RESEARCH ARTICLE

Manifold decoding for neural representations of face viewpoint and gaze direction using magnetoencephalographic data

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Abstract

The main challenge in decoding neural representations lies in linking neural activity to representational content or abstract concepts. The transformation from a neural-based to a low-dimensional representation may hold the key to encoding perceptual processes in the human brain. In this study, we developed a novel model by which to represent two changeable features of faces: face viewpoint and gaze direction. These features are embedded in spatiotemporal brain activity derived from magnetoencephalographic data. Our decoding results demonstrate that face viewpoint and gaze direction can be represented by manifold structures constructed from brain responses in the bilateral occipital face area and right superior temporal sulcus, respectively. Our results also show that the superposition of brain activity in the manifold space reveals the viewpoints of faces as well as directions of gazes as perceived by the subject. The proposed manifold representation model provides a novel opportunity to gain further insight into the processing of information in the human brain.

KEYWORDS

decoding, face viewpoint, gaze direction, manifold, MEG, neural representation, OFA, STS

1 | INTRODUCTION

Representational content, such as visual images, can be transduced into brain activity patterns. These neural representations lay the foundation for investigation into the processing of information by the brain (Kriegeskorte & Kievit, 2013). However, the decoding of neural representations containing large amounts of perceptual information is very challenging, due to the high dimensionality of the patterns associated with brain activity and the diversity of stimuli (Haxby, Connolly, & Guntupalli, 2014; Kriegeskorte & Kievit, 2013). A number of previous studies have introduced the concept of manifolds to high-level visual perception (Roweis & Saul, 2000; Seung & Lee, 2000; Tenenbaum, de Silva, & Langford, 2000), based on the assumption that a low-dimensional neural manifold within the brain could be used in the interpretation of high-level stimulus-related information. Such a manifold could be formed from sensory responses in the neural space, with

dimensionality equal to the (enormous) number of sensory neurons involved. In other words, every cardinal axis in the neural space may depend on the activity of single neurons (DiCarlo & Cox, 2007; DiCarlo, Zoccolan, & Rust, 2012; Seung & Lee, 2000). Other researchers have also assumed that object recognition involves the transformation of neural representations of an object into an untangled manifold (DiCarlo & Cox, 2007; DiCarlo et al., 2012). Manifold transformation is one approach to reducing the dimensionality of data; that is, from a high-dimensional space to a low-dimensional manifold space. A number of manifold transformation methods have been applied to the problem of image processing and pattern recognition (He & Niyogi, 2004; Roweis & Saul, 2000; Tenenbaum et al., 2000); however, few researchers have sought to apply these methods to the analysis of neural data. One study based on magnetoencephalographic (MEG) data has recently examined a neural manifold associated with simple visual patterns to enable the decoding of brain activity and the encoding of stimuli in the

primary visual cortex (Kuo, Chen, Chen, & Hsieh, 2014). They showed that the composition of two stimulus images led to the superposition of two sets of brain activity data within a manifold space. Nonetheless, it remains unclear whether this type of neural manifold could be applied to the problem of modeling representational content in face-related regions of the brain.

Face perception in the human brain is a complex process, involving representations across numerous regions of the brain with multiple temporal stages of processing (Bruce & Young, 1986; Duchaine & Yovel, 2015; Haxby, Hoffman, & Gobbini, 2000; Kietzmann, Gert, Tong, & Konig, 2016; Liu, Harris, & Kanwisher, 2002; Rossion, 2014). Face viewpoint and gaze direction are important issues in face perception, due to their roles in social communication (Perrett et al., 1985). A number of studies have used neuroimaging modalities, such as functional magnetic resonance imaging (fMRI), electroencephalography (EEG), and MEG to investigate the relationship between brain responses and face stimuli from different face viewpoints (Andrews & Ewbank, 2004; Anzellotti, Fairhall, & Caramazza, 2014; Axelrod & Yovel, 2012; Caharel, Collet, & Rossion, 2015; Caharel, d'Arripe, Ramon, Jacques, & Rossion, 2009; Dubois, de Berker, & Tsao, 2015; Ewbank, Smith, Hancock, & Andrews, 2008; Kietzmann, Swisher, König, & Tong, 2012; Kietzmann et al., 2016; Natu et al., 2010; Pourtois, Schwartz, Seghier, Lazeyras, & Vuilleumier, 2005; Ramirez, Cichy, Allefeld, & Haynes, 2014; Zimmermann & Eimer, 2013) or gaze directions (Carlin, Calder, Kriegeskorte, Nili, & Rowe, 2011; Engell & Haxby, 2007; Hoffman & Haxby, 2000; Hooker et al., 2003; Nummenmaa, Passamonti, Rowe, Engell, & Calder, 2010; Puce, Smith, & Allison, 2000; Sato, Kochiyama, Uono, & Yoshikawa, 2008; Watanabe, Kakigi, & Puce, 2001). Most of these studies obtained data from experiments based on pairs of contrasting stimuli (i.e., profile and front viewpoints, direct and averted gazes) or sets of categorized stimuli. Analysis involved comparing differences in the amplitude of brain responses and/or the use of multi-voxel pattern analysis (MVPA) to reveal the mechanisms underlying the processing of face-related data by the human brain.

Experiment results reported by (Allison, Puce, & McCarthy, 2000; Axelrod & Yovel, 2012; Haxby et al., 2000; Kietzmann et al., 2012, 2015) indicate that the inferior occipital gyri or occipital face area (OFA) is involved in the early perception of face viewpoint, whereas the superior temporal sulcus (STS) deals with movements in the eyes and mouth. Investigations into the temporal stages of face perception using EEG/MEG have indicated that the N170/M170 component is an event-related potential/field, which occurs approximately 170 ms after the stimulus onset and appears to originate in the fusiform face area (FFA) or STS (Deffke et al., 2007; Duchaine & Yovel, 2015; Nguyen & Cunningham, 2014; Sadeh, Podlipsky, Zhdanov, & Yovel, 2010). N100/M100 and N250/M250 have also been identified as important temporal components of face perception (Liu, Harris, & Kanwisher, 2002; Pitcher, Walsh, & Duchaine, 2011; Schweinberger & Burton, 2003; Zimmermann & Eimer, 2013). However, facial representations transformed from low-level neural representations in face-/gaze-related areas of the brain (OFA, FFA, and STS) have yet to be decoded at various stages in their temporal development (M100, M170, and M250).

In this study, we propose a manifold approach to the decoding of spatiotemporal information embedded within the neural representation of face images. Neural manifolds were constructed from brain responses to face images with perfectly horizontal and vertical face/gaze directions. These were then used to predict (from brain responses) the directions of faces in images containing composite face/gaze directions (i.e., with horizontal as well as vertical variations). This study addressed the following three questions. (1) Is information pertaining to face viewpoint and gaze direction embedded within a neural manifold? (2) Does the summation of the brain responses to two 1-dimensional rotations match the brain responses to 2-dimensional rotations within the neural manifold? In other words, is there a superposition of brain activity in the processing of abstract information pertaining to face viewpoint and/or gaze direction? (3) Do the temporal components M100, M170, and M250 in the OFA, FFA, and STS play essential roles in the decoding of information pertaining to face viewpoint and gaze direction.

2 | MATERIALS AND METHODS

2.1 | Participants

Eleven subjects (age: 23–39 years, 4 females) with normal or corrected-to-normal vision were included in experiments on functional localizers, face viewpoint, and gaze direction. This study was approved by the Institutional Review Board of Taipei Veterans General Hospital and all subjects provided informed consent.

2.2 | Functional localizer for face processing

Colored images of front-view faces and scrambled faces were used as stimuli in the experiment on functional localizers. As shown in Figure 1a, one front-view face image was generated using the software program FaceGen Modeler 3.1. As shown in Figure 1b, 100 phase-scrambled images were then generated from this face image by randomly scrambling phase information while retaining the amplitude spectrum of each RGB component. Each image covered a visual angle of $8.5^\circ \times 8.5^\circ$, and a gray fixation cross (visual angle of $0.5^\circ \times 0.5^\circ$) was placed in the center of each image. Each trial began with the display of a pre-stimulus white fixation cross on a black screen for 500 ms. We then displayed either the original face image or one of the scrambled images for 500 ms. Finally, a post-stimulus white fixation cross was displayed for a randomly selected duration of 400–600 ms. Each subject underwent experimental trials that included 100 face images and 100 scrambled images (randomly shuffled); that is, a total of 200 images in a period of approximately 5 min.

2.3 | Face-viewpoint experiment

In the face-viewpoint experiment, FaceGen Modeler 3.1 was again used to generate face images of the same model but from a variety of viewpoints. Figure 1a and c present two examples of the face-viewpoint stimuli. The visual angle of each image was $8.5^\circ \times 8.5^\circ$ and a fixation cross (visual angle of $0.5^\circ \times 0.5^\circ$) was superimposed in the center of each image. As shown in Figure 1e, this resulted in a total of 225

FIGURE 1 Stimulus images used in the experiment. (a) Face image with front viewpoint and direct gaze. (b) Scrambled image generated from the original face image shown in (a). (c) Face image with horizontal and vertical shifts in viewpoint (-60° , 20°). (d) Face image with gaze varied in the horizontal and vertical directions (-50° , 25°). (e) 225 face stimuli with 25 shifts in the horizontal viewpoint (ranging from -60° to 60°) and 9 shifts in the vertical viewpoint (ranging from -20° to 20°). The top-right panel presents images of a face with basic and composite viewpoints, wherein horizontal and vertical angles between -5° and 5° are regarded as basic viewpoints and all others are composite. (f) 231 stimuli related to gaze-direction, comprising 21 images rotated along the horizontal axis (ranging from -50° to the 50°) and 11 images rotated along the vertical axis (ranging from -25° to 25°). The top-right panel presents images of basic and composite gaze directions, in which horizontal and vertical shifts between -5° and 5° are specified as basic directions and all others are composite [Color figure can be viewed at wileyonlinelibrary.com]

viewpoints, covering 25 viewpoints along the horizontal plane between -60° and 60° as well as 9 viewpoints along the vertical plane between -20° and 20° . Each trial began with the display of a fixation cross on the screen for a random duration between 900 and 1,100 ms. A face image selected at random from the face-viewpoint stimulus set was then displayed on the screen for 500 ms. To enable a wide range of

viewpoints without exhausting the subjects, each stimulus image was presented only once. A total of 225 trials were presented to each subject within a period of approximately 6 min. Subjects were instructed to look at the screen passively and try to keep their eyes on the fixation cross throughout the duration of the trial. Among the 225 face viewpoints, those positioned horizontally or vertically at angles of -5° ,

0°, and 5° were defined as basic viewpoints (1-dimensional rotations), whereas all other viewpoints were defined as composite viewpoints (2-dimensional rotations), as shown in the top-right panel of Figure 1e.

2.4 | Gaze-direction experiment

The methods used in the gaze-direction experiment were the same as those used in the face-viewpoint experiment, but with a different stimulus set. FaceGen Modeler was used to generate front-view images of the same face, but with various gaze directions. Figure 1a and d present two examples of the gaze-direction stimuli. The visual angle of the stimuli covered $8.5^\circ \times 8.5^\circ$ and a fixation cross (visual angle of $0.5^\circ \times 0.5^\circ$) was superimposed in the center of each image. Figure 1f presents a partial enlargement of the eye region of each face image. Images covered 21 directions along the horizontal plane from -50° to the 50° and 11 directions along the vertical plane from -25° to 25° , which resulted in a total of 231 gaze directions. Those positioned horizontally and vertically at angles of -5° , 0° , and 5° were defined as basic directions (1-dimensional rotations), and all other directions were defined as composite directions (2-dimensional rotations), as shown in the top-right panel of Figure 1f.

2.5 | Overview of the decoding method

Figure 2 presents a schematic illustration of the manifold decoding method proposed in this work. Procedures 1 and 2 (the first box) involved the recording and preprocessing of MEG data, respectively. Each trial involving either a training or testing set can be regarded as an $N \times T$ matrix, where N denotes the number of sensors and T denotes the number of data sampled in each trial. Procedure 3 (the second box) involved the estimation of cortical brain activity from MEG signals for each of the V sampling positions in the brain, resulting in a $V \times T$ -dimensional neural space. Each trial is represented as a point within this space. Procedures 4 and 5 (the third box) involved the extraction of data from particular temporal components and regions of interest (ROIs), as determined in the localizer experiment. Procedures 6 and 7 (the final box), involved using the proposed manifold transformation method to calculate a d -dimensional neural manifold ($d = 2$ in this example) for each ROI and temporal component. Decoding capability was evaluated by projecting a testing trial (green point) into a manifold space constructed using the training data set, whereupon the predicted angles of the face in the image were compared with the actual angles in that image. Details pertaining to the decoding method are presented in the following sections.

2.6 | Data recording

MEG data were recorded in a magnetically shielded room using a 306-channel whole-head system (Vectorview, Elekta Neuromag, Helsinki, Finland) at a sampling rate of 1,001.6 Hz, with bandpass filtering of 0.03–330 Hz. Signals from 204 gradiometers were used for processing. Electrooculograms (EOGs) were also recorded to detect eye movement in the vertical and horizontal directions. Three-dimensional T1-weighted magnetic resonance imaging (MRI) with the MP-RAGE

FIGURE 2 Schematic diagram illustrating the proposed manifold decoding method. In Procedures 1 and 2 (the first box), MEG signals with T time points and N sensors evoked by face-related stimuli were first recorded and then preprocessed. The training and testing datasets were prepared separately to enable the final prediction procedures. In Procedure 3, (the second box), we calculated brain activity with T time points for each of V positions using the MCB method, wherein each brain activity datum is regarded as a point in a VT -dimensional neural space. Procedures 4 and 5 (the following box) involved the selection of temporal components and ROIs. In Procedure 6, the neural manifold was calculated using the locality preserving projection method. Procedure 7 involved the formulation of predictions for face-viewpoint/gaze-direction based on the neural manifold [Color figure can be viewed at wileyonlinelibrary.com]

sequence was performed using a 3T scanner (MAGNETOM Trio, A Tim System; Siemens Medical Solutions, Erlangen, Germany) using the following parameters: TR = 2,530 ms, TE = 3.03 ms, TI = 1,100 ms, FOV = $224 \times 256 \times 192$ mm³, matrix size = $224 \times 256 \times 192$, and voxel size = $1 \times 1 \times 1$ mm³. Coordinate systems between the MRI volume and MEG device were co-registered by locating three landmarks (nasion, left, and right pre-auricular points) in each of the systems.

2.7 | Data preprocessing

Trials were excluded from our analysis if they contained gradiometer signals with amplitudes exceeding 3,000 fT/cm or electrooculography signals with amplitudes exceeding 150 μ V. After elimination, the mean number of epochs was 193.8 out of 225 (86.1%) in the face-viewpoint experiment and 194.1 out of 231 (84.0%) in the gaze-direction experiment. MEG signals were projected onto a signal subspace using the signal space projection method (Uusitalo & Ilmoniemi, 1997) and passed through a band-pass filter (2–50 Hz). For baseline correction, the mean amplitude of the pre-stimulus interval [−250 ms, −50 ms] was subtracted from the signal of each trial. EOG-free epochs of 1,000 ms starting from 250 ms prior to stimulus onset were extracted for further analysis.

2.8 | Estimation of brain activity

We applied the maximum contrast beamformer (MCB) method (Chen, Cheng, Hsieh, & Chen, 2006) for the calculation of brain activity from MEG recordings. MCB is one of the advanced beamforming methods for source localization which can improve the estimation of dipole orientation based on the maximum contrast criterion. Attributed to its accurate estimation of dipole orientation, the source imaging results of MCB can be more focal and sensitive than conventional beamforming methods (Chen et al., 2006). For the i th trial, we denote N -channel MEG recordings at time point t ($t=1, \dots, T$) as $\mathbf{m}^i(t)$. In the first step, brain activity $y_v^i(t)$ at the v th position ($v=1, \dots, V$) sampled every four voxels in the MR image was calculated as follows:

$$y_v^i(t) = \mathbf{w}_v^T \mathbf{m}^i(t), \quad (1)$$

where, $\mathbf{w}_v$ is an $N \times 1$ spatial filter at the v th position, which was calculated by maximizing the F -statistic value (Chen et al., 2006). The F -statistic value at position v is the variance ratio (estimated in an event-related interval to that estimated in a pre-stimulus interval) of the filtered activity $y_v^i(t)$ as follows:

$$F_v = \frac{E\left\{\left(\mathbf{w}_v^T \mathbf{m}_e^i(t) - E\left\{\mathbf{w}_v^T \mathbf{m}_e^i(t)\right\}\right)^2\right\}}{E\left\{\left(\mathbf{w}_v^T \mathbf{m}_n^i(t) - E\left\{\mathbf{w}_v^T \mathbf{m}_n^i(t)\right\}\right)^2\right\}}, \quad (2)$$

where, $E\{\cdot\}$ denotes the expectation value and $\mathbf{m}_e^i(t)$ and $\mathbf{m}_n^i(t)$ are the MEG measurements in event-related and pre-stimulus intervals, respectively. We then concatenated the brain activity $y_v^i(t)$ for all time points $t=1, \dots, T$ and all positions $v=1, \dots, V$ in order to obtain the spatiotemporal activity associated with the i th trial, as vector $\mathbf{y}^i$ in the following:

$$\mathbf{y}^i = [y_1^i(1), y_1^i(2), \dots, y_1^i(T), y_2^i(1), y_2^i(2), \dots, y_2^i(T), \dots, y_V^i(1), y_V^i(2), \dots, y_V^i(T)]^T. \quad (3)$$

2.9 | Selection of latencies in temporal components

To eliminate the effects of bias imposed by the experimental data, we used data acquired in the functional localizer experiments to identify the time components for each subject. We selected peak latencies of M100, M170, and M250 according to the largest amplitudes in the MEG signals averaged across trials and channels within the following intervals: M100 [70 ms, 130 ms], M170 [130 ms, 210 ms], and M250 [210 ms, 290 ms].

2.10 | Selection of regions of interest using MEG

The parcellation of brain regions was achieved by registering the automated anatomical labeling (AAL) template (Tzourio-Mazoyer, et al., 2002) packaged with MRICro (Chris Rorden, University of Nottingham, The United Kingdom) to the MRI of each subject. ROIs in this study were defined for each subject using MEG data acquired in the functional localizer experiments. Separate ROIs were defined for each hemisphere. Face-related ROIs, including OFA, FFA, and STS, were selected using a two-sample t -test. Each position v in the inferior occipital cortex, fusiform gyrus, and STS was deemed to be within the face-related ROI if the F -statistic value for face images calculated using MCB was significantly larger than that for scrambled images ($p < .05$) (Berman et al., 2010). In the t -test, the power of brain activity under both stimulus conditions was calculated using MCB with the event-related interval specified as a 100-ms time window centered on a peak latency of M100, M170, or M250. Face-related ROIs were identified by the union of the regions identified at M100, M170, and M250. The superior frontal gyrus (SFG) and early visual cortex (EVC) were used as references in the formulation of comparisons with face-related ROIs in terms of decoding results for face viewpoints and gaze directions. SFG was defined using the AAL atlas of each subject. EVC was determined by selecting positions in the calcarine area with F -statistic values for face/scrambled images that are significantly larger than the F -statistic values for post-stimulus fixation images, as determined using a t -test ($p < .05$) (Golomb & Kanwisher, 2012). Event-related intervals were specified as 100-ms time windows centered on the M100 component evoked by the corresponding stimuli (face, scrambled, and fixation images). These ROIs were identified in most of the subjects; however, FFA was not found in one subject, and EVC was not found in two subjects. Data pertaining to unidentified ROIs were excluded from subsequent statistical analysis.

2.11 | Calculation and visualization of the neural manifold

This study adopted the manifold transformation method referred to as locality preserving projection (LPP) (He & Niyogi, 2004) to calculate the transformation matrix $\mathbf{H}_{d \times VT}$ from a $V \times T$ -dimensional neural space to a d -dimensional manifold, where d tends to be far smaller than $V \times T$. The

first step in the LPP algorithm involves the construction of an adjacency graph representing the distance relationships among data. In the adjacency graph, the K -nearest neighbors $\mathbf{y}^j$ ($j=1, \dots, K, K<20$) of each data point $\mathbf{y}^i$ are determined according to Euclidean distances in the original neural space. These are connected to $\mathbf{y}^i$ using edges with weighting $C_{i,j}$ calculated using the heat kernel, as follows:

$$C_{i,j} = \exp\left(\frac{-\|\mathbf{y}^i - \mathbf{y}^j\|^2}{u}\right), \quad (4)$$

where, the parameter of the heat kernel, u , was set to 1 in this study. A transformation matrix was then obtained by computing the eigenvectors and eigenvalues in accordance with the method proposed in (He & Niyogi, 2004). In this study, the dimensionality of the low-dimensional space (that is, d) was determined by the rate of eigenvalue accumulation (>0.9). Using transformation matrix $\mathbf{H}_{d \times VT}$, data $\mathbf{y}^i$ in the original neural space can be transformed into $\mathbf{z}^i$ in a manifold, as follows:

$$\mathbf{z}^i = \mathbf{H}\mathbf{y}^i. \quad (5)$$

The time windows of data pertaining to brain activity in each ROI were 100-ms intervals centered on the M100, M170, or M250 components. To enable the visualization of multi-dimensional data and the prediction of face-viewpoint/gaze-direction, data in the d -dimensional manifold were projected onto two one-dimensional subspaces using linear transformation with the weighting vectors $\mathbf{b}_H$ and $\mathbf{b}_V$. This was calculated using linear regression based on the face viewpoint or gaze direction, as follows:

$$\begin{aligned} r_H^i &= \mathbf{b}_H^T \mathbf{z}^i \\ r_V^i &= \mathbf{b}_V^T \mathbf{z}^i, \end{aligned} \quad (6)$$

where, r_H^i and r_V^i are coordinates in the one-dimensional subspaces associated with the i th trial, which were used to represent the horizontal and vertical angles of the face-viewpoint/gaze-direction, respectively.

2.12 | Predicting angles of face viewpoint and gaze direction

The low-dimensional manifold representation was quantitatively evaluated according to the accuracy of angle prediction. In the training stage, a neural manifold was obtained by applying the above procedure to the MEG data evoked by basic face-viewpoints/gaze-directions. Note that we obtained the spatial filter $\mathbf{w}_v$ for the estimation of brain activity, transformation matrix $\mathbf{H}_{d \times VT}$ for manifold calculation, and vectors $\mathbf{b}_H$ and $\mathbf{b}_V$ for linear projection from the basic data set.

In the testing stage, the neural manifold was used to determine the angle of composite face viewpoint or gaze direction. Spatial filter $\mathbf{w}_v$ was applied to the MEG data under examination $\mathbf{m}^0(t)$ to enable the calculation of source activity $\gamma_v^0(t)$ in each position v within an ROI:

$$\gamma_v^0(t) = \mathbf{w}_v^T \mathbf{m}^0(t), \quad (7)$$

which was then concatenated into vector $\mathbf{y}^0$, as in Equation 3. Matrix $\mathbf{H}_{d \times VT}$ was then used to calculate $\mathbf{z}^0$ in the manifold using $\mathbf{z}^0 = \mathbf{H}\mathbf{y}^0$. The horizontal and vertical angles in the face-viewpoint/gaze-direction, r_H^0

and r_V^0 , were calculated using $r_H^0 = \mathbf{b}_H^T \mathbf{z}^0$ and $r_V^0 = \mathbf{b}_V^T \mathbf{z}^0$, respectively, up to a scale factor. The decoding performance of each ROI was evaluated according to the correlation coefficient between the calculated angles and the actual angles of face-viewpoint/gaze-direction among all testing data. We also sought to determine whether there exists a shared neural representation between face viewpoint and gaze direction. This was achieved using weighting vectors $\mathbf{b}_H$ and $\mathbf{b}_V$ (calculated from face-viewpoint data) to predict the angles of gaze direction. The significance of the prediction results was determined using a random permutation test. For each subject in the test, 1,000 permutations were generated by randomly shuffling the labels of the stimuli 1,000 times. We constructed a prediction model for each permutation and performed angle prediction for each ROI. We then combined all of the prediction results from all of the subjects to construct a resampled distribution in order to determine the level of significance in accordance with this distribution.

2.13 | Comparison of LPP with other methods

We compared the LPP method with the conventional linear method, principal component analysis (PCA), and the use of original spatiotemporal brain activity in order to provide a reference by which to evaluate the suitability of the nonlinear manifold method for the modeling of brain activity. When applying PCA, we replaced the final procedure in Figure 2 (neural manifold calculation) with PCA. Parameter d of PCA was determined using the same criterion as that used in LPP, with 0.9 as the threshold of eigenvalue accumulation. When using original spatiotemporal brain activity, we accessed the data directly in the neural space without the final procedure in Figure 2.

3 | RESULTS

3.1 | Selection of ROI and temporal component in MEG

Figure 3a presents the signals from 204 gradiometers averaged across all trials from a representative subject in the functional localizer experiment. The selected M100, M170, and M250 components are indicated in the figure, with their corresponding topographies presented in the top panel. The bold circles indicate the location of Channel 2322 with a peak at M170, the signal of which is indicated by a superimposed red line in the bottom panel. The top panel in Figure 3b depicts the strength of the F -statistic value calculated from brain activity in OFA, FFA, or STS during the interval between 50 and 250 ms following stimulus onset. The bottom panel of this figure presents a temporal profile of brain activity estimated using spatial filters and MEG measurements in OFA (red), FFA (green), and STS (blue). The superimposed red, green, and blue lines indicate the signals associated with the strongest activations. The average number of voxels selected for these MEG-defined OFA, FFA, STS, and EVC regions across all subjects were 298, 68, 160, and 154, respectively. The average number of voxels for the AAL-defined SFG was 718.

FIGURE 3 Temporal profile of MEG signals and data related to estimated brain activity. (a) 204-channel MEG signals were averaged across all trials for a representative subject, wherein the superimposed red line indicates the signal of Channel 2322, which presented the strongest peak at M170. The M100, M170, and M250 components were selected in accordance with the average power of the signals. The top panel presents topographies corresponding to these components, with the white circle indicating the location of Channel 2322. (b) *F*-statistic map estimated from brain activity between 50 and 250 ms in the OFA, FFA, and STS using the MCB method. The coronal, sagittal, and axial planes are located at the peak of the *F*-map of the right hemisphere. The thick lines in the bottom panel show the temporal profiles of brain activity in the OFA, FFA, and STS. The superimposed thick lines indicate the signals with the strongest activation in these regions [Color figure can be viewed at wileyonlinelibrary.com]

3.2 | Neural manifold in a low-dimensional space

To enable the visualization of brain activity data in a manifold space, we first organized the data within a two-dimensional space and then calculated the similarity matrix between the data evoked by various stimuli. Figure 4a presents a subspace spanned by two linear combinations of coordinates in a low-dimensional neural manifold calculated for a representative subject. The colors of the data points correspond to viewpoints along the horizontal and vertical planes relative to the faces shown as stimuli, as indicated by the color map in the panel on the top-right. The information related to viewpoints along the horizontal and

vertical planes was revealed in the subspace of the neural manifold formulated using brain activity in the right OFA with a 100-ms time window centered on the M170 component. The green line connects data points (with vertical angles of -5° , 0° , and 5°) associated with horizontal viewpoints located along the horizontal axis, whereas the yellow line connects data points (with horizontal angles of -5° , 0° , and 5°) associated with vertical viewpoints located along the vertical axis. The left panel in Figure 4b presents a dissimilarity matrix, which was calculated as normalized differences in the horizontal/vertical angles of face viewpoints between image stimuli. The right panel in Figure 4b presents the averaged dissimilarity matrix obtained from brain

FIGURE 4 Low-dimensional subspace of neural manifold and dissimilarity matrix for face viewpoint. (a) Two-dimensional subspace associated with information related to face viewpoints, which was obtained from a representative subject using data related to the right OFA. The colors of the data points correspond to the particular stimuli indicated in the color map in the top-right panel. The green line connects data points (with vertical angles of -5° , 0° , and 5°) related to horizontal viewpoints along the horizontal axis; the yellow line connects data points (with horizontal angles of -5° , 0° , and 5°) related to vertical viewpoints along the vertical axis. (b) Dissimilarity matrix calculated from the difference in angles between the face viewpoints of stimulus images (left panel) and a dissimilarity matrix calculated from the difference between brain responses represented in the two-dimensional manifold subspace/original space (right panel). The correlation coefficients between two dissimilarity matrices are 0.42 ($p < .01$) and 0.06 [Color figure can be viewed at wileyonlinelibrary.com]

responses to image stimuli, which was calculated as differences in the coordinates in the two-dimensional subspace of the manifold representation shown in Figure 4a. Each element in the matrix was averaged from individual matrices for eleven subjects. The correlation coefficient between the upper triangular parts of two dissimilarity matrices was 0.41 ($p < .01$). The overall distribution of

correlations across subjects was significantly large against zero ($t = 12.3$, $p < .01$).

Figure 5a presents a subspace associated with gaze direction for a representative subject, which was obtained using data from the right STS with 100-ms time window centered on the M170 component. The colors of the data points correspond to the direction of gaze along the

FIGURE 5 Low-dimensional subspace of neural manifold and the dissimilarity matrix for gaze direction. (a) Two-dimensional subspace associated with information related to gaze direction, which was obtained from a representative subject using data related to the right STS. The colors of the data points correspond to the particular stimuli, as indicated by the color map in the bottom-right panel. Green and yellow lines connect data points related to horizontal and vertical gaze directions from -10° to 10° , respectively. (b) Dissimilarity matrix calculated from the difference in angles in gaze directions in stimulus images (left panel), and a dissimilarity matrix calculated from the differences between brain responses represented in the two-dimensional manifold subspace/original space (right panel). The correlation coefficients between these two dissimilarity matrices are 0.31 ($p < .01$) and -0.04 [Color figure can be viewed at wileyonlinelibrary.com]

horizontal and vertical planes, as indicated by the color map on the bottom-right panel. The green line connects data points associated with horizontal directions whereas the yellow line connects data points associated with vertical directions. Figure 5b presents a dissimilarity matrix obtained from the angles of horizontal/vertical gaze directions

(left panel), and the averaged dissimilarity matrix obtained from the manifold representation of brain activity across eleven subjects (right panel). The correlation coefficient between the upper triangular parts of these two matrices was 0.29 ($p < .01$) and the distribution of correlations across subjects was significantly large ($t = 10.34$, $p < .01$).

FIGURE 6 Results of face-viewpoint decoding. (a) Distribution of training and testing data in two-dimensional subspace associated with face viewpoints using data related to the M170 component in the right OFA. Circles with adjacent stimulus images indicate the decoding results with residual error of less than 15° for viewpoints along the horizontal and vertical planes. (b) Average correlation coefficients for viewpoints along the horizontal and vertical planes across all subjects using brain activity from various ROIs (***: $p < .01$, **: $p < .05$, *: $p < .1$). A paired t -test was used for comparisons between regions (**: $p < .05$). The circles and solid lines indicate the mean results for shuffled data from all subjects following 1,000 random permutations. (c) Correlation coefficients for viewpoints along the horizontal and vertical planes using the M100, M170, and M250 components in different ROIs (***: $p < .01$, **: $p < .05$, *: $p < .1$) [Color figure can be viewed at wileyonlinelibrary.com]

3.3 | Predicting angles of face-viewpoint and gaze-direction

To calculate the effect sizes for the various ROIs and temporal components, we performed angle prediction using basic stimuli as training data and composite stimuli as testing data. Figure 6a illustrates the distribution of training data (black circles, basic viewpoints) and testing data (white circles, composite viewpoints) for a representative subject in a low-dimensional subspace. This was calculated using the training data in the right OFA with a 100-ms time window centered on the M170 component. Each red circle indicates a testing data point (with residual error of less than 15° along the horizontal and vertical planes) with the corresponding image adjacent to the circle. Figure 6b presents the average correlation coefficients between the actual angles and the predicted angles using the M170 components of various ROIs across all subjects. The left and right panels of this figure respectively present the results for the horizontal and vertical angles. For each ROI, the significance level of the correlation coefficient was examined using a random permutation test (***: $p < .01$, **: $p < .05$, *: $p < .1$). The red circles and black lines indicate the results averaged from 1,000 randomly shuffled permutations. The highest correlation coefficient ($r = .3$, $p < .01$) for horizontal angles was that associated with the right OFA. This correlation coefficient was significantly higher than those with FFA (left and right) and STS (left and right) (paired t -test, $p < .05$). The highest correlation coefficient for vertical angles ($r = .11$, $p < .1$) was the one associated with the right OFA. Moreover, the correlation coefficients related to most of the regions in the right hemisphere were higher than those related to regions in the left hemisphere, with the exception of the left FFA, which scored higher than the right FFA with regard to horizontal angles. Figure 6c presents the correlation coefficients obtained using MEG components M100, M170, and M250 in the OFA, FFA, and STS regions. The highest correlation coefficient for horizontal angles was the one associated with the M170 component in the right OFA ($r = .3$, $p < .01$), whereas those obtained using the M100 component presented the lowest correlation ($r = .12$).

Figure 7a illustrates the distribution of training and testing data in a low-dimensional subspace from a representative subject, for use in the decoding of gaze direction. The data used for subspace calculation were from the right STS with a 100-ms time window centered on the M170 component. The black and white circles respectively indicate training and testing data. Red circles and their corresponding images indicate the results with residual error of less than 20°. Figure 7b presents the results related to predicted shifts in angles along the horizontal and vertical planes, which were obtained using data related to OFA, FFA, and STS across all subjects. These results were evaluated using a random permutation test (*: $p < .1$). The red circles and black lines indicate the results averaged from 1,000 randomly shuffled permutations. The significant results related to the horizontal and vertical angles were obtained from data in the right STS ($r = .13$ and $r = .11$, $p < .1$). The results associated with horizontal angles in the right STS was significantly higher than those in the OFA and FFA (paired t -test, $p < .05$). As shown in Figure 7c, M170 presented the highest correlation coefficient with regard to vertical gaze angle in the right STS.

3.4 | Shared representations between face viewpoint and gaze direction

Figure 8a illustrates the data distribution in a two-dimensional subspace of the neural manifold constructed using training data evoked by the observation of basic face images from the basic viewpoint (black circles). The data used for subspace calculation were from the right STS with a 100-ms time window centered on the M170 component. The decoding results for composite gaze-direction and face-viewpoint are indicated by white circles and gray circles, respectively. Four example pairs of testing data pertaining to face-viewpoint and gaze-direction in similar directions are also presented in this figure. As shown in Figure 8b, we calculated the average correlation coefficients between the predicted and actual angles associated with the direction of gaze. The left and right sides of this figure respectively present the horizontal and vertical angles associated with the gaze direction of all subjects (**: $p < .05$). The red circles and black lines depict the results averaged from 1,000 randomly shuffled permutations. The highest correlation coefficients for the prediction of horizontal and vertical gaze angles in the right STS were 0.07 (nonsignificant) and 0.14 ($p < .05$), respectively. The results in the right STS for the vertical direction were significantly higher than those in other regions (paired t -test, $p < .05$).

3.5 | Comparison of face-related region and early visual/superior frontal region

Comparisons of the prediction results were performed using data with the largest temporal components from the right-OFA/right-STS and EVC/left-EVC/right-EVC/SFG/left-SFG/right-SFG. Figure 9a presents the effect sizes for decoding viewpoints shifted horizontally (black bar) and vertically (white bar) using data from the right-OFA and EVC/left-EVC/right-EVC/SFG/left-SFG/right-SFG of all subjects. Data from the EVC resulted in correlation coefficients of 0.23 and 0.08 for viewpoints shifted along the horizontal and vertical planes, respectively. For viewpoints shifted along the horizontal and vertical planes, most of the results obtained using the right OFA are significantly higher than those obtained from the EVC and SFG (**: $p < .05$, *: $p < .1$). Figure 9b presents the effect sizes for decoding gaze angles shifted horizontally (black bar) and vertically (white bar) using data from the right STS and EVC/left-EVC/right-EVC/SFG/left-SFG/right-SFG of all subjects. Again, most of the results obtained from the right STS are significantly higher than those using obtained from the EVC and SFG (**: $p < .05$, *: $p < .1$).

3.6 | Comparison of LPP with other methods

Figure 9c presents the results (across all subjects) for the determination of face viewpoints shifted along the horizontal plane using the LPP method, PCA, and original spatiotemporal brain activity. In this comparison, we used data related to brain activity associated with the M170 component in the right OFA, due to its high performance in viewpoint prediction. The highest correlation was obtained using LPP ($r = .3$, $p < .01$), which was significantly higher than the values obtained using

FIGURE 7 Results of gaze-direction decoding. (a) Distribution of training and testing data in the two-dimensional subspace associated with gaze direction, using data from the M170 component in the right STS. Circles with the adjacent stimulus images indicate the decoding results with residual error of less than 20° for viewpoints along the horizontal and vertical planes. (b) Average correlation coefficients for viewpoints along the horizontal and vertical planes across all subjects using brain activity in various ROIs (*: $p < .1$). A paired t -test was used for comparisons between regions (**: $p < .05$). The circles and solid lines indicate the mean results from shuffled data from all subjects following 1,000 random permutations. (c) Correlation coefficients for viewpoints along the horizontal and vertical planes using the M100, M170, and M250 components in various ROIs (**: $p < .05$, *: $p < .1$) [Color figure can be viewed at wileyonlinelibrary.com]

FIGURE 8 Results of shared representation. (a) Distribution of data in a two-dimensional subspace constructed using training dataset of basic face viewpoints. The two testing datasets respectively comprise data from composite face viewpoints and composite gaze directions. Circles with adjacent stimulus images indicate four example pairs of testing data. Each pair contains a composite face viewpoint and a composite gaze direction with similar direction. (b) Average decoding results for composite gaze in the horizontal and vertical directions, based on a neural manifold constructed using data evoked by basic face viewpoints (**: $p < .05$). A paired t -test was used for comparisons between regions (**: $p < .05$). The circles and solid lines indicate the mean results for shuffled data from all subjects following 1,000 random permutations [Color figure can be viewed at wileyonlinelibrary.com]

PCA or raw data without the application of methods to reduce dimensionality ($p < .05$).

4 | DISCUSSION

4.1 | Superposition of brain activity in the processing of abstract information

Researchers have investigated the spatial linearity and spatial summation characteristics of low-level visual processing in the brain (Hansen, David, & Gallant, 2004; Kuo et al., 2014). The fMRI has been used to

predict BOLD responses by summing the responses to basic patches of visual stimuli containing wedges or rings in checkerboard patterns (Hansen et al., 2004). Kuo et al. (2014) used MEG to formulate a low-dimensional neural manifold based on brain activity evoked by patches of four basic checkerboard patterns in the four corners of an image. This manifold was then used to reconstruct composite patterns from brain activity evoked by visual stimuli comprising a combination of multiple basic patterns. In other words, the superposition of brain activity in a manifold implies the superposition of the corresponding stimulus images. However, this type of spatial linearity does not appear in the stimulus patterns used in the current study, due to the fact that face

FIGURE 9 (a) Comparison of decoding results for all subjects using data in the right OFA and EVC/left-EVC/right-EVC/SFG/left-SFG/right-SFG for face viewpoints along the horizontal (black bars) and vertical (white bars) planes. (b) Comparison of decoding results for all subjects using data in the right STS and EVC/left-EVC/right-EVC/SFG/left-SFG/right-SFG for horizontal (black bars) and vertical (white bars) gaze directions. (c) Comparison of decoding results for face viewpoints along the horizontal plane for all subjects using the LPP method, PCA, and the original spatiotemporal brain activity (**: $p < .05$, *: $p < .1$)

images from composite face-viewpoints/gaze-directions cannot be obtained directly through the pixel-wise combination of two or more face images from basic viewpoints/directions.

In this study, we demonstrated that the superposition of brain activity implies the superposition of abstract concepts in the stimulus images. The angles associated with composite face viewpoints and gaze directions can be derived using a neural manifold based on brain activity evoked by basic viewpoints and directions. Our decoding results suggest that neural representations in face-related areas (OFA, FFA, STS) might be used in the encoding of high-level information (such as face viewpoint and gaze direction), rather than low-level information (such as the position or edge direction of stimuli). This assumption is supported by the fact that OFA outperforms EVC with regard to decoding. Furthermore, the face-related temporal component (M170) was superior to the M100 component with regard to decoding performance. These findings support the supposition that a transformation occurs from sensory representation to perceptual representation within the human brain. This topic has been studied in the context of material representation in areas of higher-order visual processing (Hiramatsu, Goda, & Komatsu, 2011) and for valence representation in the orbito-frontal cortex (Chikazoe, Lee, Kriegeskorte, & Anderson, 2014). The neural manifold in this study can be used to decompose information pertaining to viewpoint into horizontal and vertical components. This implies that the neural manifold plays a role in the perceptual representation of images related to the human face.

4.2 | Representational space of face viewpoints

Revealing the representational geometry of neural codes is one approach to investigating the neural basis of perception (Kietzmann et al., 2016; Kriegeskorte & Kievit, 2013). Using cell recordings from two middle patches in macaque monkeys, Freiwald and Tsao (2010) identified a subspace spanned by the first two dimensions of the multi-dimensional scaling (MDS) space. In this two-dimensional subspace, data associated with a particular head orientation were clustered together. This manifest as eight clusters, the distribution of which was based on the eight corresponding head orientations. Similarly, the regional clustering of cells corresponding to face viewpoint was also observed in an optical imaging study on monkeys (Wang, Tanaka, &

Tanifuji, 1996). High-dimensional EEG data has recently been used to investigate representational dynamics in order to reveal the various temporal stages associated with viewpoint encoding (Kietzmann et al., 2016).

In the current study, MEG was used to investigate the representation of the human face in the brain of humans. Spaces calculated using the manifold transformation method can be employed in the representation of face-viewpoints/gaze-directions in two dimensions, whereas the distribution of data reveals the relationship of angles. These findings support the assertion that manifold transformation may be associated with perceptions based on the input of complex neuronal signals (Seung & Lee, 2000). The recognition of novel stimuli can be facilitated by adopting a model that approximates representations in the brain (Kriegeskorte, 2011). In a previous study, it was suggested that manifold methods could be used to reveal characteristics inherent to the appearance of objects in images (He & Niyogi, 2004; Roweis & Saul, 2000; Tenenbaum et al., 2000). In line with (Kuo et al., 2014; Kuo, Chen, & Chen, 2015), we propose that manifold methods could be a useful analytical method by which to investigate face representation within neuroimaging data of enormous dimensionality.

4.3 | Neural system for perception of faces

Face perception is a distributed process that occurs in multiple extrastriate visual regions. Discriminative response patterns constitute a core system for the functions involved in face perception, such as the processing of facial features, eye gaze, and identity (Duchaine & Yovel, 2015; Haxby et al., 2000; Haxby, Hoffman, & Gobbini, 2002). Our decoding results in this study indicate that brain responses in OFA embed more information of face viewpoints than does FFA, an area essential to face identification. We also observed a gaze representation in the right STS that were discriminative of differences in gaze direction. These findings are consistent with those of previous studies (Allison et al., 2000; Axelrod & Yovel, 2012; Duchaine & Yovel, 2015; Haxby et al., 2000; Kietzmann et al., 2012, 2015).

Researchers have reported that right lateralization in the brain activity is associated with the processing of face-related data (Axelrod & Yovel, 2012; Duchaine & Yovel, 2015; Hoffman & Haxby, 2000; Meng, Cherian, Singal, & Sinha, 2012; Pitcher et al., 2011; Rossion,

Joyce, Cottrell, & Tarr, 2003), with either stronger responses or superior classification accuracy in the right hemisphere. Our decoding results based on brain activity in the right hemisphere were more accurate than those based on data from the left hemisphere; however, we did not observe right lateralization among variations in the amplitude of MEG signals. We also found that the decoding results related to horizontal position were superior to those related to vertical positioning. This may explain the findings in one recent study based on behavioral data, wherein the range of yaw angles exceeded that of pitch angles in the process of face recognition (Favelle & Palmisano, 2012).

In this study, the decoding correlation coefficients related to the direction of gaze were lower than those related to the viewpoint of the face. This can be explained by the fact that the eyes account for only a small portion of the face. Moreover, the repeated presentation of face images with the same identity or in the same location resulted in a decrease in the amplitude of N170/M170 (Caharel et al., 2009, 2015; Ewbank et al., 2008), which would no doubt compromise decoding performance. Nonetheless, we still found that the decoding results in the right STS ($p < .01$) and STS ($p < .05$) were significantly correlated with the actual direction of gaze. These results are in agreement with previous findings in which it was indicated that STS is related to the processing of stimuli related to the direction of gaze (Hoffman & Haxby, 2000; Puce, Allison, Bentin, Gore, & McCarthy, 1998; Wicker, Michel, Henaff, & Decety, 1998).

4.4 | Perceptual representation as a face space

Researchers have yet to elucidate the means by which a multidimensional face space is represented in the human brain. Loffler, Yourganov, Wilkinson, and Wilson (2005) suggested that the identity of a person can be recognized according to its distance and direction relative to the mean face in the multidimensional face space. Based on their fMRI BOLD results, they claimed that responses to facial geometry in the FFA can be modeled as a function of face variation. More recently, Gao and Wilson (2013) applied MVPA to fMRI data obtained from the FFA and OFA. Their results suggest that the face image space could be encoded and organized using spatially distributed responses of multiple voxels, rather than those of single voxels. The regions investigated in both of these studies are related to the component that deals with invariant aspects of faces in the lateral fusiform gyrus. This belongs to the core system of the distributed model used in the perception of faces, as outlined by Haxby et al. (2000). In the current study, we used neural manifolds constructed from brain activity in the OFA and STS to reveal the perceptual representation of the viewpoint and gaze direction of faces with the same identity. These are related to components that deal with changeable aspects of faces in the STS and inferior occipital gyri, and therefore fall within the core system in the Haxby's model.

4.5 | Face processing: from view-selective to view-invariant

The mechanism in the human brain used for the recognition of faces from various viewpoints has previously been investigated using fMRI

(Andrews & Ewbank, 2004; Anzellotti et al., 2014; Axelrod & Yovel, 2012; Carlin, Calder, Kriegeskorte, Nili, & Rowe, 2011; Carlin, Rowe, Kriegeskorte, Thompson, & Calder, 2012; Kietzmann et al., 2012; Natu et al., 2010; Pourtois et al., 2005), EEG (Caharel et al., 2009, 2015; Zimmermann & Eimer, 2013), and MEG (Ewbank et al., 2008). Those studies investigated view-invariant or view-selective hypotheses related to the processing of face-related stimuli associated with different viewpoints. It is possible that both of those hypotheses are reasonable, due to the fact that brain regions involved in the hierarchical processing associated with face recognition can be as view-invariant or view-selective (Axelrod & Yovel, 2012; Duchaine & Yovel, 2015; Kietzmann et al., 2012). Freiwald and Tsao (2010) observed in cell recordings obtained from macaque monkeys that face processing is view-specific in middle patches; however, it presents partial view invariance and view invariance in anterior patches. In the current study, the high correlation coefficients obtained for decoding results in the OFA suggest that neurons in this region are view-selective, whereas the correlation of results in FFA and STS are low. This shows that most of the neurons in FFA and STS are responsive to the face stimuli but not selective to face viewpoints. To provide the evidence of viewpoint-invariance assumption for FFA and STS, further investigation in person identification is required.

4.6 | Extraction of information embedded in neuroimaging data

In previous studies, the analysis of neuroimaging data was meant to reveal how the brain processes face viewpoints and gaze directions by analyzing brain responses evoked by various stimuli. Many studies have reported that viewpoint and/or gaze direction influences the activation of the brain; however, they have been unable to observe any differences between the activations evoked by different viewpoints (Tong, Nakayama, Moscovitch, Weinrib, & Kanwisher, 2000) or between those evoked by direct gaze as opposed to averted gaze (George, Driver, & Dolan, 2001). One explanation for this inconsistency is the possibility that subtle differences are not easily revealed through direct examination of the amplitudes in BOLD responses. Classifiers in MVPA can be used to distinguish various stimulus conditions from their corresponding distributed activation patterns represented in multiple voxels (Anzellotti et al., 2014; Axelrod & Yovel, 2012; Carlin et al., 2011; Gao & Wilson, 2013). However, classifiers categorize brain responses to different stimuli, which means that they are not necessarily able to deal with stimuli presenting continuously varying parameters. This makes it difficult to apply classifiers to basic stimuli for the training of a general representation applicable to the decoding of composite stimuli. In one recent investigation into neural representations associated with viewpoint and identity, researchers demonstrated the limitations of MVPA resulting from its use of single-unit recordings on macaque monkeys (Dubois et al., 2015). As shown in Figure 9c, the low correlation coefficients obtained from the original spatiotemporal activity imply that face viewpoints cannot be determined directly from patterns in the original brain activity. However, transforming the feature space from the original neural space using LPP or PCA has been shown

to greatly improve decoding performance, far exceeding that obtained using the patterns in the original brain activity. Although good prediction performance cannot directly imply that the targeted ROIs actually process face viewpoints and gaze directions of the stimuli, the hidden structures used to deal with abstract information could conceivably be uncovered through the nonlinear transformation stream of the proposed method. The transformation from a neural space to a feature space could be regarded as a transformation from the original neural representation to a representation applicable to high-level processing in the human brain.

The MDS method (Chikazoe et al., 2014; Freiwald & Tsao, 2010) and the proposed LPP method with linear projection could both be used to visualize the representational geometry of patterns in brain activity. One major difference between these two methods is the fact that LPP obtains a nonlinear manifold through the preservation of local distances among data points. In contrast, MDS is equivalent to PCA when Euclidean distances are adopted as a similarity metric; however, it achieves a linear reduction in dimensionality by considering pairwise similarity among all of the data. Previous studies have reported that the nonlinear structure of a dataset may be invisible to PCA and MDS (Roweis & Saul, 2000; Tenenbaum et al., 2000). MDS requires a complete data set for the construction of a feature space, and is unable to transform new data from the original neural space to the feature space. Thus, the MDS approach cannot be used to predict the angles of face viewpoints or gaze directions, as is possible using the proposed method. Figure 9c presents a comparison of the results obtained using the LPP method with those obtained using PCA. The correlation coefficients obtained using LPP were higher than those obtained using PCA, which suggests that nonlinear dimensionality reduction is better than linear reduction in the formulation of low-dimensional representations from neuroimaging data.

One MEG study investigated object representation (Cichy, Pantazis, & Oliva, 2014) by using a single-trial approach and demonstrated the importance of spatiotemporal information during the processing in the brain. In their study, each kind of stimuli was repeatedly presented for a total of 40–60 times and a support vector machine was applied as a binary classifier for prediction. For classification, repetition of the same type of stimuli is essential for training. In the current study, each kind of stimuli was presented to the subject only once because the prediction was performed via regression and a well-distributed data is good for model construction.

4.7 | Roles of M100, M170, and M250 components in face processing

The high temporal resolution of MEG and EEG make it possible to investigate the temporal dynamics of face processing with short latencies. This also makes it possible to identify face-related cortical regions and their corresponding temporal components using source localization methods (Deffke et al., 2007; Nguyen & Cunnington, 2014; Shibata et al., 2002). One previous study suggested that the N170 component is related to the structural encoding mechanism involved in face perception prior to face recognition (Eimer, 2000). Investigations into the

N170/M170 components led previous researchers to propose a viewpoint-dependent representation for face processing (Caharel et al., 2015; Ewbank et al., 2008) and individual face representation from various viewpoints (Caharel et al., 2009, 2015). As in with previous research, we found that face viewpoint could be decoded with the highest accuracy when using the brain activity of M170 in OFA. We also investigated the roles of the M100 and M250 components in the processing of face viewpoints. Using M250, we observed a stronger correlation between calculated and actual viewpoints than that achieved using M100. These results may be due to N250r repetition effects, which are reportedly related to view-independent face learning processes (Zimmermann & Eimer, 2013) and face repetition priming (Schweinberger & Burton, 2003). In previous studies, it was reported that the M100 component originating in the OFA (Pitcher et al., 2011) is involved in the categorization of face-related as well as nonface-related stimuli (Liu et al., 2002). In this study, the correlation coefficient between the predicted and actual horizontal viewpoints obtained using M100 was far weaker than that obtained using M170 in OFA. These findings suggest that the M170 and M250 components carry more information in the processing of face viewpoints than does the M100 component.

Previous EEG and MEG studies dealing with the temporal components of eye-gaze processing observed differences in the amplitude or latency of brain responses at approximately 170 ms, when observing averted gazes or direct gazes (Puce et al., 2000; Sato et al., 2008; Watanabe et al., 2001). When fMRI with EEG were combined, gaze direction and pointing gestures appeared to be integrated at approximately 190 ms (Conty, Deza, Hugueville, & Grèzes, 2012). Our prediction results using M170 in the right STS were significantly correlated to the actual angles, which suggests that the M170 component is related to the processing of signals related to gaze direction.

4.8 | Shared representations associated with the perception of direction

Direction is perceived in the cues associated with social attention, such as head orientation, gaze direction, and body posture (Nummenmaa & Calder, 2009; Perrett et al., 1985; Perrett, Hietanen, Oram, Benson, & Rolls, 1992; Wachsmuth, Oram, & Perrett, 1994). Nummenmaa and Calder (2009) reported that the STS is involved in the gaze-specific analysis as well as in various processes related to attention. A direction-sensitive code in the right anterior STS has been found to differentiate leftward from rightward turns of the head (Carlin et al., 2012). It has also been proposed that high-level code used in gaze perception is related to social attention (Carlin et al., 2011). Another study based on cell recordings from macaques reported that a number of neurons respond to the specific direction of face views and gaze direction (Perrett et al., 1985). In other words, this particular group of cells is activated by stimuli associated with averted gaze and faces in profile, whereas a different group of cells is activated by direct gazes and faces in front view. In this study, our decoding results for the right STS were strongly correlated ($p < .05$) to gaze direction as well as face viewpoint. As shown in Figure 8, our results for shared representation also

demonstrate that the right STS can be used to derive the direction of gaze according to the face viewpoint representation. This can be attributed to the fact that the processing of directions related to face viewpoint and gaze direction may share a direction-sensitive representation in the right STS. Another possibility is that the direction of gaze changes with the viewpoint of the face in face images. Thus, a neural manifold trained using brain activity associated with the perception of images related to face viewpoint may contain information related to the direction of gaze, which could be used to facilitate predictions of gaze direction.

4.9 | Face recognition through a manifold

Humans are able to recognize faces despite large variations in scale, rotation, and illumination, all of which tend to produce different patterns in the evoked brain response. Nonetheless, we have yet to identify the mechanism by which the brain transforms face stimuli of a given person into an invariant representation to achieve face recognition in a wide range of contexts (Haxby et al., 2002; Riesenhuber & Poggio, 1999; Wallis & Rolls, 1997). Riesenhuber and Poggio (1999) proposed a hierarchical model based on a MAX-like mechanism to simulate higher-level recognition from view-tuned to view-invariant stages. The neural manifold proposed in this work is able to derive new face viewpoints from testing data; therefore, it may be applicable as a rotation invariant representation for face recognition. However, this work is limited by the fact that we used face images of only one person in the construction of the neural manifold. Further experimentation should be conducted to determine whether the brain responses to the images of different people result in the formation of different neural manifolds.

5 | CONCLUSIONS

This article presents a manifold method for decoding neural representations of the face viewpoint and gaze direction from MEG data. Our results demonstrate the effectiveness of using the subspaces of neural manifolds in face-related regions to represent variations in the face viewpoint and gaze direction. Moreover, the proposed manifold subspace is formulated using data related to brain activity evoked by faces from a basic viewpoint or gaze direction. Thus, it can then be used in the prediction of composite viewpoints or gaze directions from brain activity evoked by corresponding stimuli. Our evaluation results demonstrate the superiority of the proposed method over conventional methods in predicting the angles of face viewpoints and gaze directions. These results suggest that the proposed manifold decoding method is suitable for uncovering abstract information embedded in neural representations for use in investigation of how the human brain processes face-related stimuli.

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CONFLICT OF INTEREST

None.

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