity, demonstrated that activation in the fusiform gyrus correlates with the amount of fixation in the eyes and mouths (Morris et al., 2007). This amplifying role of attention on FG is congruent with both our eye-tracking data, which showed that the participants spent more time viewing both the person's eyes and mouth when observing the direct gaze portraits than the averted ones, as well as with previous eye-tracking studies (for a review see Pfeiffer, Vogeley & Schilbach, 2013). This suggests that a direct gaze prepares for face-to-face communication more than an averted gaze even in painterly (ie less realistic) artistic portraits. However, it should be noted that the individual evaluation of stimuli by our participants during debriefing showed higher arousal in direct gaze only after the eye tracking experiment, but not after the fMRI experiment. This discrepancy between these two behavioural evaluations could have been caused by the different character of the two procedures applied. We suggest that the MRI measurement itself (exceeding the length of the eye-tracking study due to morphological sequences measured consecutively after the fMRI task) could have induced decreased attention during introspection process of post-scanning debriefing.

Second, FG/FFA region has been increasingly recognized to have more important set of functions, involving processing of emotions (Ganel, Valyear, Goshen-Gottstein, & Goodale, 2005; Harry, Williams, Davis, & Kim, 2013; Kawasaki et al., 2012). Moreover, FG is now often considered an integral part of social perception and cognition (Schultz et al., 2003; Stolier & Freeman, 2016; Tso, Rutherford, Fang, Angstadt, & Taylor, 2018) and it most likely directly contributes to mentalizing processes (Baetens, Ma, Steen, & Van Overwalle, 2014; Ohnishi et al., 2004). It is thus possible to speculate that FG activation to direct vs averted gaze of painted portraits may also in part be interpreted as contributing to implicit inference of mental states of depicted persons as further discussed below.

In our study, the regions in the occipital lobe activated by the perception of the direct gaze included the cuneus and the lingual gyrus. Activation of these structures has been linked to encoding of complex images during viewing of the paintings (Vartanian & Skov, 2014). Besides its role in the visual identification, the lingual gyrus is essential for face recognition (Kozlovskiy et al., 2014). As it was demonstrated by McCarthy, Puce, Belger, and Allison (1999), the occipito-temporal cortex, including the lingual gyrus, emits ERP as a response to faces. The N200 amplitude was evoked by varying faces - colored or grayscale; normal, blurred or line-drawing faces; or by faces of different sizes.

Most importantly, we also observed parietal (angular gyrus) and prefrontal cortex brain response to direct but not averted gaze portraits. The activation in the right angular gyrus suggests the involvement of social cognitive processes, especially the theory of mind (Seghier, 2013). The angular gyrus is involved in social cognition (as a part of temporo-parietal junction) on the one hand and attentional selection on the other, but it subserves other cognitive functions as well (Carter & Huettel, 2013; Corbetta and Shulman, 2002; Igelström, Webb, & Graziano, 2015; Krall et al., 2015; Saxe & Kanwisher, 2003; Schurz, Radua, Aichhorn, Richlan, & Perner, 2014; Seghier, 2013). One can assume that eye contact with the people depicted in the portraits engages the viewers in inferring emotions and identification of the mental states of the depicted subjects (we discuss this in more detail below). In addition to the regions in the occipital and fronto-parietal lobes, we observed brain activations by direct gaze portraits in two prefrontal areas: the inferior frontal gyrus (IFG) and the middle frontal gyrus. IFG has been implicated in a number of specific cognitive functions related to the theory of mind. Importantly, a recent meta-analysis (Schurz et al., 2014, see also Schurz & Tholen, 2016) demonstrated that the left IFG was activated by the type of experimental tasks including social animations and "reading mind in the eyes". Recently, Cavallo and colleagues have found prominent IFG activation in direct gaze condition elicited by live experimenter. They interpret this IFG activity as related to the onset of a communicative intent and a preparation of a communicative response (Cavallo et al., 2015). IFG also regulates amygdala activity in emotional face processing (Horáček et al., 2015). Furthermore, it should be noted that this activation in right IFG probably anatomically overlaps with right inferior frontal junction, which

Table 2
Activation by modernist style portraits comparing to the pre-modern ones.

Cluster vx	p(FWE)	T	Z	x	y	z	R or L	Local maximum
5519	0.000	8.84	5.84	12	−85	4	R	Lingual Gyrus
	0.001	8.05	5.55	−7	−86	3	L	Lingual Gyrus
	0.006	7.21	5.21	−11	−79	2	L	Lingual Gyrus
72	0.660	4.53	3.81	26	11	63	R	Superior Frontal Gyrus
225	0.683	4.5	3.79	19	−47	−11	R	Fusiform Gyrus
	0.952	3.98	3.45	25	−36	−15	R	Fusiform Gyrus
	0.998	3.57	3.16	16	−57	−8	R	Lingual Gyrus
Activation by painterly style portraits comparing to the linear ones								
Cluster vx	p(FWE)	T	equivZ	x	y	z	R or L	Local maximum
4871	0.007	7.05	5.14	8	−86	−2	R	Lingual Gyrus
	0.008	7.02	5.13	10	−97	−3	R	Cuneus
	0.010	6.89	5.07	−5	−88	3	L	Lingual Gyrus
119	0.898	4.12	3.54	23	−47	−12	R	Fusiform Gyrus
	0.952	3.96	3.44	25	−40	−13	R	Fusiform Gyrus
	0.996	3.62	3.2	21	−57	−10	R	Lingual Gyrus
Depicted details of portraits: F > FT								
Cluster vx	p(FWE)	T	Z	x	y	z	R or L	Local maximum
20,619	0.000	14.74	7.38	15	−92	3	R	Cuneus
	0.000	12.06	6.79	19	−89	−9	R	Inferior Occipital Gyrus
	0.000	11.1	6.54	−27	−92	2	L	Middle Occipital Gyrus
141	0.275	5.11	4.16	−37	−52	60	L	Superior parietal Lobule
	0.880	4.13	3.55	−28	−57	51	L	Superior Parietal Lobule
115	0.631	4.53	3.81	39	−50	58	R	Superior Parietal Lobule
	0.937	3.98	3.46	31	−56	61	R	Superior Parietal Lobule
Depicted details of portraits: F > FTG								
Cluster vx	p(FWE)	T	Z	x	y	z	R or L	Local maximum
2230	0.017	6.67	4.97	27	−81	−12	R	Fusiform Gyrus
	0.022	6.55	4.91	17	−89	−6	R	Inferior Occipital Gyrus
	0.037	6.28	4.78	25	−89	−7	R	Inferior Occipital Gyrus
1615	0.027	6.44	4.86	−33	−85	−12	L	Inferior Occipital Gyrus
	0.083	5.85	4.57	−27	−92	4	L	Middle Occipital Gyrus
	0.102	5.75	4.51	−20	−92	−14	L	Fusiform Gyrus
Depicted details of portraits: FTG > FT								
Cluster vx	p(FWE)	T	Z	x	y	z	R or L	Local maximum
22,994	0.000	15.19	7.47	8	−90	0	R	Lingual Gyrus
	0.000	12.13	6.81	−9	−82	−7	L	Lingual Gyrus
	0.000	11.98	6.77	12	−85	−11	R	Lingual Gyrus
234	0.047	6.15	4.72	21	−29	9	R	Thalamus

Significant results at uncorrected $p \leq 0.001$ for clusters consisting of ≥ 50 voxels are displayed. Legend: cluster vx, size in voxels; p(FWE), family-wise error corrected p-value; T, T-value; Z, Z-value equivalent; *x*, *y*, *z*, Talairach coordinates of voxel of maximum significance; R or L, right or left hemisphere; F, face only; FT, face and torso; FTG, face, torso and hand gesture.

has been recently implicated in face and specifically eyes processing (Chan & Downing, 2011).

Rather unexpectedly, we found that direct gaze compared to averted gaze portraits also bilaterally activated the middle frontal gyrus, an area co-extensive with the dorsolateral prefrontal cortex (DLPFC, Fig. 1, Table 1). DLPFC has not generally been involved in gaze processing and social cognition. However, Bzdok et al. (2012) found that DLPFC also subserved recruited social judgment (trustworthiness) and age assessment of naturalistic faces. The authors hypothesize that this activity might reflect the cognitive effort involved in the decision they were required to make (comparing two faces). Activation of DLPFC was also found in an aesthetic evaluation of art works (Kirk, Dowdar, & Montague, 2011; Kirk, Skov, Hulme, Christensen, & Zeki, 2009). One way to account for our finding of activation in DLPFC would be with reference to Senju and Johnson's (2009) recent "fast-track modulator model", which hypothesizes the key role of DLPFC in the context- and task-relevant modulation of the key social brain areas involved in the detection of gaze direction, such as the superior temporal sulcus (STS), and intentionality, the medial prefrontal cortex (MPFC) and the TPJ.

Another possibility is that the DLPFC activity may be related to the fact that - contrary to several studies on gaze processing, using photographs or computer avatars (Kampe et al., 2003; Schilbach et al., 2006) - we did not find activation by direct gaze portraits in the ventromedial prefrontal cortex (VMPFC). VMPFC is a key region in anterior component of DMN and has been assigned a central role in generation of affective meaning, valuation, situated conceptualization of emotion and self-related processing (for overview see Delgado et al, 2016). VMPFC has also been associated with social cognition, and is theorized to play a role in social judgments by simulating mental states that evaluate one's own and others' behaviours (Flagan & Beer, 2013; Schurz et al., 2014). The absence of VMPFC activity can be attributed to two factors. First, the fact that our participants were merely required to watch paintings as if they were in a gallery and were not explicitly requested to evaluate the social or emotional content of the portraits during fMRI paradigm that would evoke activity in more extensive parts of the social brain network. Incidentally (as observed by Senju & Johnson, 2009) in studies reporting VMPFC activation in response to a direct gaze, participants were explicitly asked to decode the intention of the face to communicate, which may have elicited greater activation for the direct gaze. Secondly, also relevant is the fact that emotional processing in VMPFC can be attenuated by DLPFC in evaluation processes (Hare, Camerer, Rangel, & Hare, 2009; Kirk et al., 2011) and

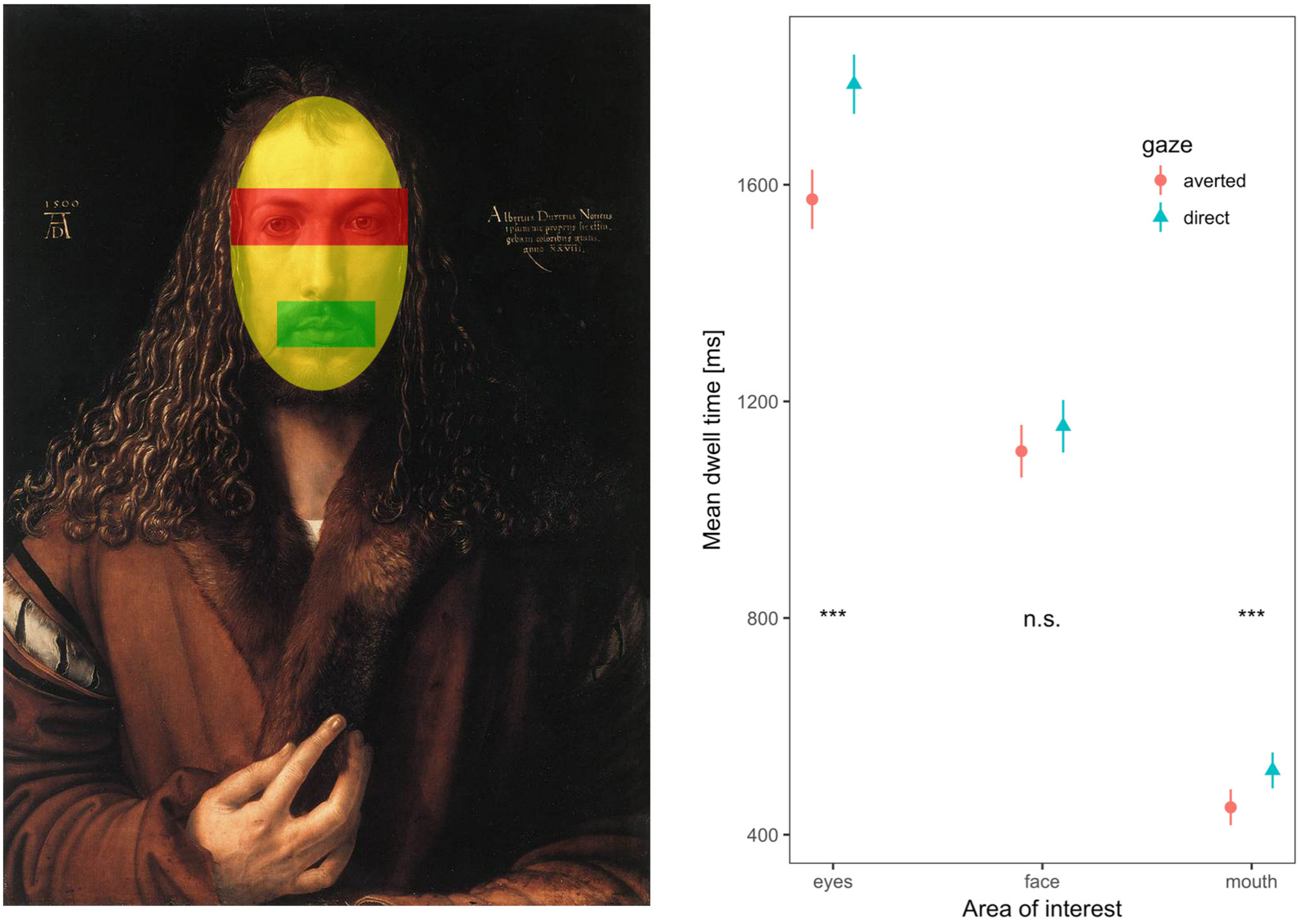

Fig. 3. The illustration of the selected AOI of the face features (left) and the AOI dwell times compared for direct and everted gaze portraits (right). Left: a portrait with areas of interest: face (yellow), eyes (red), mouth (green). Right: differences in dwell time for portraits with averted/direct gaze and for each area of interest. Error bars represent Fisher's Least Significant Difference. $^{*}p < .05$, $^{**}p < .01$, $^{***}p < .001$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

specifically in context of art perception (Kirk & Freedberg, 2015; Kirk et al., 2009). It is therefore possible that our finding of DLPFC activity similarly reflects implicit evaluation process, which inhibited the emotional response to portraits in VMPFC. However, these differences in parietal and frontal cortices should be interpreted cautiously because in direct comparison between direct and averted gaze portraits they did not survive the conservative FWE correction.

4.1.2. Effect of direct and averted gaze on selected AOI dwell time

The complementary eye-tracking measurement confirmed that participants spent more time viewing depicted person's eyes when viewing the direct gaze portraits than the averted ones. This finding is in agreement with our neuroimaging results: the activation of the abovementioned brain regions connected to social cognition and face processing increased in the direct gaze condition. Heightened attention to the direct gaze thus supports the neuroimaging findings and confirms that the gaze is a crucial feature to driving face processing and social engagement. The relationship between increased activation of fusiform region and higher number of fixations on eyes has been previously shown in patients with autism (Dalton et al., 2005) and in healthy subjects (Morris, Pelphrey, & McCarthy, 2006). Our eye-tracking findings, indicating correlation between the direct gaze condition and longer dwell time on the eyes area, may be supported also by the individual evaluations of stimuli by the participants (debriefing after the experiment) that showed higher arousal after viewing the direct gaze portraits in line with previous research (e.g. Akechi et al., 2013; Myllyneva & Hietanen, 2015a, 2015b).

On the other hand, we did not observe any significant differences between the dwell times spent in the whole face AOI in direct versus averted gaze portraits. It contradicts the study by Palanica and Itier (2012), which found that faces with a direct gaze were viewed longer than faces with an averted gaze regardless of body context, background, and task demands. The discrepancy might be caused by the character of our stimuli: whereas the stimuli from the study of Palanica and Itier (2012) were proportionally balanced in types (portraits, details and full figures) and visual correspondence (varying only in gaze direction), our stimuli were not balanced, and thus the AOI varied in size. The discrepancy might be thus caused by the visual variability of our stimuli. Nevertheless, this is an unresolved dilemma regarding the use of authentic stimuli such as art works. For example, Dukewich, Klein, and Christie (2008) used original art works for examining the viewers' preference for following the direction of the depicted gaze, but the gaze of depicted people was digitally manipulated. The authors achieved the perfectly balanced triplets varying only in the gaze direction, while losing authenticity of paintings. We choose the opposite approach, while sacrificing the exact visual correspondence.

Interestingly, in the direct gaze condition participants also spent more time viewing mouth, representing a communication signal and the most important cue for discrimination of both static and dynamic facial expressions of the depicted person (Blais, Jack, Scheepers, Fiset, & Caldara, 2008). This may also suggest that direct gaze stimulates face-to-face communication, or preparedness for such action, in comparison to averted gaze. Nevertheless, to our knowledge, no study yet reported, if the gaze direction affects the fixation of mouth area and in which way. Another recent evidence to consider is the observation of individual differences in the style how mouth-eyes stimuli are viewed (Coutrot, Binetti, Harrison, Mareschal, & Johnston, 2016; Peterson & Eckstein, 2013; Rogers, Speelman, Guidetti, & Longmuir, 2018). Some people showed a strong preference for eye gaze, whereas others a strong preference for mouth gaze, and others distributed their gaze between the eyes and mouth to varying extents. This shows that both eyes and mouth are essential for face processing across individuals, and preference for either of them depends on personal style.

In this context we should also mention that due to the variable emotions of portrayed persons in the stimuli set, no correlation was observed between gaze direction and emotional valence of presented stimuli. Nevertheless, the expected strong relationship between emotional valence and arousal produced by the emotions depicted in individual portraits was identified in both experimental samples, demonstrating that the depicted emotion was recognised and was affecting emotional state of tested participants.

4.2. Face processing in general

Direct gaze versus fixation also yielded activation in the hippocampus bilaterally, an area which has not been reported in other studies on gaze processing. The medial temporal lobe and particularly the hippocampus are traditionally involved predominantly in memory functions and also in higher-order spatial perception and conjunctions of features that constitute spatial scenes (for a review see Lee, Yeung, & Barense, 2012). In contrast, some authors demonstrated the role of the hippocampus both in perception and recollection of objects and faces (Fried, MacDonald, & Wilson, 1997; Ishai, Schmidt, & Boesiger, 2005). Our experimental paradigm did not allow for a strict distinction between perception and memory functions. Nevertheless, during free viewing of images these two processes cannot be considered to operate independently, as during the viewing of art portraits beholders probably implicitly compare representations of socially salient features (faces, gestures) with memory representations of such objects. This might also explain the activation of DLPFC, which is involved in processing and coordination of these processes.

Contrary to other studies, we did not detect the effect of a direct gaze on amygdala and this finding thus corresponds to the results of authors who similarly did not report amygdala response to a direct gaze (Pageler et al., 2003; Schilbach et al., 2006). The absence of amygdala activation can be explained by the small number of portraits with *clearly expressed emotions* in our set of stimuli (only 14% according to post-experiment evaluation, in contrast to 66% of portraits with "*subtle emotional expression"* and 20% of them labelled as an *"inexpressive mask"*). An additional factor could be the variability in emotional expressions of the portrayed persons in the stimuli set (including only a few with explicitly negative facial emotions). Nevertheless, the expected strong relationship between the evaluated emotional valence and arousal produced by the emotions depicted in the individual portraits was identified in both experimental samples, demonstrating that the depicted emotion was recognized and affected the emotional state of the tested participants.

4.3. Comparison to other studies on gaze perception: effect of representational medium

Interestingly, the pattern of brain activation discrimination of direct and averted gaze portraits in our study (Fig. 1) is more similar to an imagery task with famous faces than to the gaze experiments using naturalistic stimuli. Visual imagery of famous faces activates a network of regions that includes the calcarine, precuneus, hippocampus, intraparietal sulcus, and inferior frontal gyrus (Ishai, Haxby, & Ungerleider, 2002). Besides the fact that only a small fraction of pictures used in our study was known to volunteers, the similarity of our results with visual imagery findings suggests the role of mental imagination in the perception of artistic portraits. In addition, the same study identified that focusing attention on features of the imagined faces (e.g., eyes, lips, or nose) resulted in increased activation in the right intraparietal sulcus (adjacent to the angular gyrus) and the right inferior frontal gyrus (Ishai et al., 2002), which responded specifically to the direct gaze portraits.

Overall, our findings (especially activation in the angular gyrus and the frontal cortex, absence of amygdale and VMPFC activation) seem to correspond to the general characteristics of a set of painted portraits used in this experiment compared to standard stimuli used in previous gaze experiments. Firstly, there is much greater variability of expression in our set along both essential axes of valence and intensity of emotions, with some facial configurations clearly signaling complex mental states, rather than prototypical basic emotion. On a phenomenological level, the painted artistic portraits elicit a wide range of meanings, to signal communicative intent, social interest, dominance, hostility, and attraction. In general terms, it can be argued that in most painted portraits the representational medium (compared to naturalistic photographs or video clips) significantly increased an element of ambiguity of expression, which is present even in naturalistic stimuli (Back & Jordan, 2014), thus preventing a response in the amygdalae.

4.4. Effect of painting style, period and pictorial context of the portraits

Our results also confirm the substantial influence of representational medium on brain activity. Consistent with our hypothesis, images categorized as being depicted in a painterly ("less realistic") style exerted higher activation of the medial and inferior surfaces of the occipital lobe (calcarine fissure, cuneus, lingual and fusiform gyri) than a linear style. The most likely explanation is that a more pronounced BOLD signal reflects more intense processing in the visual cortex required by those portraits, in which faces and gaze are rendered in a less realistic manner (or must be extracted from the painterly medium). This assumption is also supported by the comparison of pre-modern and modernist portraits in our group showing that the modern paintings (in which the painterly style predominates) activate the specific visual areas for face processing (lingual and fusiform gyrus) more intensively than the premodern paintings.

The finding that the activity of the visual cortex was substantially influenced by the pictorial context of stimuli was consistent with our expectation. Perception of the portraits featuring faces only (compared to those depicting faces with torso and hand gestures) activated the visual cortex and particularly, the fusiform cortex more intensively (Fig. 2), which suggests an exclusive attention on faces. The increased activity of the lingual cortex in portraits with visible hand gestures (in contrast to face and body only) is in concordance with previous studies that identified engagement of the lingual gyrus when participants perceived body-only (as opposed to face or face and body of actors; Morris et al., 2006) or during face-blurred gestures (Saggar, Shelly, Lepage, Hoeft, & Reiss, 2014). Therefore, participants were attending to visuospatial aspects of stimuli, especially motion-related information from gestures.

5. Limitations

There are several limitations in our study. First, we have not attempted a direct comparison between gaze perception of painted portraits and more naturalistic (photographic) stimuli. This future direct comparison will require creating a set of photographic portraits, emulating the posture, emotional expression and gaze behavior, as well as overall composition of painted models. We were thus unable to confirm the specificity of our findings for artistic portraits. Second, our study utilized separate fMRI and eye-tracking measurements that required enrollment of two different participant samples in order to avoid repeated exposure bias. This design did not allow a direct comparison of separate data sets of the same subjects which could be obtained in simultaneous fMRI and eye-tracking experiment. Third, our set of stimuli was selected (and balanced) to test the influence of direction of gaze in painterly portraits. This approach enabled us also to test the effect of painting techniques and characteristics on fMRI activation. However, the design (and number of stimuli) did not allow us to test the interactions between factor of gaze and factors of painting characteristics under control of possible technical confounds (artist, luminance, and RGB color components). Hence, the interaction between gaze and painting techniques should be addressed by future specifically designed study. Fourth, to avoid movement artefacts, we did not register direct behavioral response during scanning, hence the behavioral data collected during the post-scanning debriefing would be interpreted cautiously. It is thus not possible to relate the indices of a subjectively felt response with neuroimaging data and exploring such a link clearly suggest itself as a topic for future research. Fifth, because the luminance and some other characteristics of individual portraits were not fully counterbalanced for some of the secondary tested conditions (date of the painting; influence of style, pictorial context of the portrait), a control fMRI measurement was performed. We analyzed the possible effect of luminance on reported brain activation. All portraits used in the original MRI measurement were sorted according to their average luminance and divided into two sets of blocks containing portraits with high or low luminance. Their comparison showed luminance specific activity only in the primary visual cortex V1/V2 areas. We therefore argue that luminance of the paintings is not related to the brain activity reported as specific for painting style, pictorial context or time period of the paintings. Another limitation of the study is the quality of art reproductions presented during the fMRI experiment. To achieve acceptable comparability of the obtained results from fMRI and eye-tracking measurements, both the resolution and field of view (screen size) characteristics have been decreased during the eye-tracking measurement. Finally, while several studies have recently found an effect of head orientation on the perception of gaze direction (Laube, Kamphuis, Dicke, & Thier, 2011; Pageler et al., 2003), we did not analyze the effect of head orientation on gaze direction, as the directional variability of faces among our stimuli was too great.

6. Conclusion

Our findings shed some additional light on the vexing problem of the nature of interaction with depicted human beings. Art historians have claimed that the imagination enables viewers to react to a depicted gaze as if they were confronting the live person (e.g. Belting, 2007) and such views have been reiterated in many literary and anecdotal accounts of viewers establishing some form of emotional (and even verbal) rapport with the people depicted in the portraits. Within social neuroscience, an emerging consensus insists on the fundamental difference between the first-person and second-person perspective in social interaction, or between social observation and social interaction (Przyrembel, Smallwood, Pauen, & Singer, 2012; Schilbach et al., 2013; Tylén, Allen, Hunter, & Roepstorff, 2012). Our results, demonstrating the activation of angular gyrus/TPJ, middle and inferior frontal gyri by direct gaze portraits, suggest that static and in some cases highly stylized depictions of human beings in artistic portraits elicit brain activation commensurate with the experience of being observed and potentially addressed by intelligent sentient being and involve observers in implicit inferences of the painted subject's mental states and emotions, and possibly even a prefiguration of communicative intent. Future research may thus focus on disentangling the effects of specific viewing conditions (instructions) and priming of subjects on mentalizing and an empathic response to the subjects depicted in portraits.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.bandc.2018.06.004.

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