

Neural representation of familiar faces in human visual cortex

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September 14, 2020

Acknowledgment

Foremost, I wish to express my sincere appreciation to my adviser, Dr. Reza Rajimehr, you have been a tremendous mentor for me. I would like to thank you for your consistent support and guidance in all the time of this project. Words cannot express how grateful I am to you for all of your patience, motivation, and immense knowledge. I could not have imagined having a better adviser and mentor for my Ph.D study.

I would also like to say a special thanks to scientific committee of the Institute for Research in Fundamental Sciences (IPM) for all their supports that let me the chance to continue my research.

My sincere thanks also goes to Dr. Gholam Reza Hosseinzadeh, Dr. Elaheh Yargholi, Dr. Hossein Vahabi, Dr. Mohammad Reza Abolghasemi, Dr. Shima Seidalaiee, Dr. Mojtaba Abbaszadeh, Dr. Mayam Vaziri, Dr. Karim Rajaei and all academic members of the school of cognitive science for their priceless help.

Last but not the least, I would like to thank my best friend and life companion, Ali Samiee and also my parents for all the great and persistent supports at all stages of this work.

Abstract

Extensive research has shown that perceptual information of faces is processed in a network of hierarchically-organized areas within ventral temporal cortex. For familiar and famous faces, perceptual processing of faces is normally accompanied by extraction of semantic knowledge about the social status of persons. Semantic processing of familiar faces could entail progressive stages of information abstraction. However, the cortical mechanisms supporting multi-stage processing of familiar faces have not been characterized. Here using an event-related fMRI experiment, familiar faces from four celebrity groups (actors, singers, politicians, and football players) and unfamiliar faces were presented to the subjects while they were engaged in a face categorization task. We systematically explored the cortical representations for faces, familiar faces, subcategories of familiar faces, and familiar face identities using whole-brain univariate analysis and searchlight-based multivariate pattern analysis. Convergent evidence from all these analyses revealed a network of overlapping and hierarchically-organized areas in posterior cingulate cortex (PCC) that contained decodable fMRI responses for representing different levels of semantic knowledge about familiar faces. Our results suggest a hierarchical organization in PCC for processing the semantic information of faces analogous to the hierarchical organization within ventral temporal cortex for processing the perceptual information of faces.

Contents

1	Introduction	8
1.1	Face-specificity hypothesis	9
1.2	Cognitive model of face processing	11
1.3	Neural model of face processing	13
1.3.1	Core system of face processing	13
1.3.2	Extended system of face processing	14
1.3.3	Revisions to neural model	16
1.4	Familiar and unfamiliar face processing similarity and differences	18
1.4.1	Perceptual information	19
1.4.2	Conceptual information	20
1.5	Different types of familiarity	21
1.6	Neuroimaging evidences for familiar face recognition	22
1.6.1	Core system	22
1.6.2	Extended system	23
1.7	Thesis outline	24
2	First experiment	25
2.1	Methods	25
2.1.1	Subjects	25
2.1.2	Visual stimuli	25
2.1.3	Experimental procedures	26
2.1.4	Data acquisition	28

2.2	Data analysis	28
2.2.1	Preprocessing	28
2.2.2	ROI localization	30
2.2.3	Pattern information analysis	32
2.2.4	Classification distance for similarity analysis	32
2.2.5	Correlation distance for similarity analysis	33
2.2.6	Test for low-level feature similarity	34
2.2.7	Surface-based searchlight	36
2.3	Results	37
2.3.1	Behavioral assessment of familiarity	37
2.3.2	Univariate analysis	37
2.3.3	Pattern analysis	38
2.3.4	Searchlight analysis	39
2.4	Discussion	40
3	Second experiment	44
3.1	Methods	44
3.1.1	Subjects	44
3.1.2	Visual stimuli	44
3.1.3	Procedure	45
3.1.4	Data acquisition	47
3.1.5	Data analysis	47
3.2	Results	50
3.2.1	Univariate analysis	50
3.2.2	Multivariate analysis	51
3.3	Discussion	52
4	Third experiment	55
4.1	Introduction	55
4.2	Methods	58
4.2.1	Subjects	58

4.2.2	Visual stimuli	58
4.2.3	Experimental procedure	61
4.2.4	Data acquisition	62
4.2.5	Data analysis	63
4.3	Results	69
4.3.1	Behavioral results	69
4.3.2	Cortical representations of familiar faces	70
4.3.3	Cortical representations of familiar face subcategories	70
4.3.4	ROI analysis	72
4.3.5	Cortical representations of familiar face identities	75
4.3.6	Topographic organization of semantic face representations in PCC	76
5	Discussion	81
5.1	Representation of information for familiar faces	82
5.2	Representation of information for subcategories of familiar faces	84
5.3	Representation of information for familiar face identities	85
5.4	Representation of perceptual information for faces in PCC	86
5.5	Hierarchical organization of semantic face representations in PCC	87
5.6	The role of OFA and FFA in semantic face processing	88
5.7	The role of ATL in semantic face processing	88
6	Appendix Figures	91

List of Figures

1.1	Cognitive model of face processing	12
1.2	The neural model of face processing	14
1.3	Core system Face preferential regions	15
1.4	Extension of core system face-selective areas	18
1.5	Neuroimaging evidence for different types of familiar persons	21
2.1	Face stimuli and task design	27
2.2	Behavioral assessment of familiarity	29
2.3	Whole-brain univariate analysis	31
2.4	ROI-based multivariate pattern analysis	35
2.5	Surface sub-sampling	37
2.6	Whole-brain searchlight representing information for familiar face sub-categories	41
3.1	Face stimuli and task design	46
3.2	Whole brain univariate analysis	51
3.3	Whole-brain searchlight representing information for familiar face sub-categories	52
4.1	Face stimuli and task design	59
4.2	Spatial frequency matching of face stimuli, and results of the V1 model	60
4.3	Face-selective ROIs	68
4.4	Whole-brain univariate analysis	71

4.5	Whole-brain searchlight analysis for identifying regions that encode familiar face subcategories	72
4.6	ROI-based MVPA for familiar face subcategories	74
4.7	CDI for familiar face subcategories in selected ROIs	75
4.8	Whole-brain searchlight analysis for identifying regions that encode familiar face identities	77
4.9	Topographic organization of semantic face representations in PCC . .	79
6.1	All samples of face stimuli used in the fMRI experiment 1	92
6.2	All samples of face stimuli used in the fMRI experiment 2	93
6.3	All samples of face stimuli used in the fMRI experiment 3	94

Chapter 1

Introduction

Every day life is full of interactions with different kinds of objects along time and space. Appropriate interactions necessitate the ability to distinguish objects based of physical features, and categorization of them to general conceptual categories such as animate, inanimate, tools, plants, conspecifics, etc. [Rosch et al., 1976]. Efficient recognition of these conceptual categories convey relevant information that is critical for the adaptive control of action. This capacity had vital role in all kinds of species and was so crucial for survival that became a fundamental feature in the evolution of animal species [Rhodes et al., 2012, Contreras et al., 2012]. Conceptual categorization of objects could be either constrained by evolutionary pressures or shaped from correlated experiences in the environment that gradually lead to more abstract factual knowledge [Binder et al., 2009, Mahon and Caramazza, 2009].

Among these conceptual categories, recognition of conspecifics category and its social subcategories has been the most critical ability for social species [Rosch et al., 1976]. Psychologists have stated that categorizing conspecifics to social subcategories induces inferences and assumptions about individuals and consequently specifies acceptable interactions with them [Dovidio et al., 2008]]. Conspecifics recognition can be based on different visual aspects of individuals such as face and body. Analysis of the face leads to the fastest and the most accurate identification [Rhodes et al., 2012]. Moreover, face recognition appears to be a fundamental cognitive task in everyday life of social species, and it has an important role in their social communications.

Given the importance of faces in our social life, one main goal of human visual system is to process different aspects of faces. Models of face perception proposed that flexible and efficient extraction of face-related categorical information could be possible by having dedicated neural representations for faces that are separable from the representations for other object categories.

Human and non-human primates also need to recognize social categorical information in addition to perceiving general appearance of faces, facial features, expressions, speech articulation and individual identification [Ross and Olson, 2012]. Familiar faces can be readily categorized based on various social, semantic, and contextual factors. For example, we can label a group of faces as a distinct celebrity group (actors/actresses, musicians, politicians, scientists, athletes, etc.). Although, previous studies have found hierarchical and multi-stage representations within ventral temporal cortex for perceptual processing of faces, it remains an open question how and where in the brain multiple categorical levels of familiar face-related semantic knowledge are represented. Using neuroimaging, this thesis investigated how semantic information of familiar faces is extracted in the human face processing system.

This chapter is organized as follows. First, we begin with studies reporting specialized and distinct mechanism for face processing. Then, we explain briefly the cognitive and neural models for face recognition. Next, we present studies which have addressed differences for familiar and unfamiliar face recognition.

1.1 Face-specificity hypothesis

The earliest studies suggesting distinct mechanism for recognition of faces than the other objects were based on neuropsychological case reports that showed brain injuries could lead to selective impairment in face perception [Florence and Ellis, 1990]. The reports demonstrating existence of object agnosia without prosopagnosia also confirmed these hypothesis [Duchaine et al., 2006, Sergent et al., 1992, Rezlescu

et al., 2012].

The first evidence for face specificity in the normal brain came from studies investigating the effects of inversion. Yin's (1969) study showed that turning faces upside down affected performance of face recognition more than did inversion of other objects [Yin, 1969]. Later studies proposed that this difference was provided by holistic representation of faces that is absent in object recognition [Tanaka and Farah, 1993, Young et al., 1987].

In line with behavioral reports, electrophysiological studies also showed different processing for face and objects in healthy subjects using electroencephalogram (EEG). Actually, presenting faces and objects to participants led to a greater negative evoked potential around 170ms after stimulus onset (N170) [Bentin et al., 1996].

In the nonhuman primate brain, Charles Gross and colleagues were the first groups reporting the face-selective neurons [Desimone et al., 1984, Gross et al., 1972]. This evidence was confirmed by Rolls, Perrett, and others [Perrett et al., 1982]. Neuroimaging studies also demonstrated that regions in the superior temporal sulcus of the macaque revealed especially strong responses to faces [McCarthy et al., 1997, Tsao et al., 2003]. In a study by Tsao and colleagues, fMRI and single-cell recording were combined. Specifically, they localized face-selective regions using fMRI method in the macaque brain and then evaluated their responses to faces using single-cell recording. The results showed that 97% of the neurons in the pre-defined regions were selective for faces [Tsao et al., 2006]. This finding was replicated in the following study and provided the evidence to claim that macaque face patches are composed almost entirely of face-selective neurons [Freiwald and Tsao, 2010].

In humans, the pioneering study by (Kanwisher et al., 1997) described a method for detecting a face-selective area using a functional localizer including faces and non-face objects stimuli. Findings from this study revealed a cluster of voxels in the fusiform gyrus which showed significant responses to faces than to the nonface objects, named as Fusiform face area (FFA) [Kanwisher et al., 1997]. Further studies

showed that two other clusters of voxels also are selective to faces. One area which is located topographically within inferior occipital gyrus is named as OFA [Haxby et al., 1999]. This area was proposed to be involved in the early detection of faces [Haxby et al., 2000]. The other face-selective area is located in the posterior part of the superior temporal sulcus (pSTS) [Hoffman and Haxby, 2000].

Experimental disruption using transcranial magnetic stimulation (TMS) during behavioral performance provided causal evidence for the face specificity of these regions. Studies targeted the right occipital face area (OFA) using TMS showed that this manipulation typically disrupted face perception. However, TMS of neighboring regions did not affect the face processing [Pitcher et al., 2007, Pitcher et al., 2009]; but see [Pitcher et al., 2011]. The similar results were observed by intracranial stimulation of the right OFA [Jonas et al., 2014] and right fusiform gyrus [Jacques and Bruno, 2015, Rangarajan et al., 2014].

In conclusion, all these findings revealed that faces differ from other object categories. Faces elicit different behavior, their processing can be selectively impaired, and comparing to other object categories, they evoke different brain responses.

1.2 Cognitive model of face processing

Bruce & Young proposed a cognitive model for face processing which suggests two distinct streams of processes for identification of faces and recognition of face expression [Bruce and Young, 1986]. The model is shown in figure 1.1.

Behavioral cognitive studies motivate this framework and have shown that recognition of invariant information of faces (e.g. identity) and changeable aspects of faces (e.g. face expressions) are processed independently. Data from normal individuals revealed that judgments of facial expressions do not depend on face identity [Bauer, 1984]. The other study also showed repetition priming enhances the accuracy and the speed of recognition on face perception tasks. However, such priming produces no detectable changes on tasks that involve processing face expression [Ellis et al., 1990].

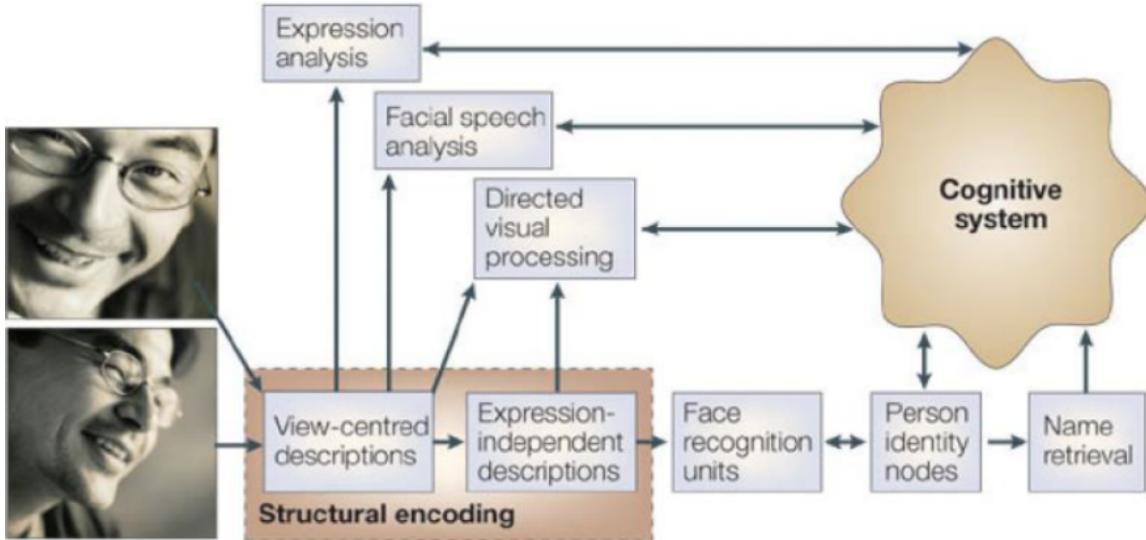


Figure 1.1: The Bruce & Young (1986) model of face processing [Young et al., 1986].

Neuropsychological studies of patients suffering from prosopagnosia also support this division. Specifically, some cases of such patients can not recognize identities without any impairment in facial expression recognition [Tranel et al., 1988].

The first route for identity recognition is proposed to comprises of several stages that gradually process more abstract information. First, faces were represented pictorially and similar to its original image. However, this level of representation is only sufficient for recognizing the similar image [Bruce, 1982] but not provide enough information for actual face recognition which includes different changes such as viewing angle, hairstyle, or facial expression. For efficient face recognition, it was needed to a more abstract level of representation which is named as the structural code. Such representation is proposed to encode faces invariantly across features which is constant across different images of the same identity. It was proposed that this encoded representation is maintained in face recognition units (FRUs) and then projected to corresponding person identity nodes (PINs). Additionally, retrieval of associated person knowledge with each of faces (such as names and other semantic information) is retrievable by activating this PINs [Weibert, 2016].

To sum up, Bruce & young cognitive model suggests differential processing of face identity and changeable aspects such as expressions. The identity representation gradually becomes more abstract and provide necessary information for recognition across different images. This model did not incorporate the neuroanatomical basis for its separate components, because the model was proposed when the sources of information about the neural basis of cognitive function were only limited to monkey electrophysiology and human and monkey lesion studies [Calder and Young, 2005, Young and Bruce, 2011]. However, the next neuroimaging studies provided more neuroanatomical information for face processing. In the next sections, we will introduce concepts which was proposed by these studies and will explain the Haxbys model which was proposed based on underlying cognitive and neural findings.

1.3 Neural model of face processing

Based on early neuroimaging studies and evoked potential research, Haxby and colleagues proposed a model for the human neural systems that mediate face perception [Haxby et al., 2000]. This model shares some aspects with Bruce and youngs cognitive model. The model has a branching structure which represents changeable aspects of faces distinctly from the identity information. The model also has a hierarchical framework comprising a core system for visual analysis of faces and a distinct extended system for processing the personal knowledge attached to each face.

1.3.1 Core system of face processing

The original model proposed that the core system is consisting of three distinct areas in the ventral cortex including orbitofrontal cortex (OFA), fusiform face area (FFA) and posterior superior temporal sulcus (PSTS) which carries out visual information of faces.

In the Haxbys model analogs to Bruce and Youngs model, the information of detected faces in OFA is then passed to two distinct pathways. The first pathway,

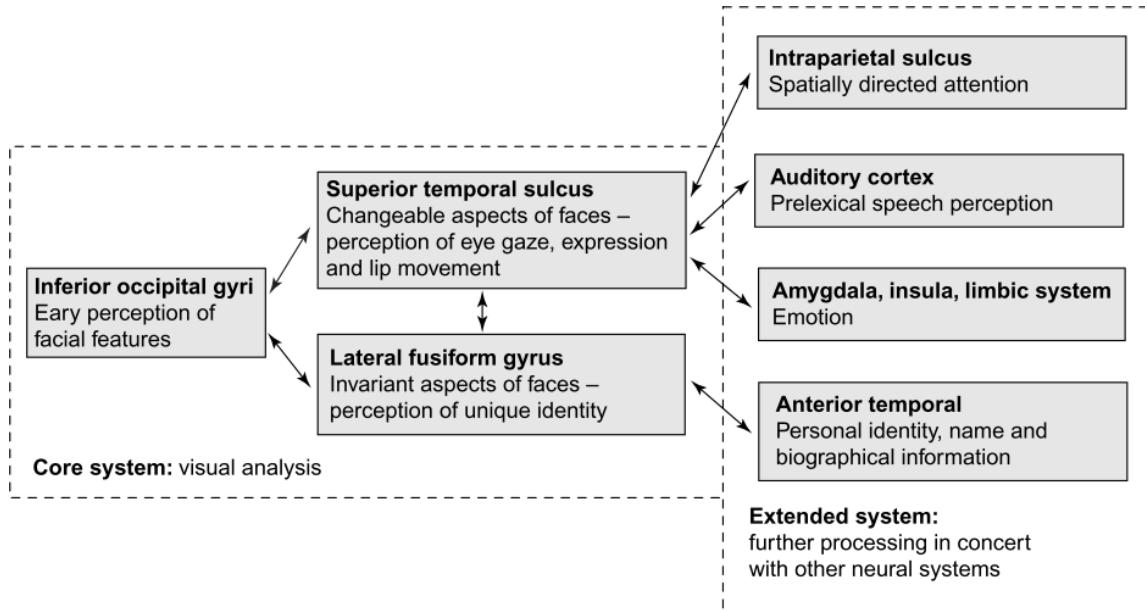


Figure 1.2: The neural model of face processing proposed by [Haxby et al., 2000]. The model included two distinct divisions: Core system and extended system.

which projects dorsally to the STS, processes changeable aspects which are important for social communications, such as facial expressions, eye gaze detection, and lip movements [Allison et al., 2000]. The other pathway, which projects ventrally to the FFA, is involved in processing invariant aspects of faces such as identity and gender.

1.3.2 Extended system of face processing

Haxby's model also proposed that information of faces is also processed by another distributed network of areas named as the extended face network. They suggested that these areas are not dedicated to the processing of visual information. Instead, these regions extract different types of information from faces. This hypothesis was based on observed connections to the core areas.

In the original model, the extended system included neural structures within intraparietal sulcus (IPS), the auditory cortex, amygdala, limbic system, and anterior

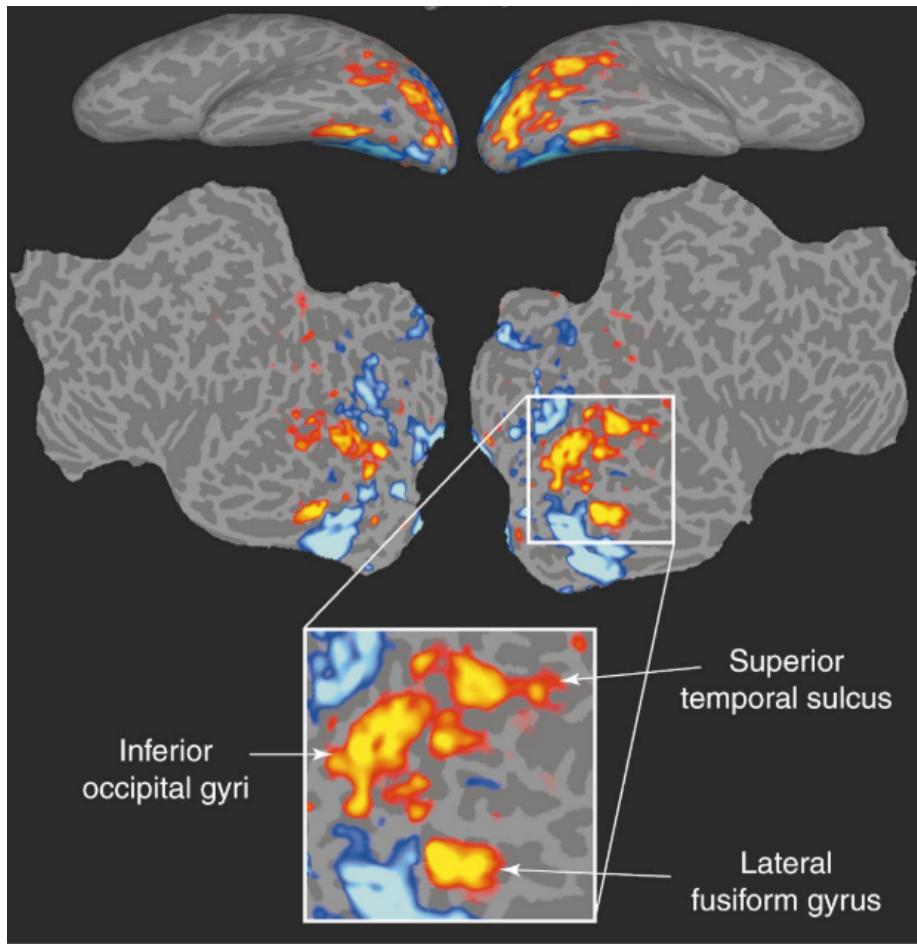


Figure 1.3: In the [Haxby et al., 2000] original neural model of face processing, core system included the OFA, FFA and pSTS.

temporal lobe (ATL). Specifically, the model proposed that IPS which has interconnections with pSTS provides the means to direct attention according to the gaze direction [Puce et al., 1998]. The auditory cortex is another neural element that is similarly interconnected to pSTS and is involved with speech perception. The model also included the medial prefrontal cortex (mPFC) and temporoparietal junction (TPJ) associating with Theory of Mind [Frith and Frith, 2012, Saxe and Kanwisher, 2003], precuneus for information retrieval from long term memory [Burgess et al., 2001, Fletcher et al., 1995, Gorno-Tempini et al., 1998, Ishai et al., 2000, Leveroni et al.,

2000], and amygdala which process emotional information from faces [Adolphs et al., 1998].

ATL is another neural structure that is linked with FFA and was proposed to be involved in processing semantic information of faces.

1.3.3 Revisions to neural model

The core system of Haxby's model included three face-selective areas (OFA, FFA, and pSTS). However, the other studies reported additional regions which were similarly responsive to faces.

1.3.3.1 Anterior temporal lobe (ATL) face area

Neuropsychological studies reported cases with prosopagnosia resulting from lesions to the ATL [Barton et al., 2002]. Neuro-imaging studies using Positron emission tomography (PET) also revealed that ATL was responsive to faces [Sergent et al., 1992]. Despite the low signal-to-noise ratio of fMRI data within this region, previous research could also detect and report a face-selective area in the ATL (named anterior temporal face patch - ATFP) [Rajimehr et al., 2009, Tsao et al., 2008]. Further support for the role of ATL for face processing comes from human studies that used face localizer with emotional or familiar face stimuli [Avidan et al., 2014], coronal scanning [Axelrod and Yovel, 2013], and dynamic emotional faces [Yang et al., 2016]. Additionally, evidence from multivoxel pattern analysis (MVPA) which revealed decodable information of face identities within this region confirm the role of this area in face processing [Anzellotti et al., 2014, Kriegeskorte et al., 2007, Nestor et al., 2011]. These findings suggested that a critical face area is located in ATL which could be considered in the ventral pathway of the core system [Duchaine and Yovel, 2015].

1.3.3.2 Anterior superior temporal sulcus (aSTS) face area

While findings of studies using static localizer rarely detected an activation in the neural structures located in the anterior superior sulcus, those used dynamic localizer showed that this area modulated selectively by faces [Pitcher et al., 2011, Fox et al., 2009]. The strong response of anterior STS to dynamic faces provided evidence for the hypothesis that previous methods of face selectivity detection have a limited and maybe even inaccurate view of its role in face processing [Duchaine and Yovel, 2015]. Additionally, the results from studies using static faces but with more sensitive methods of analysis such as adaptation experiment or MVPA analysis demonstrated also that this region contained information of gaze direction [Calder et al., 2007]. The sensitivity of this area to gaze direction was corroborated by the result of single-cell recording studies in macaque aSTS that were responsive to particular gaze directions [Perrett et al., 1985]. The discussed findings suggested that aSTS was a face selective area that could be included to the dorsal pathway of the core system [Duchaine and Yovel, 2015].

1.3.3.3 Inferior frontal gyrus (IFG) face area

The earliest evidence of face-selective area in the prefrontal cortex are based on single-cell recording of the macaque monkey brain [Ó Scalaidhe et al., 1997]. Similar to temporal face-selective areas these neurons revealed weak responses to objects but responded strongly when presented with faces. Neuro-imaging studies also reported three face areas in the prefrontal cortex of macaque brain [Tsao et al., 2008].

In line with the evidence in macaque monkeys, several human neuro-imaging studies reported face-selective activation in the lateral prefrontal cortex [Rajimehr and Tootell, 2008, Chan and Downing, 2011, Chan, 2013]. Studies using dynamic face localizer showed that the prefrontal face area was more sensitive to dynamic faces than the static ones. This finding suggested that this area maybe associated with the neural structures that process dynamic faces in the STS [Fox et al., 2009, Pitcher et al., 2011].

In a study, they showed that experimental disruption of a patient's right PFC

with TMS resulted in face-specific visual illusion and hallucination [Vignal et al., 2000]. Another evidence for the role of frontal area for face processing came from study of the same subject after the right anterior lateral prefrontal resection. This lesion led to the selective deficit for fearful face recognition [Moscovitch et al., 1997].

Chan & Downing tried to investigate the functional role of this area in face recognition. They demonstrated that eyes alone evoked greater responses than whole faces. Thus, they speculated that this area might be associated with the processing of gaze information [Chan and Downing, 2011].

Taken together, Duchaine & Yovel suggested that the dorsal pathway of the core system rather than pSTS consisted of the IFG face area ([Duchaine and Yovel, 2015]).

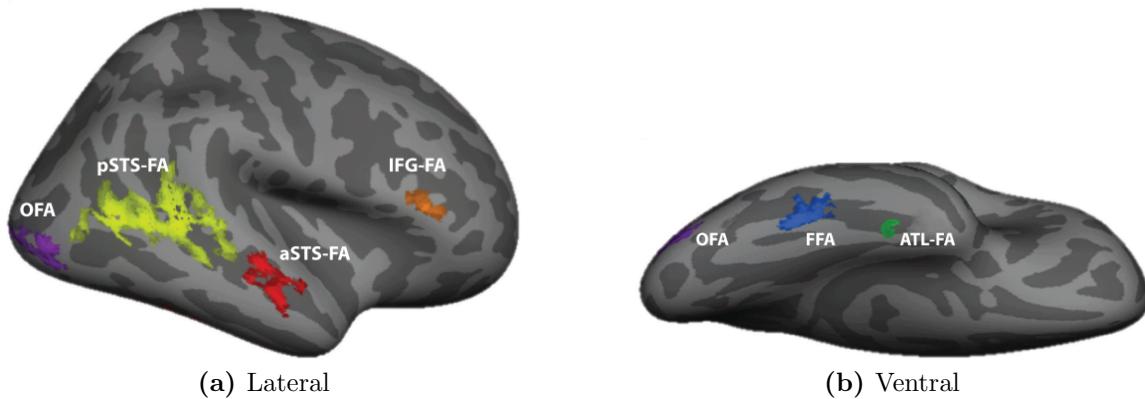


Figure 1.4: Extension of core system face-selective areas. While original Haxby's model included OFA, FFA, and pSTS in the core system, recent research has identified additional face-preferential regions in the anterior temporal and right inferior frontal cortices, considered as components of the core system [Guntupalli et al., 2017, Duchaine and Yovel, 2015].

1.4 Familiar and unfamiliar face processing similarity and differences

The most important goal of face processing for social species is recognition of familiar faces. However, most of previous neuropsychological and neuroanatomical

studies on face processing use unfamiliar face stimuli. Using such stimuli provided the chance to concentrate on visual analysis of faces and diminish the effect of other streams of information such as semantic or emotional information which are typically associated with familiar faces [Gobbini and Haxby, 2007]. While lots of the basic phenomena of face processing are common across familiar and unfamiliar faces, they differ in various aspects.

1.4.1 Perceptual information

Behavioral studies have shown that some of the basic properties of face processing, such as the Thatcher illusion effect, face inversion effect, and the composite face effect are common across familiar and unfamiliar faces [Johnston and Edmonds, 2009]. Findings from the other studies also revealed that recognition of faces was impaired by contrast negation for both familiar and Unfamiliar faces [Freiwald et al., 2016, Bruce et al., 1987, Johnston and Edmonds, 2009]. Some neuropsychological evidence from prosopagnosic individuals also revealed that the difficulty in recognizing faces is common for both familiar and unfamiliar faces [Dalrymple et al., 2011, Duchaine et al., 2007]. Despite these common characteristics, there is a clear discrepancy between these two distinct categories of faces.

It has been shown that the accuracy of visual discrimination between two images of faces, which depict the same face, are significantly higher for familiar than unfamiliar faces [Davies-Thompson et al., 2009, Jenkins et al., 2011]. Specifically, making judgment about similarity of two images of unfamiliar faces associates with more mistakes. Differences in orientation, viewpoint, or lightening, affect the accuracy of unfamiliar face matching [Hancock et al., 2000]. By contrast, recognition of familiar faces is highly accurate even for low-quality images with lots of variations [Natu and O'Toole, 2011].

Bruce & Young proposed faces are first encoded on pictorial code. This represen-

tation is sufficient for recognition of familiar or unfamiliar faces from identical images. However, it is not sufficient for recognition of faces with different image variations. In this model the source of invariance for familiar face recognition was attributed to distinct kind of representation named as structural code [Bruce and Young, 1986] that in contrary to pictorial code is more abstract and less susceptible to Image variations.

Neuropsychological studies also provide evidence for differential neural processing of familiar and unfamiliar faces [Benton, 1980]. For example, while a neuropsychological patient was unable to recognize familiar faces yet was able to match unfamiliar faces. The inverse pattern also observed in another patient, who was unable to match unfamiliar faces yet was able to recognize familiar faces [Malone et al., 1982]. This double dissociation suggested that there might exist a differential neural processing for familiar and unfamiliar faces.

1.4.2 Conceptual information

Familiar faces and unfamiliar faces not only have qualitative differences in perceptual information, but also differ with respect to associated context, person knowledge, personal relationships, and emotional information. This additional information can enhance face recognition. For instance, in a behavioral experiment, Curtois & Mueller showed that participants can better remember a face when they were asked to judge their personality than when they made just perceptual judgment [Courtois and Mueller, 1979]. The same effect was reported in another study that associated faces with unique labels [McGugin et al., 2011]. In addition, the other study revealed our superior ability to recognize faces associated with semantic information comparing to the condition following to exposure to rich visual information of faces from multiple views [Schwartz and Yovel, 2016].

These findings suggest that social, emotional, and higher-level categorizations all contribute in face recognition.

1.5 Different types of familiarity

The concept of familiarity itself includes different categories including personally familiar, visually familiar, experimentally familiarized, and famous faces. While, numerous studies with the goal of investigating familiar face processing each used one of these categories and ignored their differences, the results were inconsistent [Gobbini and Haxby, 2007].

In some studies, familiarity associated with personally familiar faces [Bartels and Zeki, 2000, Gobbini et al., 2004, Leibenluft et al., 2004, Nakamura et al., 2000, Visconti Di Oleggio Castello et al., 2017a, Ramon and Gobbini, 2018], in others the familiar stimuli included individuals known through the media [Gorno-Tempini et al., 1998, Leveroni et al., 2000, Sergent et al., 1992]) and other cases investigated the effect of experimentally familiarized faces [Dubois et al., 1999, Leveroni et al., 2000, Rossion et al., 2001].

Some studies systematically explored the differences among different types of familiarity [Sugiura et al., 2011, Taylor et al., 2009]. However, the number of these studies is still limited and thus it's a great obstacle to reveal their differences.

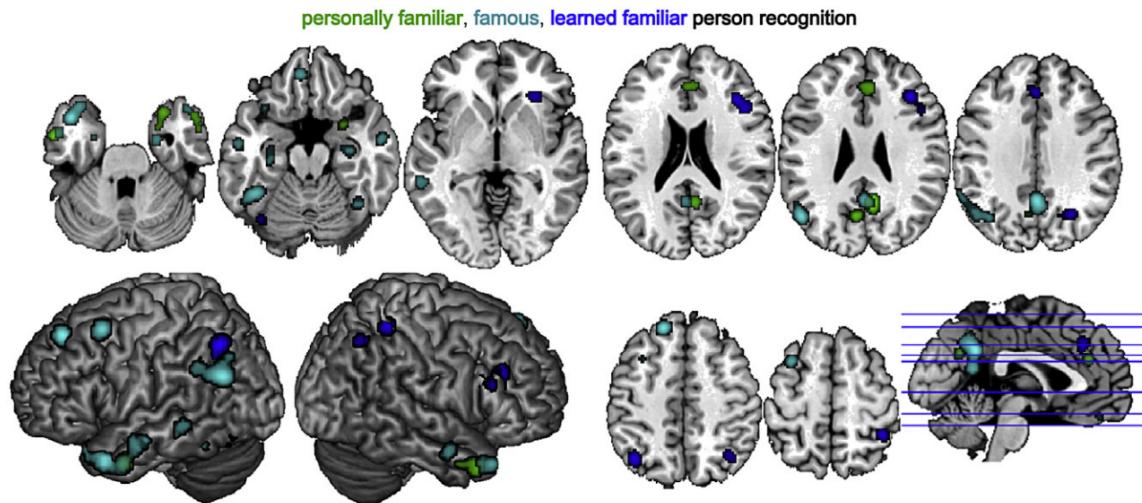


Figure 1.5: Brain regions involved in recognition of different types of familiar faces. These areas identified by a meta-analysis on healthy subjects [Blank et al., 2014a]. Personally familiar (light green), famous (cyan), and learned-familiar (dark blue) persons.

1.6 Neuroimaging evidences for familiar face recognition

The results from functional neuroimaging studies using PET and fMRI have shown that familiar faces strongly modulated a distributed network of brain regions including regions within the core system and extended system of face processing [Ramon and Gobbini, 2018].

1.6.1 Core system

In many studies, brain activity elicited by familiar and unfamiliar faces were compared to localize regions differentiating between the two. In behavioral studies, it has been shown that familiar faces identified in higher speed and precision than unfamiliar faces. Thus, FFA is an area which has been mainly focused by researchers, since it was reported to be involved in processing invariant aspects of faces [Haxby et al., 2000]. However, the results from these studies have not shown consistent differences in the overall strength of activity in response to familiar versus unfamiliar faces in posterior regions of the core system (OFA, FFA, pSTS) [Natu and O'Toole, 2011]. While some studies associated familiarity with decreased neural activity [Rossion et al., 2003], the others reported no relevant changes [Dubois et al., 1999].

Although posterior regions of the core system revealed inconsistent and weak manipulations in response to familiarity attribute, neural structures within ATL emerged in lots of studies. This region exhibited enhanced activity comparing familiar/famous faces versus unfamiliar faces [Gobbini and Haxby, 2007, Gobbini et al., 2004, Ramon et al., 2015], revealed an adaptation response to repetition of familiar faces [Sugiura et al., 2011], and showed sensitivity to association of semantic information to faces [Von Der Heide et al., 2013]. Thus, it was suggested that ATL is a well-suited area to bound perceptual information of faces with semantic knowledge of individuals including their names or biographical information [Collins and Olson, 2014].

1.6.2 Extended system

Familiarity-dependent modulation in areas beyond the core system has been reported in a number of additional regions such as structures within the posterior cingulate cortex (PCC), anterior cingulate cortex (ACC), medial temporal lobe (MTL), hippocampus, and amygdala [Ramon et al., 2015, Weibert et al., 2016].

Posterior cingulate cortex (PCC): The human neuroimaging studies have found that this area is face responsive in perceptual learning paradigm [Leveroni et al., 2000, Gobbini et al., 2004, Maguire et al., 2001, Katanoda et al., 2000, Kosaka et al., 2003, Natu and O'Toole, 2015, Cloutier et al., 2011, Anzellotti and Caramazza, 2016], fMRI-adaptation paradigm [Weibert et al., 2016, Pourtois et al., 2005], visual imagery [Ishai et al., 2000], functional localizers with dynamic facial stimuli [Fox et al., 2009], and functional localizers with a working memory task [Anzellotti and Caramazza, 2017]. This region also revealed stronger responses to different types of familiar faces including: self face [Kircher et al., 2000, Platek et al., 2008, Sugiura, 2015], personally familiar faces [Sugiura et al., 2009a, Leibenluft et al., 2004, Pierce et al., 2004, Gobbini et al., 2004, Lee et al., 2013, Blank et al., 2014b] and famous faces [Leveroni et al., 2000, Eger et al., 2005, Bernard et al., 2004].

Anterior cingulate cortex (ACC): Prior studies have suggested that personally familiar faces spontaneously activate representations of person knowledge in the ACC [Cloutier et al., 2011, Gobbini and Haxby, 2007, Todorov et al., 2007]. In a recent meta-analysis by Blank and colleagues it was shown that personal familiar face identification activated extended brain network including clusters in the right anterior cingulate cortex. Furthermore, famous person identification also activated anterior cingulate cortex but in the left hemisphere.

Hippocampus: Previous research comparing activity of different types of familiar faces including famous or personally familiar faces with unfamiliar faces showed

that the extent of hippocampal activity was higher for familiar faces than unfamiliar faces [Elfgren et al., 2006, Leveroni et al., 2000, Pierce et al., 2004, Sergent et al., 1992]. Quiroga et al. also showed that so-called concept neurons of this area activated by very different pictures of a familiar individual, its name written in letters, and even faces associated with it. Thus it was suggested that this area encode abstract information of different identities [Quiroga et al., 2005]. Hence, the hippocampus might represent some type of person knowledge including associated semantic information with faces, such as the name or profession.

Amygdala & insula: While the activation within the other discussed area was stronger for different types of familiar faces than unfamiliar faces, the response in the amygdala and insula were weaker. Personally familiar faces evoked weaker responses than famous faces and famous faces evoked weaker responses than unfamiliar faces. Thus, these areas which are associated with emotional response, showed weaker activation when faces associated with more emotion [Gobbini et al., 2004, Gobbini and Haxby, 2006], but see [Leibenluft et al., 2004].

1.7 Thesis outline

We designed three fMRI experiments to address the main question of this study. These experiments had similarities and differences with regard to paradigm, data acquisition, and scanning parameters. Specifically, we gradually optimized the parameters of experiments to overcome the weaknesses of designs and achieve more reliable results.

Chapter 2 & 3 provide details of the two preliminary experiments (experiment 2 & 3).

Chapter 4 summarizes methods and results of the most optimized design (experiment 3) to address the main questions of this study.

Chapter 5 provides a discussion of the experiment 3 results and presents possibilities for future work.

Chapter 2

First experiment

2.1 Methods

2.1.1 Subjects

Fourteen adult subjects with normal vision participated in the imaging sessions. Collected data from four of these participants were excluded from the analysis due to large head movements (more than a voxel) and technical problems. Therefore, data of 10 subjects were analyzed (6 males, 4 females, mean age = 27.4 years, std = 4.45 years). Informed written consent was obtained from each subject. All experimental procedures conformed to NIH guidelines.

2.1.2 Visual stimuli

Stimuli were images of two main categories of faces: familiar faces and unfamiliar faces (Figure 2.1A). The familiar face category itself was composed of 4 subcategories: cinema, music, politics, and sport. Familiar faces of each subcategory were selected on the basis of high ratings of face familiarity. Unfamiliar faces were selected from celebrities that were unknown to the subjects. In total, 76 different faces (4×16 familiar + 12 unfamiliar) were selected. In politics and sport categories,

all the faces were male. In cinema and music categories, half of the faces were female.

All face images, collected from the web, were edited to be in grayscale format, frontal view, approximately equal size (9 degrees of visual angle; image size: 500×500 pixels), and a natural hairstyle. The background of faces was set to be black. A red fixation point (radius = 10 pixels) was superimposed at the center of stimuli.

2.1.3 Experimental procedures

Familiarity of each subject with the faces was tested before the scan session. Only subjects who were able to categorize at least 12 faces, out of 16 faces in each category of familiar faces, participated in the study. Thus, for each subject, 60 images (4×12 familiar faces + 12 unfamiliar faces) were used as visual stimuli.

Before scanning session, subjects were presented with all the 60 face stimuli and were instructed to make a judgment about the category of each stimulus. Subjects recorded their judgment by pressing one of the five buttons associated with the five fingers of their dominant hand.

After scanning session, the familiarity of subjects with face stimuli was quantitatively assessed through an online survey/questionnaire (Figure 6.1).

During the imaging experiment, subjects were asked to fixate on a fixation point and perform a categorization task. A response box with five buttons was used for recording the responses of subjects. The stimuli were displayed on a black background and projected onto a screen. Subjects viewed the screen via a mounted mirror over the head coil.

Each session consisted of 10 functional runs. A fast event-related design was used for presenting the stimuli in each run. The sequence of stimuli contained 90 trials (60 face trials + 30 null trials). The null stimulus was a fixation point on a blank

A

Familiar				Unfamiliar
Cinema	Music	Politics	Sport	
				

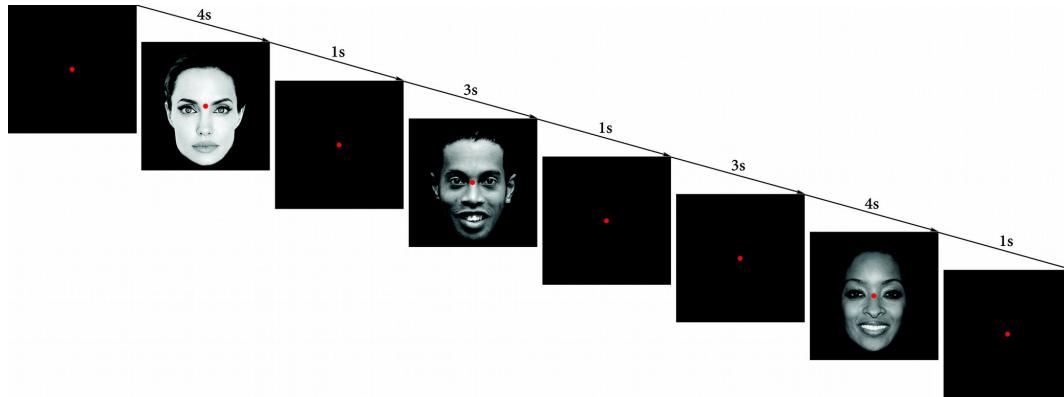
B

Figure 2.1: Face stimuli and task design. **A**, Stimuli were from two main categories of faces: familiar and unfamiliar. The familiar face category itself consisted of four subcategories: cinema, music, politics, and sport. A red fixation point was positioned at the center of each image. **B**, Fast event-related design. Trials, either stimulus or null, were presented randomly in the run sequence. Each trial consisted of 1-second stimulus or blank event followed by 3-second fixation event.

background. The first 6 and the last 4 trials of the sequence were always nulls. The other trials were presented randomly in the sequence. Each trial, either stimulus or null, was presented for one second followed by a 3-second fixation event. Different stimulus sequences were used across runs. Stimulus sequences were generated using Psychtoolbox-3 [Brainard, 1997]. An example of the functional run is shown in Figure 2.1B.

2.1.4 Data acquisition

Data were collected using a Siemens 3T Tim Trio MRI system with a 32-channel head coil at Medical Imaging Center of Imam Khomeini Hospital Complex (Tehran, Iran).

For each subject, a whole-brain anatomical scan was acquired using T1-weighted MP-RAGE sequence (TR = 1.8 s, TE = 3.44 ms, isotropic voxel size = $1 \times 1 \times 1$ mm 3 , 256 sagittal slices, flip angle = 7°).

The functional scans were based on a GE-EPI sequence (TR = 2 s, TE = 30 ms, voxel size = $3 \times 3 \times 4$ mm 3 , 30 semi-axial slices, flip angle = 90°). The slices were obtained in an even-odd interleaved order.

2.2 Data analysis

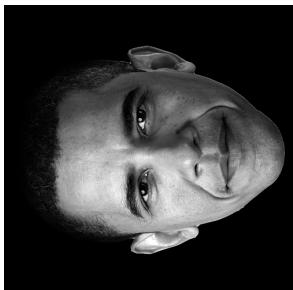
Functional and anatomical data preprocessing and voxel-wise analysis were done using Freesurfer and FS-FAST (<http://surfer.nmr.mgh.harvard.edu/>).

2.2.1 Preprocessing

For each subject, the cortical surfaces were computationally reconstructed by analyzing the anatomical T1 images.

Functional data were first skull-stripped using FSL's brain extraction tool to generate brain mask [Smith, 2002]. Then using the middle time-point of each run as the reference, the functional images were aligned using AFNI's motion correction algorithm [Cox, 1996]. For each subject, only runs with less than 2 mm motion in any direction were included in the fMRI analyses. In the next step, intensity values of all voxels were converted to a standard intensity scale. The mean intensity of

Behavioral assessment of familiarity of subjects with face stimuli

Name		* Email address
Please answer the questions. Attention: For answering just rely on your knowledge and don't look for it in the other sources.		
Stimulus 1		
Choose the category of above stimulus: Mark only one oval: <input type="radio"/> Cinema <input checked="" type="radio"/> Music <input type="radio"/> Politics <input type="radio"/> Sport <input type="radio"/> Unfamiliar		

		Confusion Matrix				
		Cinema	Music	Politics	Sport	Unfamiliar
Response Class	Cinema	19.8% 119	0.0% 0	0.0% 0	0.0% 0	0.3% 2
	Music	0.2% 1	19.7% 118	0.0% 0	0.0% 0	0.7% 4
Response Class	Politics	0.0% 0	0.0% 0	19.8% 119	0.0% 0	0.2% 1
	Sport	0.0% 0	0.0% 0	0.0% 0	20.0% 120	0.3% 2
Response Class	Unfamiliar	0.0% 0	0.3% 2	0.2% 1	0.0% 0	18.5% 111
		0.8% 99.2%	1.7% 98.3%	0.8% 99.2%	0.0% 100%	7.5% 92.5%
		Cinema	Music	Politics	Sport	Unfamiliar

Figure 2.2: Behavioral assessment of familiarity. **Left panel**, Each subject completed an online survey after scan session. In the survey, 60 face images were presented to the subjects, and they indicated which category (out of 5 categories) each image belonged to. **Right panel**, Stimulus-response confusion matrix. Data from all subjects were pooled (total number of stimuli/responses = $60 \times 10 = 600$). In the absence of any confusion, a diagonal element (a dark green cell) would have the value of 120 ($120/600 = 20\%$).

all voxels across all time-points inside the eroded brain mask was computed. Then, the intensity value of each voxel at each time-point was divided by the mean intensity and multiplied by 100. The functional volumes were rigidly coregistered to the same-subject anatomical volumes using boundary-based registration method. After registration, the functional data were resampled/projected on an average cortical surface (fsaverage).

Time-series modeling was done using general linear model (GLM) considering hemodynamic response overlap of events in rapid event-related designs [Friston et al., 1995, Bar, 2004]. The time-series of each run was modeled as a sum of weighted response variables plus an error term. Response variables included task regressors (i.e. regressors for stimulus conditions) and nuisance regressors (three head motion parameters, mean confound, linear and quadratic trends, and time-point exclusion). The first four time-points of each run were discarded to avoid inhomogeneity effects of the magnetic field. Task regressors were modeled as a boxcar function convolved with a canonical hemodynamic response function. The time-series were whitened by removing temporal autocorrelations.

2.2.2 ROI localization

Familiar face-selective regions were localized using a two-stage univariate analysis in the common anatomical space (fsaverage). First in the subject-level analysis, a single model was estimated for time-series of each voxel along a session. In this model, time-series of all runs within a session were concatenated, and the design matrix was composed of task regressors and run-related nuisance regressors. Subject-level statistical maps were computed by pairwise t-test comparisons between familiar and unfamiliar face conditions. The resulting statistical maps were spatially smoothed using a Gaussian filter (full width at half maximum = 6 mm). Then in the group-level analysis, familiar face-selective regions were defined by mixed-effects averaging of individual subjects' maps. The group-average maps were thresholded at p value

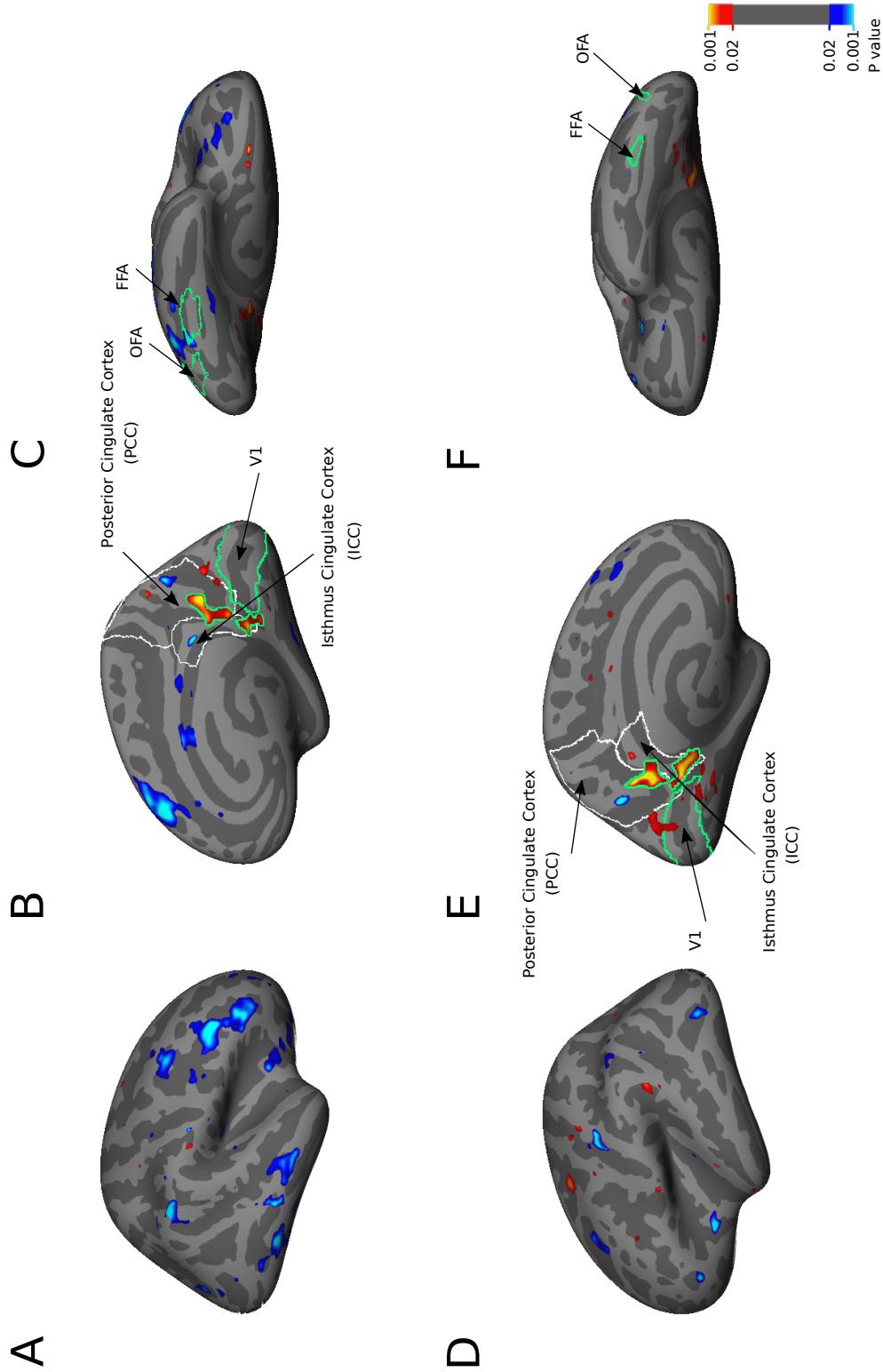


Figure 2.3: Whole-brain univariate analysis. The maps show significant ($p < 0.02$, t-test) activations for familiar (red/yellow) versus unfamiliar (blue/cyan) faces in right (A-C) and left (D-F) hemispheres. The activation maps are based on mixed-effects group-average of data from 10 subjects, and are displayed on lateral (A,D), medial (B,E), and ventral (C,F) views of an inflated cortical surface ('saverage' surface). The familiarity activated two distinct cortical regions in medial occipital cortex in both hemispheres. These regions were named posterior cingulate cortex (PCC) and isthmus cingulate cortex (ICC). FFA, OFA, and V1 labels are also shown on the cortical surface of both hemispheres.

$|>0.02$ (uncorrected threshold). The maps were intersected with parcels from an anatomical parcellation atlas [Desikan et al., 2006]. The functional activation within precuneus cortex was defined as PCC, and the activation within isthmus cingulate cortex was defined as ICC.

General face-selective regions were derived from an average functional atlas [Julian et al., 2012]. These regions included fusiform face area (FFA) and occipital face area (OFA). As a control region, V1 was defined using an automatic V1 localization in Freesurfer [Hinds et al., 2008].

2.2.3 Pattern information analysis

Two different methods of pattern similarity analysis were used to reveal fine-grained categorical information of familiar face subcategories in the familiar face-selective and general face-selective regions.

2.2.4 Classification distance for similarity analysis

ROIs for pattern analysis: Each surface-based ROI mask, computed using univariate analysis in the common anatomical space, was mapped onto native space of each subject. Since surface-based masks contained vertices with redundant information, volume-based voxels corresponding to those vertices were selected.

Time-series analysis: This analysis was similar to GLM in the subject-level univariate analysis except that time-series modeling was done in the voxel space and separately for each run.

Pattern generation: For each condition, beta values were estimated for all voxels within each ROI mask and were concatenated to form a vector. To prevent loss of fine-grained pattern information, no spatial smoothing was applied, and data were analyzed in individual subjects. In each subject, data from two hemispheres were combined.

Normalization: Beta values were normalized by subtracting the mean across con-

ditions, to remove common response pattern ??.

Dimension reduction: Principal component analysis (PCA) was performed to extract a more compact representation of data. Using PCA, zero-centered functional data were projected from the high-dimensional voxel space into a low-dimensional (15-dimensional) feature space without loss of information.

Data splitting: Functional data were splitted into two independent sets: training and test set. The two sets were selected from different runs that had independent stimulus sequences and independent preprocessing. Efficient splitting of data was done by a leave-one-run-out cross-validation method.

Training the classifier: To investigate whether patterns of activity in each ROI mask could discriminate four different conditions (cinema, music, politics, and sport categories), six pairwise classifiers were trained (cinema vs. music, cinema vs. politics, and so on). Support vector machine (SVM) with a linear kernel was used for training the classifiers. SVM has several advantages over other classifiers; it does not depend on the distribution of training data and it can handle limited data in high-dimensional spaces [Allefeld, 2015].

Testing the classifier: Decision boundaries obtained from training the classifiers were applied to an independent test set (a single run), so that the generalizability of the decision boundary could be evaluated. By this procedure, circular inferences and overfitting would be avoided.

Classification performance: The classification performance was defined as an average performance across all repetitions of cross-validation. Finally, to determine whether significant information is encoded for different classes of data, accuracy of each classifier was compared to chance accuracy (50% performance) using t-test analysis.

Decoding matrix: All pairwise classification performance values were converted to error values and were shown in a decoding matrix.

2.2.5 Correlation distance for similarity analysis

The initial steps of this method (ROI selection, time-series analysis, and pattern generation) were similar to the procedure described for the classification method.

Data splitting: All runs of each subject were splitted into two complimentary sets of runs. Within each set and for each condition, beta values were normalized (mean-subtracted) and then averaged across runs.

Similarity analysis: Pairwise correlation between patterns of activity was computed for all subcategories of familiar faces. To determine whether there was any discriminative information in the patterns of activity, between-category correlations were computed and compared to within-category correlations [Roth and Zohary, 2015]. For instance, the similarity between patterns of activity for music and sport faces was computed by estimating within-category correlations, averaging them, and subtracting it from the correlation between these two categories.

Generalizing similarity values: To avoid arbitrariness in data splitting, the correlation distance was calculated for all possible permutations of run splitting (252 permutations for 10 runs). The correlation values were averaged across all permutations.

Correlation matrix: All pairwise correlation values were shown in a correlation matrix.

2.2.6 Test for low-level feature similarity

To make sure that patterns were discriminated based on categorical information, and not physical similarity of stimuli (low-level features), an additional analysis was performed. In this analysis, faces were first segmented from the background, then low-level features (pixel-wise mean luminance and RMS contrast) were computed for all face stimuli. The values were used as external regressors in the GLM time-series modeling after normalizing and convolving with a canonical hemodynamic response function. To avoid the collinearity problem [Monti, 2011], a two-step method was used for time-series modeling. In the first step, the time-series were modeled using low-level feature variables and nuisance variables. In the second step, the residuals extracted from the first step were modeled using the category variable.

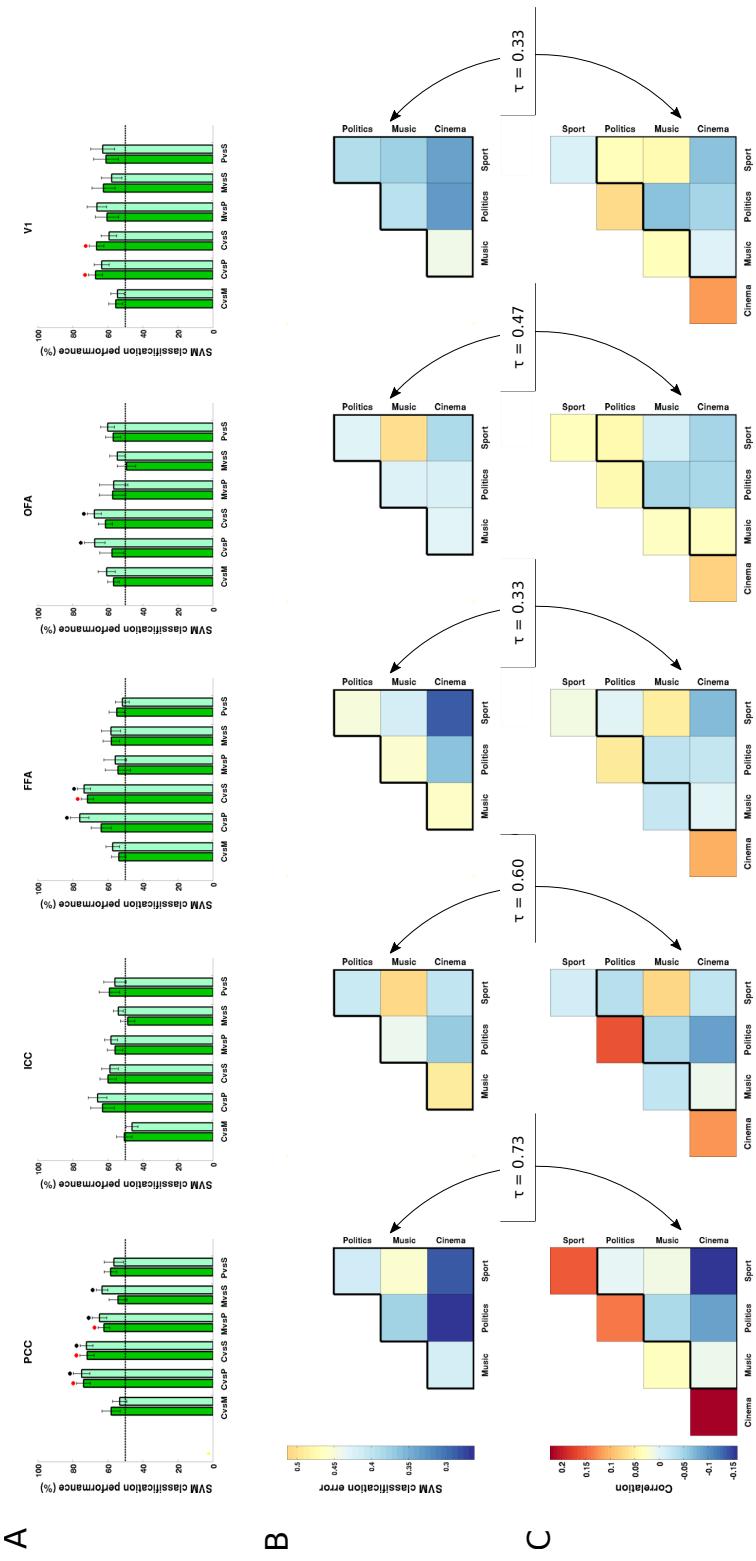


Figure 2.4: ROI-based multivariate pattern analysis. From left to right, graphs depict results of similarity analysis for different ROIs including PCC, ICC, FFA, OFA, and V1. **A**, Pairwise discrimination rates based on SVM classification analysis. C, M, P, and S correspond to cinema, music, politics, and sport categories, respectively. Dark green and light green bars show results of classification analysis without and with including the regressors of low-level features, respectively. Red and black dots indicate FDR-corrected significant performance for dark green and light green bars, respectively. Dashed black line indicates the chance level of 50%. Error bars denote the standard error of the mean calculated across subjects. **B**, Decoding matrix. Pairwise classification performance values were converted to error values and were shown in a decoding matrix. **C**, Similarity analysis based on correlation distance between patterns of activity. The correlation matrix is an average matrix across subjects. The color scale bar represents Pearson correlation coefficient values. Within-category correlations were subtracted from between-category correlations before computing Kendall's Tau correlation between decoding matrix in **B** and off-diagonal elements of correlation matrix in **C**.

2.2.7 Surface-based searchlight

Surface-based searchlight analysis provided the means for pattern localization. This analysis involved several steps which are explained clearly below.

First, the cortical surface was extracted by Freesurfer. Then, A 2-dimensional disk with a specific radius were defined around each point/vertex on the cortical surface. In this level, vertices were sampled according to the distance along the cortical surface considering the surface curvature [Chen et al., 2010]. Then for pattern extraction from functional image using the provided 2-dimensional disc structure, set of vertices were projected to the functional image space. Thus, the functional image was coregistered to the T1-weighted image which was used for surface reconstruction. Because the surface meshes created in the tessellation step of the surface reconstruction have fine spatial resolution, sampling information of all vertices within each mask would result in redundant features for pattern analysis [Oosterhof et al., 2011]. Hence, to disallow this multiple occurrences of the same information, the masks were mapped to the native space and all voxels intersecting the mapped disk were sampled. Then estimated beta values of those voxels were concatenated to generate the response patterns for face categories. To quantify amount of categorical information in each mask we used a category discriminability index (CDI). The CDI metric was defined as the average of within-condition pattern correlations (diagonal elements of correlation matrix) minus the average of between-condition pattern correlations (off-diagonal elements of correlation matrix). Finally, a map of regions with highest categorical information was obtained. To evaluate significance of the categorical information, estimates of all subjects were combined to perform random-effects group-level statistical analysis using t-test. To correct for multiple comparisons, the Benjamini-Hochberg procedure for controlling the false discovery rate was used [Benjamini and Hochberg, 1995].

To overcome computational burden of searchlight analysis for all regions/disks around cortical vertices, a cortical subsampling procedure was designed which is explained bellow. The surfaces were graphs from vertices and faces. Each face interconnected 4 adjacent vertices with weighted edges. Based on this weighted representation and

information of vertices corresponding to each face, adjacent vertices belonging to the same face and closer than 2mm were excluded. Figure 2.5 illustrated the sub-sampled surface.

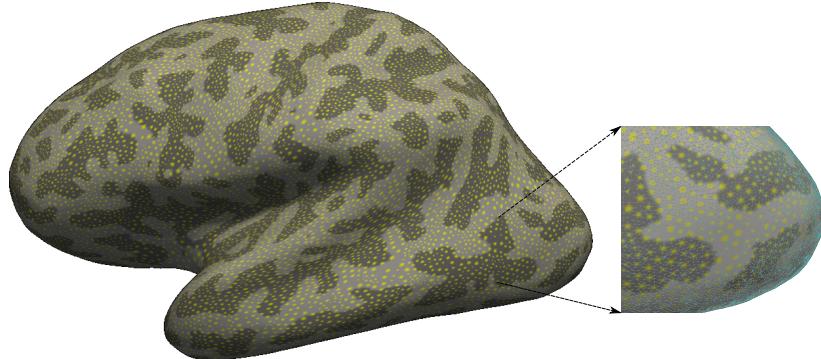


Figure 2.5: Surface sub-sampling.

2.3 Results

2.3.1 Behavioral assessment of familiarity

In a quantitative test, subjects showed a high performance in recognizing face categories (overall performance = 97.8%, Figure 6.1). The confusion matrix demonstrated that subjects were highly accurate in recognizing cinema, politics, and sport categories (performance $\geq 98\%$), while they had few errors in recognizing music and unfamiliar faces.

2.3.2 Univariate analysis

Group-level analysis for the contrast between familiar faces versus unfamiliar faces showed a higher response to familiar faces in posterior cingulate cortex (PCC) (Figure 2.3). This result is consistent with previous findings on selectivity for familiarity in PCC [Gobbini et al., 2004, Leveroni et al., 2000]. In addition to PCC, a

region within isthmus cingulate cortex (ICC) was also responsive for familiar faces (Figure 2.3).

Unfamiliar faces produced a higher activation mainly in inferior frontal sulcus in right hemisphere (Figure 2.3). This region has been reported to be a part of face-processing network [Rajimehr et al., 2009].

In the group-level analysis, general face-selective regions FFA and OFA did not show a significantly higher response to either familiar or unfamiliar faces (Figure 2.3). This result is consistent with the view that familiarity weakly modulates the core system of face processing [Dubois et al., 1999, Leveroni et al., 2000, Gorno-Tempini and Price, 2001, Eger et al., 2005, Ramon et al., 2015]; but see [Sergent et al., 1992, Rossion et al., 2003, Kosaka et al., 2003, Gobbini and Haxby, 2006].

2.3.3 Pattern analysis

Familiar face-selective and general face-selective regions may contain distributed information about familiar face subcategories. To test this, two different methods of multi-voxel pattern analysis were used (Figure 2.4).

Both classification and correlation methods consistently showed that PCC is more sensitive than the other areas to the social category of face stimuli. In PCC, SVM classification performance was significantly higher than chance in three (out of six) pairwise comparisons between face categories ($p < 0.05$, t-test, FDR-corrected). After removing the effects of low-level features, SVM performance increased and became significant in four pairwise comparisons ($p < 0.05$, t-test, FDR-corrected). The correlation analysis also showed that within-category patterns were more similar than between-category patterns (diagonal vs. off-diagonal cells in the correlation matrix). All these results suggest that PCC is sensitive not only to the familiarity of faces but also to their categorical knowledge. Moreover, the patterns of responses in PCC

were not induced by low-level feature similarities.

In contrast, pattern analysis in ICC revealed no categorical information. This result implies that ICC just carries modulatory effects of familiarity (as shown in the univariate analysis) and it has no involvement in the representation of categorical information.

Categorical information were weakly represented in FFA and OFA. In these two regions, SVM classification performance was significant in two pairwise comparisons only after removing the effects of low-level features ($p < 0.05$, t-test, FDR-corrected). In V1, no categorical information was observed after removing the effects of low-level features ($p > 0.05$, t-test, FDR-corrected).

The relationship between decoding matrix (SVM classification error) and off-diagonal elements of correlation matrix was evaluated using Kendall's Tau rank correlation. Tau correlation coefficient was highest in PCC, suggesting that PCC contains reliable information about face categories.

2.3.4 Searchlight analysis

Previous levels of analysis were focused on investigating representational information of familiar face subcategories in the specific functional ROIs. These ROIs were either localized regions (PCC and ICC) extracted using conventional univariate methods or general face-selective regions (FFA and OFA) derived from a functional atlas. However, representational information could be encoded in a distributed way, with weak or no effect of regional-average activation changes.

In this analysis, using pattern-based whole-brain searchlight analysis [Kriegeskorte et al., 2006] we localized regions where response patterns distinguish between subcategories of familiar faces. Specifically, we used the CDI metric (the difference between the correlation values in diagonal and off-diagonal cells of the correlation matrix).

The searchlight maps from group-level analysis are shown on the inflated surfaces of the right hemispheres in Figure 2.6.

In the right hemisphere, a high amount of categorical information was observed medially in the posterior cingulate cortex which was located posterior and ventral to the obtained area from univariate analysis (PCC). Information of familiar face subcategories also observed significantly in the multiple regions in the lateral surface including the lateral prefrontal cortex (LPFC), precentral gyrus, and postcentral gyrus.

In the left hemisphere, also a significant area was observed medially in the posterior cingulate cortex. However, this area was located anterior to (PCC) which was localized in the familiar versus unfamiliar comparison. A high amount of categorical information also observed in multiple areas within lateral surface including the lateral prefrontal cortex (LPFC), central gyrus, and precentral gyrus.

This analysis revealed no categorical information on the ventral surface for both hemispheres.

2.4 Discussion

The main goal of this experiment was to investigate where in the brain represents information of subcategories of familiar faces. To that end, we presented a set of stimuli from two main categories of familiar and unfamiliar faces. The familiar category itself contained (male/female) faces from 4 subcategories of cinema, music, politics, and sport. We used whole-brain univariate and multivariate searchlight analysis to discover regions representing information of familiar faces and subcategories of familiar faces, respectively. The key finding from these analyses was that regions within posterior cingulate cortex carry information of familiar faces and subcategories of familiar faces.

Previous neuroimaging studies using univariate analysis showed that information of familiar faces was represented in the posterior cingulate cortex ([Gobbini et al., 2004]). In this study, we also found a significant activity in the PCC replicating pre-

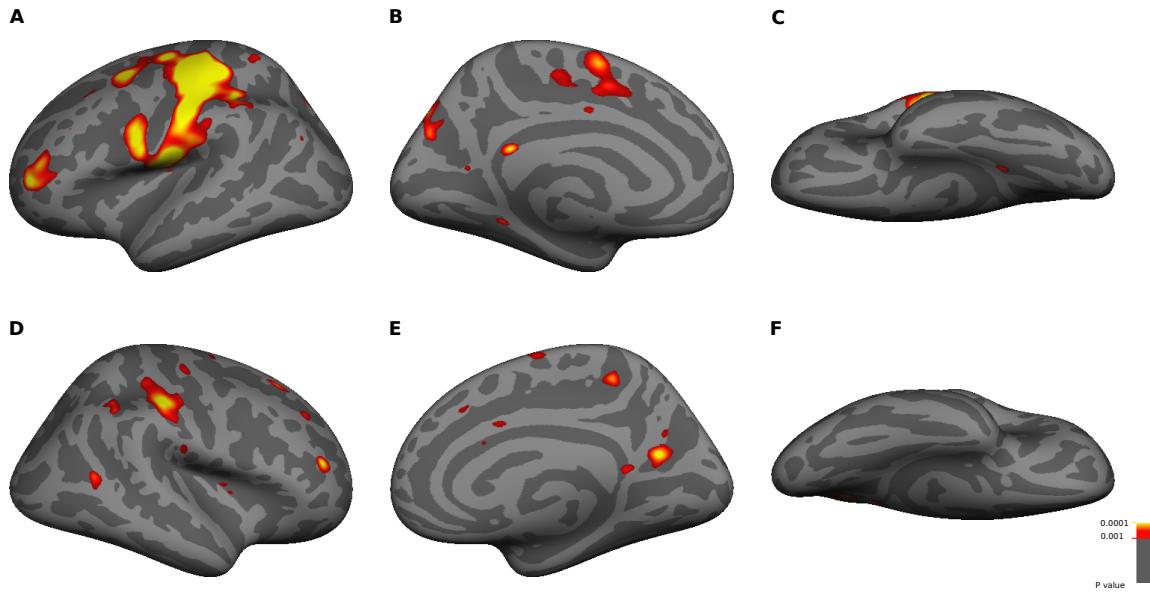


Figure 2.6: Whole-brain searchlight representing information for familiar face subcategories. **A**, The maps show significant ($p < 0.05$, t-test, FDR corrected) whole-brain searchlight results in left (A-C) and right (D-F) hemispheres. The activation maps show averaged categorical information based on category dissimilarity index (CDI) metric from 17 subjects and displayed on lateral (A,D), medial (B,E), and ventral (C,F) views of an inflated cortical surface (fsaverage surface). Information of subcategories of familiar faces is represented medially in an area located in the posterior cingulate cortex in both hemispheres as well as lateral areas within LPFC and postcentral/precentral gyrus.

vious results. More importantly, this study using the rich set of familiar stimuli and MVPA approaches provided us the chance to extend the analysis to finer grained semantic information of familiar faces within this region. We found that PCC also carry neural information of subcategories of familiar faces which was more distinguishable and significant than the general face selective regions (OFA and FFA), ICC, and V1. The finding from whole brain searchlight analysis also revealed that a cluster of activity in the posterior cingulate cortex represented categorical information of faces.

Using two different methods of ROI-based MVPA analysis and whole brain searchlight let us to explore further the role of general face selective regions for representation of categorical information of familiar faces. The results showed that neural information of subcategories of familiar faces was weakly distinguishable in the general face selective regions (OFA and FFA). Even, the detected information was pronounced less when the effect of low-level information was regressed out. This finding

plus the result from the univariate analysis confirmed the hypothesis that general face selective areas in the ventral visual cortex were not sensitive to familiarity information of faces ([Dubois et al., 1999, Leveroni et al., 2000, Gorno-Tempini and Price, 2001, Eger et al., 2005, Ramon et al., 2015]).

Apart from a successful above chance discrimination of familiar face subcategories in the PCC, we also found an unexpected highly significant activity in the pre/post central cortex. This finding could be explained by distinct task based motor responses that were associated with each stimulus category in the current design. Wide-spread reciprocal connections of PCC to cortical and sub-cortical areas including V4, DLPFC, parahippocampal cortex, and other association cortices suggest this area is an association area that may subserve a variety of behavioural functions ([Cavanna and Trimble, 2006]). Thus, to conclude that PCC carry information of subcategories of faces, the caveat of this design with respect to motor activity deserved to be modified.

The results of ROI-based analysis in the V1 showed that observed information was independent of the perceptual properties of the faces. However, to address this point several steps were taken. Specifically, rather preliminary matching steps of images to avoid the possible low-level information, we found weak but distinguishable differences. Thus, following this observation we used two-step regress-out procedure that exclude associated mean luminance and contrast of images. Although this approach let us to diminish the effect of perceptual information, it might be better to control this parameters in advance.

The other caveat of this experiment was unbalanced distribution of face stimuli based on gender property which might results in discriminative information and could be considered as a confounding factor. Although, exclusion of gender property was not qualitatively affect the results, it was recommended to be considered in advance for the future studies.

The set of unexpected discoveries suggested further research using the design controlled for possible confounding factors could shed light on whether PCC contain categorical information for familiar faces.

Chapter 3

Second experiment

3.1 Methods

3.1.1 Subjects

Twenty two adult subjects with normal vision (11 males, 6 females, mean age = 26.29 years, std = 3.99 years) were recruited for the imaging sessions. Informed written consent was obtained from each subject, which was approved by the local ethics committee. All experimental procedures conformed to NIH guidelines.

3.1.2 Visual stimuli

Similar to experiment 1 stimuli were selected from two main categories of faces: familiar faces and unfamiliar faces (Figure 3.1 A). The familiar face category also was similarly composed of 4 subcategories: cinema, music, politics, and sport. However, in this experiment the selected stimuli were fixed across subjects. Thus, familiar faces of each subcategory were selected based on high ratings of face familiarity. Unfamiliar faces were selected from celebrities that were unknown to the subjects. In total, 40 different faces (48 familiar + 8 unfamiliar) were selected. The other modification with respect to experiment 1 is related to the gender of the selected

stimuli. To control for the possible effect of gender, all the faces were chosen from the male category. Original face images, which were obtained from the Internet, were frontal views of faces with direct gaze, natural hairstyle, and approximately neutral expressions. Background of stimuli was erased and made gray. Faces were then edited to be in gray-scale format and equal size (horizontal and vertical visual angles were about 7 and 10 degrees, respectively). After that, to control for low level pixel wise information of stimuli, faces were histogram equalized to a sample face using Matlab toolbox. Finally, a red fixation point (radius = 1 degree visual angle) was superimposed at the center of edited stimuli.

3.1.3 Procedure

Familiarity of each subject with face stimuli was quantitatively assessed through an online survey/questionnaire. Only subjects who were able to categorize all images of familiar faces were recruited in the study. Before scanning session, subjects were presented with all the 40 face stimuli, including familiar and unfamiliar ones. Then, they were administered to practice one experimental run outside the scanner. In the scanner, subjects completed 20 experimental runs as well as two category localizer runs.

All stimuli were presented using a block design while subjects were engaged in an oddball detection task. An example of the functional run is shown in (Figure 3.1 B). In each experimental run, the sequence of typical blocks and one additional dummy or catch block were repeated two times ($2 * (5 + 1) = 12$ blocks). Each typical block contained 8 different images of the same category, each presented for 1 second without any gap (Figure 3.1 C). The order of images within each block was arranged randomly. On the catch block, one of the eight images was selected from the other category stimuli. The dummy block was produced similar to one of the typical blocks. To make sure that subjects paid attention to the category of the presented stimuli, they were asked to report any oddball images within each block. To eliminate the contribution of the probable motor confound they were administered

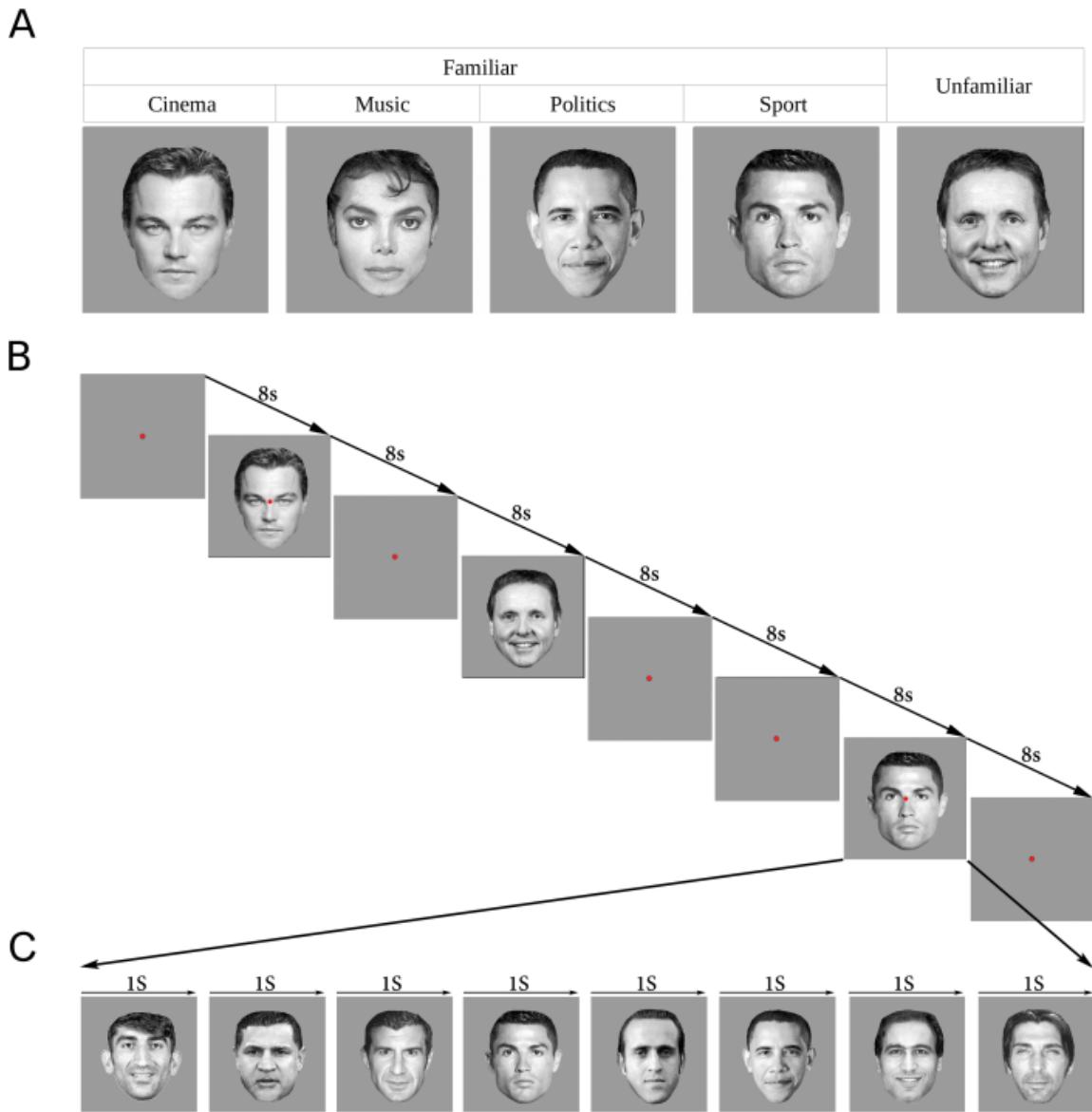


Figure 3.1: Face stimuli and task design. **A**, Stimuli were from two main categories of faces: familiar and unfamiliar. The familiar face category itself consisted of four subcategories: cinema, music, politics, and sport. A red fixation point was positioned at the center of each image. **B**, Block design. The sequence included stimulus blocks interleaved with blank blocks (8 seconds each). The order of stimulus blocks were random. **C**, In each stimulus block, 8 stimuli were presented sequentially without any gap.

to report their response not during the stimuli presentation, but just following to the next fixation condition. Blocks were presented with 8 seconds gap. The first,

middle, and the last part of each run consisted of 8 seconds nulls.

In the same session, a category localizer was used to localize face-selective regions, including OFA, FFA, and ATFP. In each localizer run, blocks of three categories (faces, scenes, and objects) were sequentially presented. The sequence of each run contained 4 repetitions of each category block, which the order of blocks was counterbalanced within each run. Stimuli included gray-scale images of faces (either male or female faces), objects (e.g., cars, tools, and chairs) and scenes (either indoor or outdoor scenes). In each block, 20 images were shown to the subjects, which each image lasted for 750 ms and followed by an inter-trial interval of 50 ms. Subjects were instructed to report any spatial motion wiggle in images. The first, middle and end of each run consisted of 8-second fixation blocks.

3.1.4 Data acquisition

Data were collected using a Siemens 3T Tim Trio MRI system with a 32-channel head coil at medical imaging center of institute of fundamental sciences (Tehran, Iran).

For each subject, a whole-brain anatomical scan was acquired using T1-weighted MP-RAGE sequence (TR = 1.9 s, TE = 2.5 ms, isotropic voxel size = $1 \times 1 \times 1$, 256 sagittal slices, flip angle = 9).

The functional scans were acquired using a typical GE-EPI sequence (TR = 2 s, TE = 30 ms, voxel size = $3 \times 3 \times 4$, 30 semi-axial slices, flip angle = 90). The slices were obtained in an even-odd interleaved order.

3.1.5 Data analysis

Functional and anatomical data preprocessing and voxel-wise analysis were done using Freesurfer and FS-FAST (<http://surfer.nmr.mgh.harvard.edu/>).

3.1.5.1 Preprocessing

To better estimate the Bold signal, data were preprocessed according to a standard set of steps. To diminish the effects of noise from different sources, we pre-processed data similar to experiment 1 which is explained clearly in the previous chapter. However, during collecting these series of data because of the instability of the scanner, some additive and artificial noise were observed. Thus, we performed extra steps of data quality check which are explained briefly below.

All functional runs of subjects were despiked to remove any high values not attributable to physiological activities, thus excluding the runs with scanner noise. Additionally, functional signal to noise ratio (fSNR) of all functional runs was evaluated and those runs with lower quality of signal were excluded (the first run of each session).

In the motion correction step of each run data, time points with the motion greater than 1 mm in any direction were excluded. Then, the runs with less than 5 excluded time points were included in the fMRI analyses.

3.1.5.2 Univariate analysis:

In the univariate analysis, the preprocessed functional data were resampled/projected to an average cortical surface (fsaverage). Projected data were then spatially smoothed using a Gaussian filter (full width at half maximum = 6 mm). Time-series modeling was done using general linear model (GLM) [Friston et al., 1995, Bar, 2004]. The time-series of each run was modeled as a sum of weighted response variables plus an error term. Response variables included task regressors (i.e. regressors for stimulus conditions including cinema, music, politics, sport, and unfamiliar conditions) and nuisance regressors (three head motion parameters, mean confound, linear and quadratic trends, and time-point exclusion). The first four time-points of each run were discarded to avoid inhomogeneity effects of the magnetic field. Task regressors were modeled as a boxcar function convolved with a canonical hemodynamic response function. The time-series were whitened by removing temporal autocorrelations.

To localize regions containing information of familiar faces, we did a two-stage univariate analysis in the common anatomical space (fsaverage). In the subject-level analysis, a single model was estimated for time-series of each voxel along a session. In this model, time-series of all runs within a session were concatenated, and the design matrix was composed of task regressors and run-related nuisance regressors. Subject-level statistical maps were computed by pairwise t-test comparisons between familiar and unfamiliar face conditions. The resulting statistical maps were spatially smoothed using a Gaussian filter (full width at half maximum = 6 mm). Then in the group-level analysis, familiar face-selective regions were defined by mixed-effects averaging of individual subjects maps. The group-average maps were thresholded at p-value < 0.01 (corrected threshold).

3.1.5.3 Multivariate analysis:

To localize regions containing information of subcategories of familiar faces, whole-brain MVPA searchlight analysis was performed. This analysis was carried out using the CosmoMVPA toolbox [Oosterhof et al., 2016]. Specifically, a curved cylinder was defined around each point/vertex between two cortical surfaces (Freesurfers Pial and White surfaces), which sampled a constant number of voxels (100 voxels in our analysis). The estimated values of these voxels were used to generate the response patterns for different conditions. To quantify the amount of categorical information in each region we used a category discriminability index (CDI) [Roth and Zohary, 2015]. The CDI metric was defined as the average of within-condition pattern correlations (diagonal elements of correlation matrix) minus the average of between-condition pattern correlations (off-diagonal elements of correlation matrix). Pattern analysis was performed for all possible regions and the estimated CDI values were assigned to the central vertex of each region. Finally, a map of vertices with the highest amount of categorical information was obtained in each subject, and the results were transformed into the standard space (fsaverage) for group analysis. To evaluate the

significance of the categorical information, estimates of all subjects were combined to perform random-effects group-level statistical analysis using t-test. To correct for multiple comparisons, the Benjamini-Hochberg procedure for controlling the false discovery rate was used [Benjamini and Hochberg, 1995]. The procedure of functional data processing to generate patterns for this analysis is explained below.

Time-series analysis: The first step in calculating multivariate pattern information was to model time series using GLM method. In the multivariate pattern analyses, to prevent loss of fine-grained pattern information, preprocessed data were analyzed in the subjects native anatomical space without applying any spatial smoothing. Using a procedure described in the univariate analysis, beta values associated with task events were estimated. Here estimation of beta values was performed in the voxel space and separately for each run. To evaluate pattern information for subcategories of familiar faces, the design matrix included 5 distinct task regressors (cinema, music, politics, sport, and unfamiliar faces).

Data splitting: All runs of each subject were splitted into two complementary sets of runs. Within each set and for each condition, beta values were normalized (mean-subtracted) and then averaged across runs. Then, estimated values corresponding to each region were concatenated to generate the response patterns for different conditions.

3.2 Results

3.2.1 Univariate analysis

To define regions that were more responsive to familiar faces, we used univariate analysis. In the group-level analysis, for the contrast between familiar faces versus unfamiliar faces, we found greater activities in multiple areas within the cortex. Figure 3.2 shows the resulting statistical maps on the average surface (fsaverage).

In the medial surface, familiar faces evoked greater activities in the posterior cingulate cortex for both hemispheres. This result is consistent with previous findings on

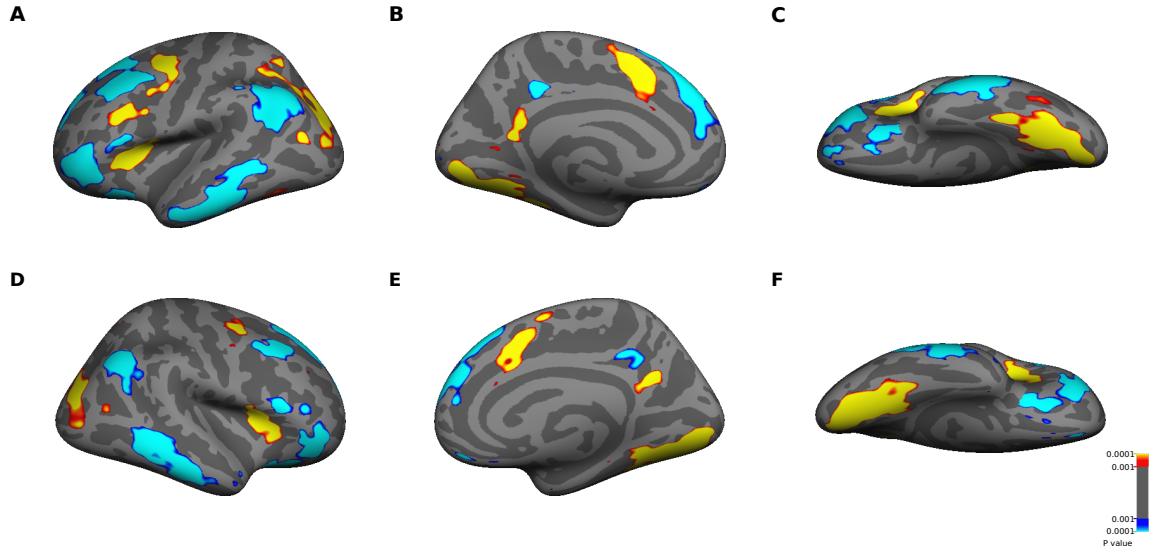


Figure 3.2: Whole brain univariate analysis. **A**, The maps show significant ($p < 0.01$, t-test, FDR corrected) activation for familiar (red/yellow) versus unfamiliar (blue/cyan) faces in left (A-C) and right (D-F) hemispheres. The activation maps are based on mixed-effects group-average of data from 22 subjects, and are displayed on lateral (A,D), medial (B,E), and ventral (C,F) views of an inflated cortical surface (fsaverage surface). The familiarity activated two distinct cortical regions in medial cortex in both hemispheres.

selectivity for familiarity in PCC [Gobbini et al., 2004, Leveroni et al., 2000]. Additionally, a region within superior frontal cortex was also responsive for familiar faces. Other lateral regions in the LPFC and parietal cortex also revealed modulation by familiarity attribute. This selectivity to familiar faces was significant in both hemispheres.

On the ventral surface, we also observe a highly significant activity in the early visual cortex and fusiform gyrus.

3.2.2 Multivariate analysis

To localize regions, decoding subcategories of familiar faces, we performed a whole-brain MVPA using surface-based searchlight. Specifically, we used the CDI metric (the difference between the correlation values in diagonal and off-diagonal cells of the correlation matrix). The searchlight maps from the group-level analysis are shown on the inflated surfaces of both hemispheres in Figure 3.3.

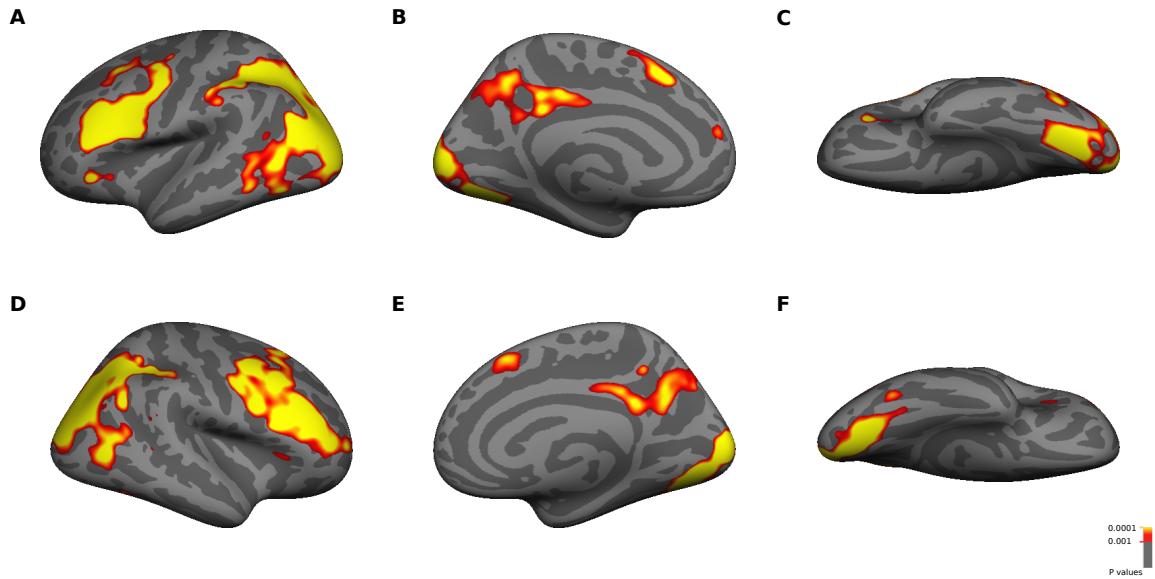


Figure 3.3: Whole-brain searchlight representing information for familiar face subcategories. The maps show significant ($p < 0.05$, t-test, FDR corrected) whole-brain searchlight results based on CDI method from 22 subjects in the left (**A-C**) and right (**D-F**) hemispheres. Information of subcategories of familiar faces is represented in multiple regions including posterior cingulate cortex, temporal cortex, and two highly significant areas within fronto-parietal network in both hemispheres.

In the medial cortex, high amount of categorical information was observed medially in the posterior cingulate cortex which overlapped and extended posteriorly and superiorly to the obtained area from univariate analysis.

In the ventral cortex, categorical information of faces was found significantly in the bilateral visual cortex starting in the early visual cortex and extending to occipital, posterior, and mid fusiform cortices. Significant information also observed in the broad regions in the lateral cortex including the lateral prefrontal cortex (LPFC) and parietal cortex.

3.3 Discussion

In this experiment, a face set was designed to investigate the neural structures representing information of familiar faces and subcategories of familiar faces. Similar to the (experiment 1) the face set included stimuli from two main categories:

familiar and unfamiliar faces. Faces of the familiar category were also selected from the most famous identities associated to four distinct social categories (cinema, music, politics, and sport). However, bearing in mind caveats of (experiment 1), some modifications were considered (see methods). The results from univariate analysis revealed that an area within the posterior cingulate cortex represented information of familiar faces replicating our previous result. Interestingly, findings of whole-brain searchlight analysis also showed that this area carries distinguishable information of familiar face categories. These findings suggest that posterior cingulate cortex not only is sensitive to familiarity attribute of faces but also represents distinctly finer-grained information of faces with respect to social information.

In the (experiment 1), to make sure subjects paid attention to the social category of presented stimulus, they were administered to report their response with an associated finger. Thus, information other than conceptual information of familiar faces could contribute to the decoding. However, the new design not only let us make sure that subjects paid attention to the category of presented stimuli but also resolved the problem of motor confound. Clearly, despite the (experiment 1) results, we did not detect any decodable information in the pre/post central cortex.

When a face is familiar, the recognition procedure involves processing both perceptual and conceptual aspects of that face. Thus to make sure that the observed activity was related to the conceptual aspect, the perceptual aspect should be controlled. In (experiment 1), we observed general face-selective regions weakly represented information of subcategories of familiar faces which was excluded using a two-step regress out procedure. In this experiment, we increased our controls with respect to low-level features including size, luminance, and contrast. Unexpectedly, the results revealed highly significant and decodable information in multiple areas in the cortex including the dorsal and ventral pathways of the visual cortex which were absent in the previous experiment. Possibly, the face set of (experiment 1) included decodable perceptual information rather than those that were controlled in the current design. However, because of the lower statistical power of event-related

design they couldn't be detected.

In conclusion, we found that regions within the posterior cortex discriminate subcategories of familiar faces replicating the (experiment 1) results. The current design was a strength in that it provides the chance to overcome the problem of motor confound. However, it was a weakness in that we failed to control for perceptual confound.

Chapter 4

Third experiment

4.1 Introduction

Face recognition is a fundamental cognitive ability which plays an important role in social communications in everyday life. Faces, as complex visual stimuli, contain various types of information along different perceptual dimensions. One main goal of human visual system is to flexibly extract perceptual information of faces at multiple levels, including early visual processing for face detection, analysis of facial features and their configuration, analysis of facial viewpoints and expressions, and finally view-invariant processing for face identification. For familiar and famous faces, this cascade of perceptual analysis is followed by a process of retrieving semantic information or semantic knowledge about faces (Young et al., 1986). This process can be viewed as a continuum comprising multiple stages of information extraction, from the general facts about people to the specific facts about individuals. In light of such multi-stage abstraction of semantic information, familiar and famous faces can be processed hierarchically at different semantic levels: they can be processed as a general category of human faces, they can be categorized/distinguished from unfamiliar faces, they can be classified into specific subcategories of familiar faces based on social and contextual factors (e.g. celebrity groups such as actors and politicians), and they can be identified as unique individuals (e.g. the face of Brad

Pitt or Barack Obama). Flexible and efficient extraction of face-related semantic information could be possible by having dedicated neural representations for every level of semantic processing. Although, previous studies have found hierarchical and multi-stage representations within ventral temporal cortex for perceptual processing of faces, it remains an open question how and where in the brain multiple categorical levels of face-related semantic knowledge are represented, and whether there is a hierarchical topographic organization for such representations.

Previous studies have shown that perceptual information of faces is processed by a distributed network of brain regions. These areas, which are considered as the core system of face processing, hierarchically transform perceptual information of individual face identity, either familiar or unfamiliar, from view-specific to identity-specific information (Gobbini & Haxby, 2007; Haxby et al., 2000). Indeed, perceptual information of faces elicits high activities in bilateral face-selective areas within occipitotemporal cortex: the occipital face area (OFA) (Gauthier et al., 2000), the fusiform face area (FFA) (Kanwisher et al., 1997), and the posterior superior temporal sulcus (pSTS) (Chao et al., 1999; Grill-Spector & Weiner, 2014). Further research has reported that a distinct face-selective region in the ventral part of the anterior temporal cortex (named as anterior temporal face patch (ATFP)) (Rajimehr et al., 2009) is also involved in visual and perceptual encoding of faces. More specifically, ATPF appears to be an important region for recognition and discrimination of facial identities (Anzellotti et al., 2014; Goesaert & Op de Beeck, 2013; Kriegeskorte et al., 2007; Nestor et al., 2011).

While activity of posterior regions (OFA, FFA, and pSTS) revealed inconsistent and weak differences in response to cognitive manipulations such as familiarity (Dubois et al., 1999; V. Natu & OToole, 2011; Ramon & Gobbini, 2018), neural structures within anterior temporal lobe (ATL) exhibited enhanced activation to familiar/famous faces than unfamiliar faces (Gobbini & Haxby, 2007; Gobbini et al., 2004; Ramon et al., 2015). These structures also revealed an adaptation response to repetition of familiar faces (Sugiura et al., 2011) and showed sensitivity to association of semantic information to faces (Von Der Heide et al., 2013). Thus, it has been suggested that ATL is a well-suited area to bound perceptual information of

faces with semantic knowledge of individuals including their names or biographical information (Collins & Olson, 2014).

Neuroimaging studies have also shown that beyond the ATL, a number of additional regions such as structures within posterior cingulate cortex (PCC), anterior cingulate cortex (ACC), medial temporal lobe (MTL), hippocampus, and amygdala are engaged in the processing of familiar/famous faces (Ramon et al., 2015; Weibert et al., 2016). These regions, which are located outside of classical visual areas, are part of a broad group of face patches defined as the extended system of face processing (Gobbini & Haxby, 2007; Haxby et al., 2000). The results from a meta-analysis also suggests that semantic information and person knowledge are mainly represented in the extended face network (Binder et al., 2009). These studies provide valuable insights into which areas of the brain contain the neural code for semantic knowledge of familiar faces. However, it still remains an open question whether and how those areas represent the continuum of person-related semantic knowledge from general information about people to more abstract information about specific individuals.

In the study reported here, therefore, we aimed to address how semantic information of familiar faces is extracted in the human face processing system. To address this question, we needed an experimental paradigm to ensure that we target the neural structures that are involved in processing the fine-grained and abstract information of familiar faces with respect to social attributes. Thus, we designed an experiment to present multiple face identities from two main categories of familiar and unfamiliar faces, with familiar stimuli selected from four different subcategories of famous faces (four celebrity groups). This rich set of face stimuli provided us with the opportunity to investigate the neural structures representing and disentangling semantic information of faces in multiple levels of abstraction. The human subjects were engaged in a celebrity categorization task, and their brain responses were collected using an event-related fMRI experiment. We systematically increased the sensitivity of the analysis from univariate to multivariate analysis to evaluate the gradual changes in the neural representations of faces, from the coarse level of face and familiar face encoding to a more fine-grained level of representing familiar face subcategories and familiar face identities. Additionally, we examined whether

the cortical areas involved in such representations display a hierarchical topologic organization.

4.2 Methods

4.2.1 Subjects

Sixteen human adult subjects (11 males, 5 females, mean age = 26.29 ± 3.99 years) with normal vision were recruited for the imaging sessions. Informed written consent was obtained from each subject. All experimental procedures conformed to NIH guidelines and were approved by the local ethics committee.

4.2.2 Visual stimuli

Stimuli consisted of images from two main categories of faces: familiar faces and unfamiliar faces (Figure 4.1A). The familiar face category included celebrity faces from four subcategories: cinema, music, politics, and sport. Familiar faces of each subcategory were selected based on high ratings of familiarity for our subjects (some of them were national celebrities). Unfamiliar faces were selected from celebrities that were unfamiliar for our subjects. In total, 40 different faces (48 familiar + 8 unfamiliar) were selected. All faces were male. Supplementary Figure 6.3 shows all face images.

Original face images, which were obtained from the Internet, were frontal views of faces with direct gaze, natural hairstyle, and approximately neutral expression. Background of faces was segmented and filled by black color. Faces were then converted to the grayscale format, and their size was adjusted so that they can fit within an oval-shaped frame (the horizontal and vertical visual angles of the frame were 6.5 and 9 degrees, respectively). The hairs were almost covered by this mask.

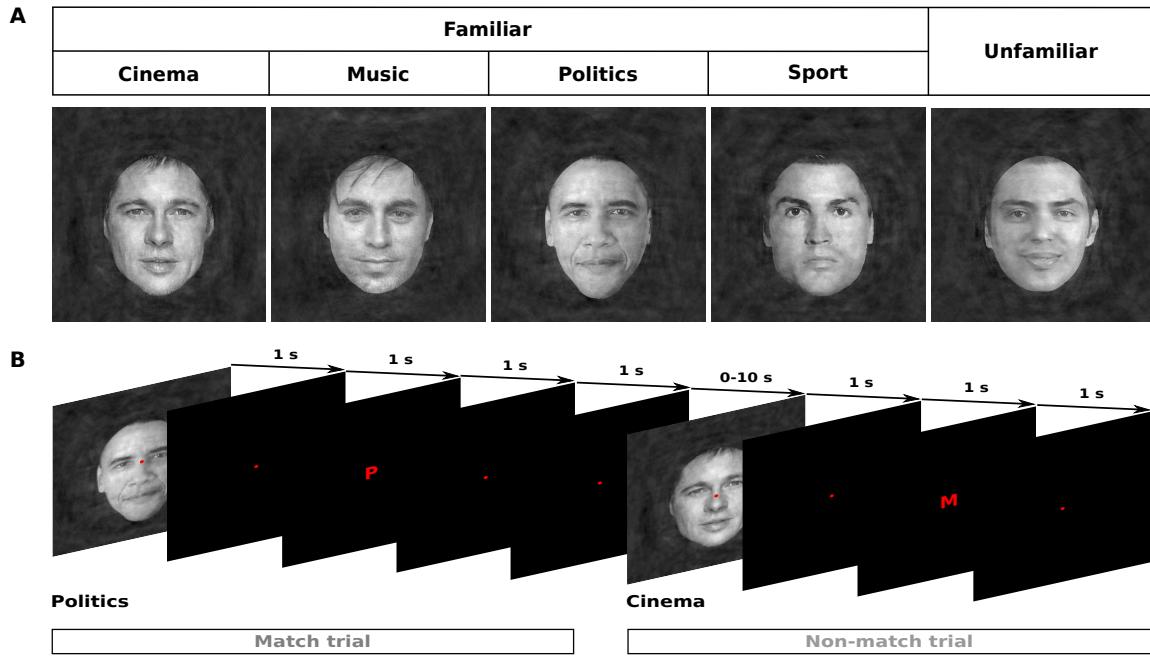


Figure 4.1: Face stimuli and task design. A, Stimuli consisted of images from two main categories of faces: familiar faces and unfamiliar faces. The familiar face category included celebrity faces from four subcategories: cinema, music, politics, and sport. A red fixation point was positioned at the center of each image. B, The sequence of events in a functional run. Each stimulus trial was composed of a face event (1-second face stimulus presentation, followed by a 1-second blank) and a letter event (1-second letter presentation, followed by a 1-second blank). The letter indicated a category label (e.g. P - Politics, M - Music, etc.). During the letter event, subjects had to compare the category label with the actual category of the face stimulus and report their match/non-match response by pressing a key on the response box. In addition to the stimulus trials, a number of null trials (delay periods) with variable durations were presented throughout the run.

The framed faces were embedded within a squared-shape black area (size = 12.5 degrees visual angle), then the brightness, contrast, luminance histogram, and power spectrum of all face stimuli (including their surrounding black area) were physically matched/equalized using the Shine toolbox (Figure 4.2A-B, Willenbockel et al., 2010). Finally, a red fixation point (radius = 1 degree visual angle) was superimposed at the center of face stimuli, and the stimuli were presented on a uniform black screen.

To quantitatively measure the discriminability of face categories based on low-level visual features (such as retinotopic shape information and spatial frequency), we evaluated the performance of a V1 model in classifying faces into five seman-

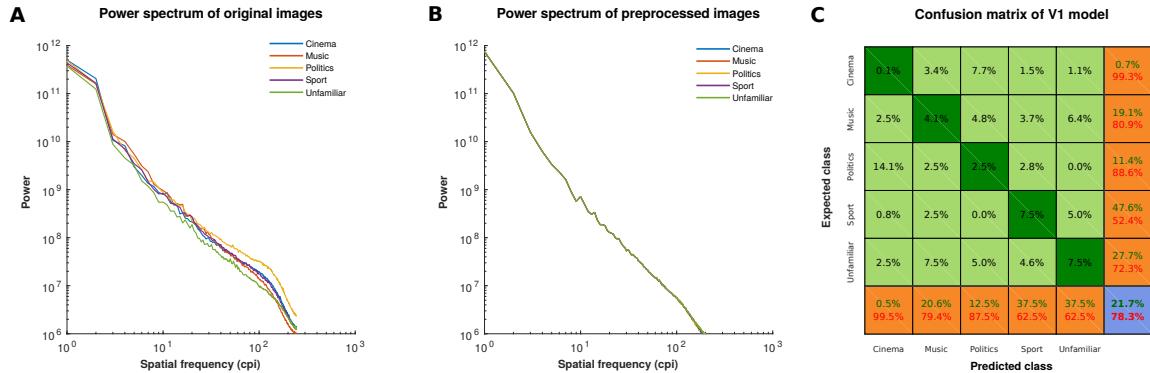


Figure 4.2: Spatial frequency matching of face stimuli, and results of the V1 model. A-B, The log-log plots show the averaged power of the Fourier transform at each spatial frequency for images of each face category before (A) and after (B) power spectrum equalization in the SHINE toolbox. The 1-D power spectra were obtained by averaging power across all orientations (i.e. radial averaging) in the 2-D power spectra of the images. C, The confusion matrix summarizes the performance of V1 model in classifying the preprocessed face images into five semantic categories/classes. The rows of the matrix correspond to expected classes, and the columns of the matrix correspond to predicted classes. The diagonal cells show the pattern of correct classifications, and the off-diagonal cells show the pattern of misclassifications. The metrics of positive predictive value and false discovery rate are shown in the last row, and the metrics of true positive rate and false negative rate are shown in the last column. The overall accuracy and error of the multi-class classification are shown in the blue cell (the values in green and red colors, respectively).

tic categories. For this, we first simulated V1 cortical neurons using HMAX model (Serre et al., 2007). Images were modeled with a set of simple-like (S1) and complex-like (C1) cells in the second layer of the HMAX model, then the responses of these cells were used as input patterns for classification of images. Linear support vector machine (SVM), which was implemented in the LIBSVM toolbox, was used as a classifier for multi-class classification. The classification performance was assessed using leave-one-sample-out cross-validation method, in which one sample from each class was used for testing the classifier, and all remaining samples were used for training the classifier. The overall performance of the classifier was 21.7% correct rate, which was not significantly different from the chance-level performance (20%) ($p > 0.05$, permutation test). Additionally, to investigate the contribution of each of pairwise comparisons to total performance, the confusion matrix was plotted (Supplementary Figure 2C). The correct rate for most pairwise comparisons was around the chance-level performance. Thus, the observed total accuracy was not dependent on a specific comparison. Overall, these analyses confirmed that the face categories were not distinguishable based on low-level pixel-wise information.

4.2.3 Experimental procedure

Familiarity of each subject with face stimuli was quantitatively assessed through an online survey/questionnaire. Only subjects who were able to categorize all images of familiar faces were recruited in the study. In the scanning session, subjects completed 16 functional runs of the main fMRI experiment and 2 functional runs of the category localizer experiment. Before scanning and outside the scanner, subjects were presented with all the 40 face stimuli (including familiar and unfamiliar faces), and they practiced the task of the main experiment.

A fast event-related fMRI design was used for presenting the stimuli in each functional run of the main experiment. An example functional run is shown in Figure 4.1B. The sequence of stimuli contained 40 stimulus trials (8 repetitions of 5 category conditions) and 35-39 null trials. Null trials were blank periods in which only fixation point was presented on a uniform black screen. To have the most optimized estimation of hemodynamic response, the order of stimulus and null trials for each run was generated using the Freesurfer OptSeq2 algorithm (<http://surfer.nmr.mgh.harvard.edu/optseq/>). The first 10 and the last 4 seconds of the sequence were always nulls. Duration of stimulus trials was 4 seconds, and duration of null trials varied between 0 and 10 seconds. Each stimulus trial included a face event and a letter event, which were presented sequentially. In the face event, a randomly-chosen face stimulus (one out of 40 possible examples) was presented for 1 second, followed by a 1-second blank. In the letter event, a letter (size = 0.5 degree visual angle) was presented at the center of screen for 1 second, followed by a 1-second blank. The letter was either C, M, P, S, or U representing a category name. The reason for using the first letter of the category names (instead of the whole names) was to minimize confounding visual activations not related to face and semantic representations. Half of the stimulus trials were match trials (the letter correctly represented the stimulus category), and the remaining stimulus trials were

non-match trials. The order of match and non-match trials was random. Subjects were instructed to make a judgment about the category of each face stimulus and perform a match/non-match task. They indicated the match/non-match response by pressing a key with their right or left index finger. The responding hand for the match (and non-match) response was alternated and counterbalanced across subjects. Subjects were also asked to fixate on the fixation point throughout the scans. This design ensured that subjects paid attention to the semantic category of the face stimuli without making an association between a particular motor response and a particular face category. Such associations could impose problems during the multi-variate pattern analysis of fMRI responses.

In the same fMRI session, a category localizer was used to localize face-selective regions including OFA, FFA, and ATFP. In each localizer run, four repetitions of three category blocks (faces, scenes, and objects) were presented. In each repetition, the order of blocks was random. Stimuli included grayscale images of faces (male and female faces), objects (e.g. tools, cars, and chairs) and scenes (indoor and outdoor scenes). In each block, 20 images were presented sequentially. Each image lasted 750 ms, followed by a blank interval of 50 ms. Subjects were instructed to report any spatial wiggle in images. There was an 8-second fixation block in the beginning, middle, and end of each run.

4.2.4 Data acquisition

Data were collected using a Siemens MAGNETOM Prisma 3T scanner with a 64-channel head coil at the National Brain Mapping Laboratory (NBML) (Tehran, Iran). Subjects laid back in the scanner and viewed back-projected screen via a mounted mirror over the head coil. All stimuli were presented using MATLAB and Psychtoolbox (<http://psychtoolbox.org/>).

For each subject, a whole-brain anatomical scan was acquired using T1-weighted

MP-RAGE sequence (TR = 2 s, TE = 3.47 ms, isotropic voxel size = $1 \times 1 \times 1$, 256 sagittal slices, flip angle = 7, GRAPPA acquisition with acceleration factor = 2).

The functional scans for the main experiment and category localizer were based on a GE-EPI sequence (TR = 2 s, TE = 30 ms, voxel size = $3.5 \times 3.5 \times 3.5$, 34 semi-axial slices, distance factor = 10%, flip angle = 90, GRAPPA acquisition with acceleration factor = 2). The slices were obtained in an even-odd interleaved order. The first 3 volumes of each run were discarded to allow for MR signal equilibration.

4.2.5 Data analysis

Using recon-all in Freesurfer (<http://surfer.nmr.mgh.harvard.edu/>), structural T1 images of each subject were processed, subcortical structures were automatically segmented, and cortical surfaces were computationally reconstructed. FS-FAST (<https://surfer.nmr.mgh.harvard.edu/fswiki/FsFast>) was used for preprocessing and voxel-wise analysis of functional data.

4.2.5.1 Preprocessing

Functional data were first skull-stripped using FSLs brain extraction tool to generate a brain mask (Smith, 2002). Then using the middle time-point of each run as the reference and applying AFNI's motion correction algorithm, the functional images were aligned (Cox, 1996). For each subject, only runs with less than 1 mm motion in any direction were included in the fMRI analyses. In the next step, intensity values of all voxels inside the brain mask were converted to a standard intensity scale. For this, the mean intensity of all voxels across all time-points was first computed. Then, the intensity value of each voxel at each time-point was divided by the mean intensity and multiplied by 100. The functional volumes were then rigidly co-registered to the same-subject anatomical volumes using boundary-based registration method.

4.2.5.2 Univariate analysis

In the univariate analysis, the preprocessed functional data were resampled/projected to an average cortical surface (fsaverage). Projected data were then spatially smoothed using a Gaussian filter (full width at half maximum = 6 mm). For each surface vertex, activations for different category conditions were calculated using a general linear model (GLM). In this model, time-series of all runs within a session were concatenated, and a design matrix composed of task regressors and run-related nuisance regressors was constructed. Time-series were whitened by removing temporal auto-correlations. Task regressors represented temporal patterns of five face events (cinema, music, politics, sport, and unfamiliar faces) and one letter event, which were all convolved with a canonical hemodynamic response function. The three head motion parameters produced during realignment were used in the GLM model as nuisance regressors to account for residual effects of subjects movements. Additional nuisance variables included linear trends, quadratic trends, and mean confound. Prior to estimating beta values of the model, the first four time-points of each run were discarded to avoid inhomogeneity effects of the magnetic field. Finally, beta values for the task regressors were obtained.

We performed a two-stage surface-based univariate analysis to localize regions selective for familiar faces in the common anatomical space (fsaverage). In the subject-level analysis, statistical maps were computed by t-test comparison between beta values in the contrast of familiar versus unfamiliar faces. Then, in the group analysis, the familiar face regions were defined based on mixed-effects averaging of individual subject maps. The group-average map was thresholded at FDR-corrected $p - value < 0.05$.

4.2.5.3 Multivariate analysis

In the multivariate pattern analyses (MVPA), to prevent loss of fine-grained pattern information, preprocessed data were analyzed in the subjects native anatomical

space without applying any spatial smoothing. Using a procedure described in the univariate analysis, beta values associated with task events were estimated. Here estimation of beta values was performed in the voxel space and separately for each run. To evaluate pattern information for subcategories of familiar faces, the design matrix included 6 distinct task regressors for five face events (cinema, music, politics, sport, and unfamiliar faces) and one letter event. To evaluate pattern information for familiar face identities, the design matrix included 41 distinct task regressors for 40 individual face events and one letter event. After fitting the GLM, estimated beta values of all voxels within a given ROI mask were concatenated to form an fMRI pattern vector for each condition in each run. To remove the common response pattern, beta values were normalized by subtracting the mean across conditions. To test whether neural patterns could distinguish between different stimulus conditions, we used two decoding approaches: correlation method and SVM classification method.

In the correlation method, 16 runs of each subject were split into two complementary sets of 8 runs (e.g. odd and even runs). Within each set and for each condition, fMRI activation patterns were averaged across runs. In each ROI mask, patterns of activities (one pattern for each condition) in one half of data were correlated with patterns of activities in the other half of data, which resulted in a split-data representational similarity matrix (sdRSM) with the size (rows and columns of the matrix corresponded to N conditions). Pearsons r was used for computing pairwise correlations. To avoid arbitrariness in data splitting, the sdRSMs were calculated for 100 permutations of run splitting, which were selected randomly out of all possible permutations. The correlation values were then averaged across all permutations. The amount of categorical information in each ROI was quantified using a category discriminability index (CDI). The CDI metric was defined as the average of within-condition pattern correlations (diagonal elements of sdRSMs) minus the average of between-condition pattern correlations (off-diagonal elements of sdRSMs).

To evaluate different hypotheses about neural representations, categorical models were designed, and sdRSMs were correlated with these model matrices using Kendalls

tau rank correlation (Kriegeskorte, 2014; Nili et al., 2014, 2016). To examine whether the correlations between categorical models and sdRSMs were significant, estimates of all subjects were combined to perform random-effects group-level statistical analysis using t-test. To correct for multiple comparisons, the Benjamini-Hochberg procedure for controlling the false discovery rate was used (citeBenjamini1995).

In the classification method, the functional runs were split into two independent sets. In each round of data splitting, the training set included 15 runs, and the test set included the left-out run. The two sets of runs had independent stimulus sequences and independent preprocessing – the two important factors for avoiding circular inferences and overfitting. To test whether categorical information could be encoded in each ROI mask, six pairwise classifiers (cinema vs. music, cinema vs. politics, and so on) were trained on responses to four category conditions (cinema, music, politics, and sport categories) in the training set. For training the classifiers, SVM with a linear kernel was implemented in LIBSVM. SVM has several advantages over other classifiers; it does not depend on the distribution of training data, and it can handle limited data in high-dimensional spaces ([Allefeld and J-D Haynes, 2015]). Decision boundaries obtained from training the classifiers were applied to an independent test set (a single run), so that the generalizability of the decision boundary could be evaluated. The classification performance was based on leave-one-run-out cross-validation method, and it was defined as an average performance across all folds of cross-validation. Finally, to determine whether significant information was encoded for different stimulus classes, accuracy of each classifier was compared to the chance-level accuracy (50% performance) using t-test across subjects.

4.2.5.4 Searchlight analysis

A surface-based searchlight method was used to localize regions that could distinguish between activity patterns of different stimulus conditions. This analysis was performed in the native space of subjects using the CosmoMVPA toolbox (Oosterhof

et al., 2016). Specifically, a curved cylinder was defined around each point/vertex between two cortical surfaces (Freesurfer’s Pial and White surfaces), which sampled a constant number of voxels (100 voxels in our analysis). Then, the estimated beta values of these voxels were concatenated to generate the response patterns for different conditions. Pattern analysis was performed for all possible regions on the cortical surface using correlation with the categorical model approach. For each region, the correlation value was assigned to the central vertex of that region. Finally, a vertex-wise map of correlation values (a map of categorical information) was obtained in each subject, and the results were transformed into the standard space (fsaverage) for group analysis.

4.2.5.5 ROI definitions

Classic face-selective areas, including OFA, FFA, and ATFP, were localized using category localizer scans. We performed the same steps of preprocessing and GLM analysis as the univariate analysis, except that the design matrix included distinct task regressors for three category blocks: faces, scenes, and objects. The face-selective ROIs were defined based on the contrast of faces versus scenes. For localizing OFA and FFA, the group-average maps were thresholded at p-value $\leq .05$. OFA/FFA were identified as cluster of voxels in posterior/anterior parts of the bilateral fusiform gyrus showing higher activation for faces than scenes (Figure 4.3).

For localizing ATFP, the group-average maps were thresholded at p-value ≤ 0.001 . The activation in ATFP is generally weak presumably due to susceptibility-induced loss of MR signal in the anterior temporal lobe (Rajimehr et al., 2009). Thus, a low threshold of statistical significance was used for detecting ATFP.

The anatomical region of Brodmann area 23 (one of the subdivisions of PCC) was also defined using PALS-B12 atlas of human cerebral cortex (Van Essen, 2005) on the fsaverage surface. For the multivariate analysis, these surface-based ROIs were projected from the common anatomical space onto native anatomical space of each subject.

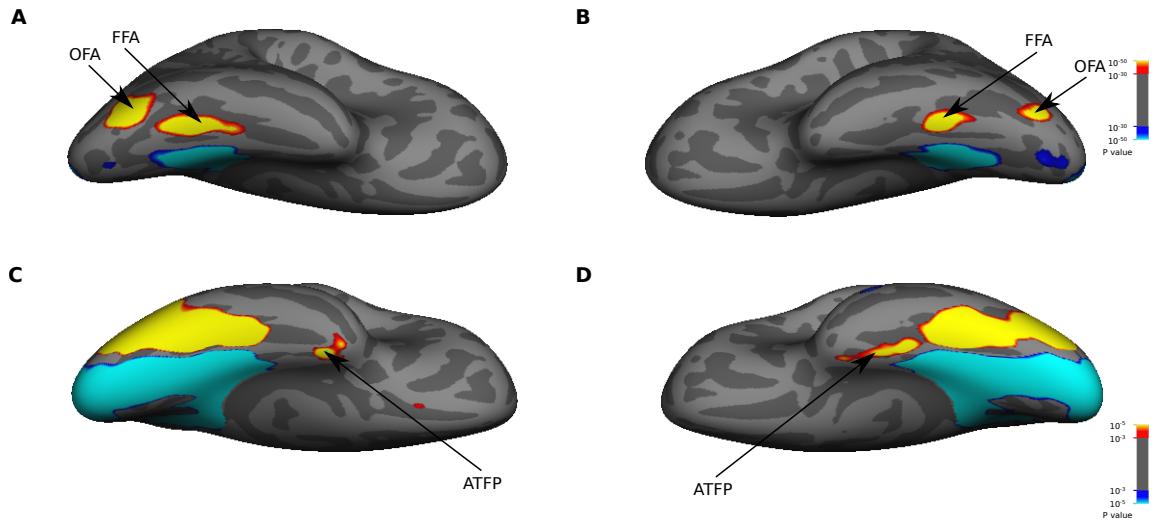


Figure 4.3: Face-selective ROIs. The maps show significant activations for face (red/yellow) versus scene (blue/cyan) stimuli in right (A,C) and left (B,D) hemispheres. The activation maps are based on mixed-effects group-average of face localizer data from 16 subjects, and are displayed on ventral views of an inflated cortical surface (the fsaverage space). The colorbars indicate the significance values. For thresholding the significance maps, two values were used: a high threshold for defining the strongly activated face-selective areas OFA and FFA (A,B), and a low threshold for defining the weakly activated face-selective area ATFP (C,D). These ROIs were projected/transformed from the fsaverage space to the native anatomical space of each subject.

In a control analysis, discriminability of face categories was assessed in the low-level visual cortical area V1. The visually responsive V1 ROI was defined in each hemisphere of each subject using the following procedure. First, the maps of visually responsive voxels were derived based on the contrast of faces versus fixation (faces > fixation) in the main fMRI experiment. Then, the resulting maps were intersected with anatomical V1 ROIs generated by the Freesurfer parcellation (Hinds et al., 2008).

Two subcortical ROIs (hippocampus and amygdala), which were obtained for each subject through Freesurfer's automated subcortical segmentation, were also included in the multivariate ROI analysis.

4.2.5.6 Face-selective maps from Human Connectome Project (HCP) database

To compare our activations with a broader network of face areas, face-selective maps were obtained from the HCP task fMRI dataset (<https://www.humanconnectome.org/study/hcp-young-adult>). Details of data acquisition have been described elsewhere (Glasser et al., 2016). We used data from the working memory task. For the working memory task, 787 subjects underwent 2 runs of functional scanning while performing an N-back (0-2 back) task. In each run, subjects were presented with blocks of images from four categories (faces, places, tools, and body parts). The blocks had either 0-back or 2-back working memory task, as indicated by a cue at the beginning of the block. Each block contained 10 trials. In each trial, an image was presented for 2 seconds, followed by a 500 ms inter-trial interval. Data were preprocessed and analyzed using the HCP pipelines (Glasser et al., 2013). Specifically, the preprocessed data were projected to a standard space, the surface data were spatially smoothed by a 2mm FWHM Gaussian kernel, and GLM was used to estimate functional activities in each vertex. In the subject-level analysis, face-selective maps were obtained based on the contrast of faces versus all other categories, collapsing across the memory conditions. Maps of individual subjects were averaged in the standard space. The face-selective vertices were defined as the top 1% of vertices, which had the highest z-values in the contrast of faces versus all other categories (Abbasi et al., 2020). The 99th percentile corresponded to the cutoff-point z-value of 12.38 in the group-average map. The final map was transformed into the fsaverage surface.

4.3 Results

4.3.1 Behavioral results

During the functional runs of the main fMRI experiment, subjects performed a match/non-match task. The overall performance and reaction time of subjects in this

task were 96.31% 4.23% and 558 ms 54 ms, respectively. This high performance, which was observed in all individual subjects, confirmed that subjects were performing the task correctly. In the analysis of behavioral data, we found no significant difference in performance between the five category conditions [one-way ANOVA; $F(4,75) = 1.01$, $p > 0.05$]. Likewise, there was no significant difference in reaction time between the five category conditions [one-way ANOVA; $F(4,75) = 0.31$, $p > 0.05$]. These results indicated that the five face categories were matched in terms of task difficulty and attentional engagement of subjects.

4.3.2 Cortical representations of familiar faces

Based on the univariate analysis, we defined cortical regions that were activated by familiar faces. In the group-average maps (Figure 4.4), we found significantly greater activation in PCC and ACC for familiar than unfamiliar faces. The ACC activation extended to anterior medial prefrontal cortex in the left hemisphere. Two other spots in the lateral part of ATL and temporoparietal junction (TPJ) also revealed modulation by familiarity. For all these regions, the selectivity to familiar faces was significant in both hemispheres. However, the extent of activity was more pronounced in the left hemisphere. On the ventral surface, face-selective areas OFA, FFA, and ATFP did not show a significantly higher response to either familiar or unfamiliar faces. The responses to familiar and unfamiliar faces were not significantly different in the early visual cortex, confirming that these faces were well matched in terms of low-level visual features.

4.3.3 Cortical representations of familiar face subcategories

To identify regions which could distinguish between subcategories of familiar faces, we performed a whole-brain MVPA using a surface-based searchlight method (Figure 4.5A). Specifically, we used correlation with the categorical model approach. For each region on the cortical surface, sdRSM with the size 4×4 was computed.

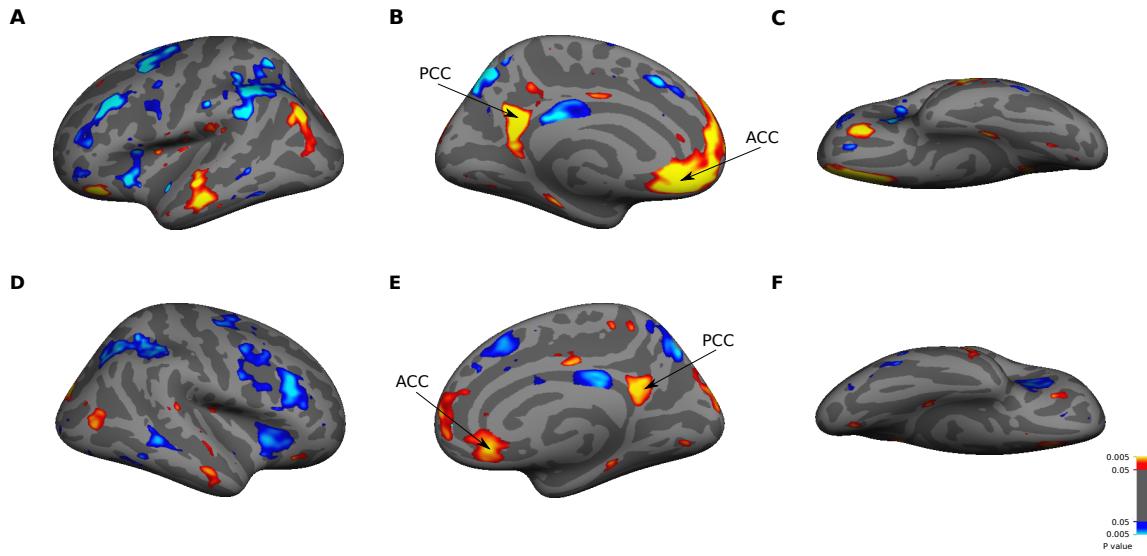


Figure 4.4: Whole-brain univariate analysis. The maps show significant ($p < 0.05$, t-test, FDR-corrected) activations for familiar (red/yellow) versus unfamiliar (blue/cyan) faces in left (A-C) and right (D-F) hemispheres. The activation maps are based on mixed-effects group-average of data from 16 subjects, and are displayed on lateral (A,D), medial (B,E), and ventral (C,F) views of an inflated cortical surface (fsaverage surface). The familiarity activated two distinct cortical regions (PCC and ACC) in medial cortex of both hemispheres.

Rows and columns of the matrix corresponded to four subcategories of familiar faces (cinema, music, politics, and sport). Each element of the matrix represented the correlation between response patterns for two category conditions in two complementary sets of runs (e.g. cinema condition in odd runs and politics condition in even runs). An ideal categorical model was an identity matrix in which the diagonal elements had maximum correlation of one and the off-diagonal elements had zero correlation. The rank correlation between neural sdRSM and the categorical model indicated how much each region contained information about subcategories of familiar faces. The searchlight maps from group analysis are shown on the inflated surfaces of both hemispheres in Figure 4.5B-G. Subcategories of familiar faces could be decoded significantly in PCC of both hemispheres, in a region that highly overlapped with Brodmann area 23. Two other significant clusters were located in posterior parietal cortex (PPC) and lateral prefrontal cortex (LPFC) of left hemisphere. On the ventral surface, no significant cluster was observed.

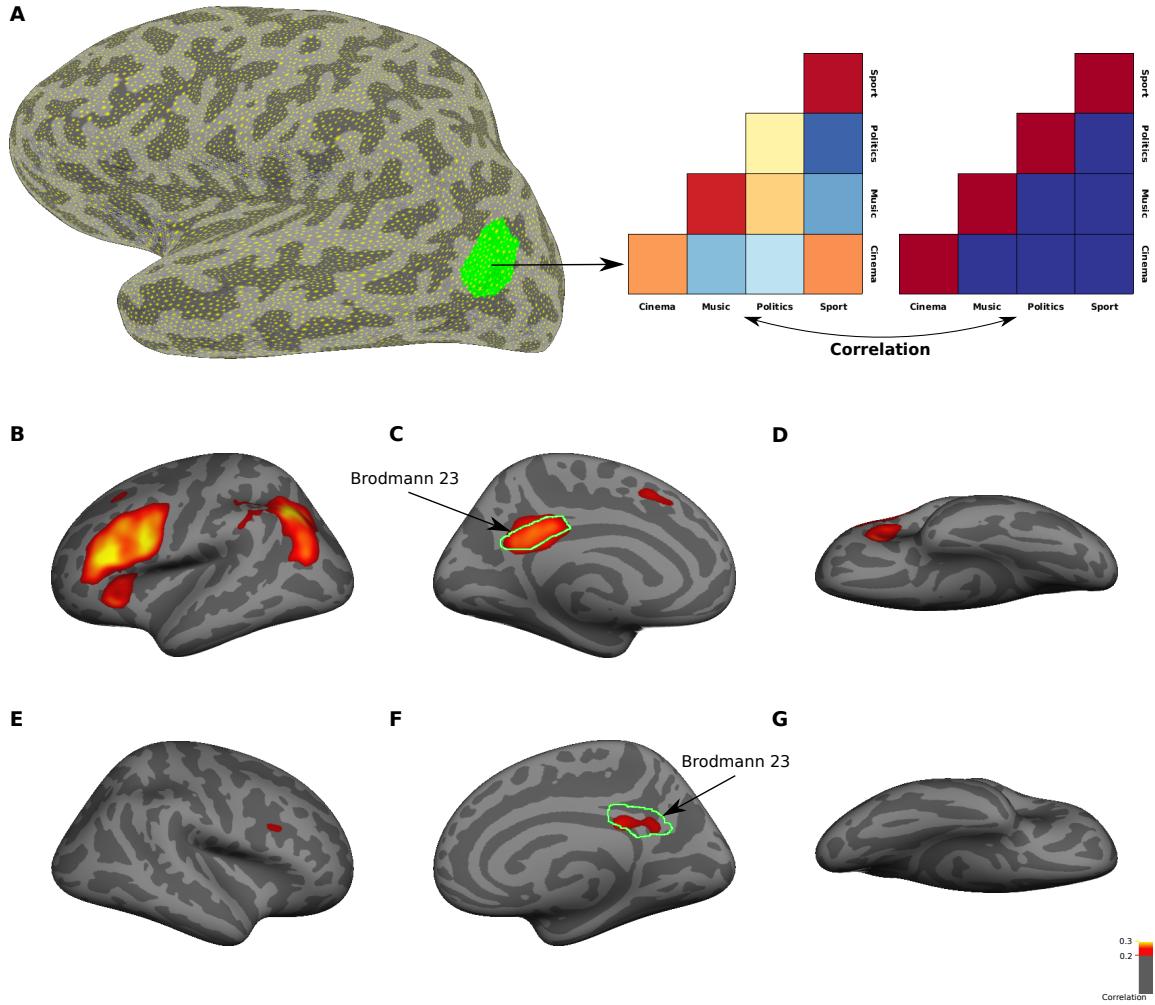


Figure 4.5: Whole-brain searchlight analysis for identifying regions that encode familiar face subcategories. A, The procedure for surface-based searchlight analysis. For each surface mask, Kendalls tau correlation between neural sdRSM and categorical model was computed. Here we used a model to test pattern information for familiar face subcategories. The green region is an example surface mask in a representative subject. B-G, The maps show averaged correlation coefficient values from 16 subjects in left (B-D) and right (E-G) hemispheres. Only vertices with a significant ($p < 0.05$, t-test, FDR-corrected) correlation are included in the maps. The correlation maps are displayed on lateral (B,E), medial (C,F), and ventral (D,G) views of an inflated cortical surface (fsaverage surface). The border of Brodmann area 23 was defined in both hemispheres of fsaverage surface based on PALS-B12 atlas.

4.3.4 ROI analysis

The results of searchlight analysis showed that categorical information of familiar face subcategories was strongly represented in Brodmann area 23 a subdivision of

PCC. However, this analysis did not reveal any representations of categorical information in visual cortical regions. We therefore used an ROI analysis approach to further explore the sensitivity of visual cortical regions (including V1, OFA, FFA and, ATFP) to the categorical information of familiar faces. We also included Brodmann area 23 in the ROI analysis. The ROI analysis differs from the searchlight analysis in two important ways. First, the pattern analysis is performed for voxels within functionally (or anatomically) defined areas. These areas may not necessarily have a circular shape, as it is assumed in the searchlight analysis. Second, the number of voxels in a given ROI can be higher than a predefined number used in the searchlight analysis.

Pattern information in each ROI was assessed using two different methods of MVPA: correlation method and classification method (see Methods). Figure 4.6 shows the results of ROI analysis. In the correlation matrices of Brodmann area 23, the activations were more similar in within-category conditions than between-category conditions (diagonal vs. off-diagonal cells in the correlation matrix), especially in the left hemisphere. Such pattern was not observed in the correlation matrices of other ROIs. This result confirmed that Brodmann area 23, but not the selected visual cortical regions, contained information about familiar face categories. In Brodmann area 23 of both hemispheres, the SVM classification performance was also significantly higher than chance level in five (out of six) pairwise comparisons between face categories again demonstrating that this area had separable representations of familiar face categories. In contrast, no pairwise comparisons showed significant performance in FFA and ATFP. Categorical information was weakly represented in OFA and V1. The SVM classification performance was significantly above chance level in two pairwise comparisons in right OFA, and in two pairwise comparisons in left and right V1. This result confirmed that low-level visual features, which were predominantly represented in V1, had minimal contributions to the discrimination of familiar face categories.

In each ROI, the categorical information for familiar faces was also quantified us-

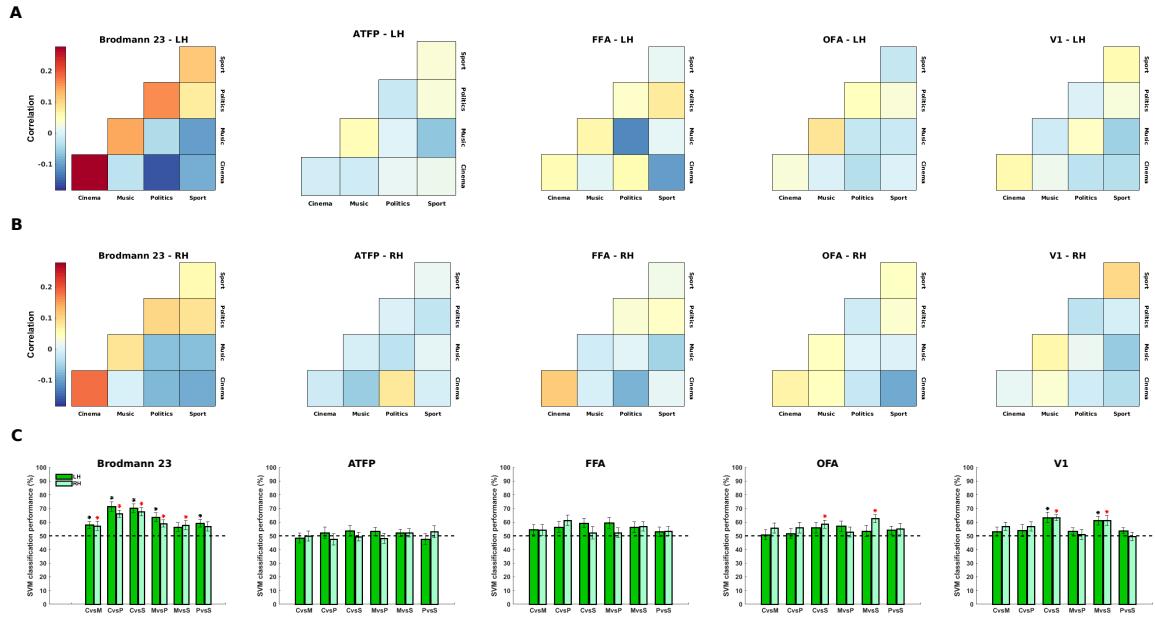


Figure 4.6: ROI-based MVPA for familiar face subcategories. From left to right, graphs depict results of multivariate analysis for different ROIs including Brodmann area 23, ATFP, FFA, OFA, and V1. The matrices in panels A and B are averaged neural sdRSMs across 16 subjects in left (A) and right (B) hemispheres. sdRSM in each subject was obtained by averaging sdRSMs across 100 random permutations of run splitting. The matrices are triangular because corresponding elements in upper triangular and lower triangular parts of sdRSMs have been averaged. The color scale bar represents Pearson correlation coefficient values. Some of the correlation values are negative mainly because normalized data have been used (see Methods). The bar plots in panel C show SVM classification performance for six pairwise comparisons between face categories (C: cinema, M: music, P: politics, S: sport). Dark green and light green bars show results of classification analysis in left and right hemispheres, respectively. Black and red asterisks indicate significant performance ($p < 0.05$, t-test, FDR-corrected) for dark green and light green bars, respectively. Dashed black line indicates the chance level of 50%. Error bars denote the standard error of the mean calculated across subjects.

ing CDI metric (difference between the correlation values in diagonal and off-diagonal cells of the correlation matrix). In this analysis, we included two subcortical areas (amygdala and hippocampus), which were previously reported to have selective activation for familiar faces (Ramon et al., 2015; Viskontas et al., 2009). The result of this analysis is shown in Figure 4.7. As expected, Brodmann area 23 contained the highest amount of categorical information in both hemispheres. All other cortical areas (V1, OFA, FFA, and ATFP) and subcortical areas (amygdala and hippocampus) contained weak and non-significant categorical information.

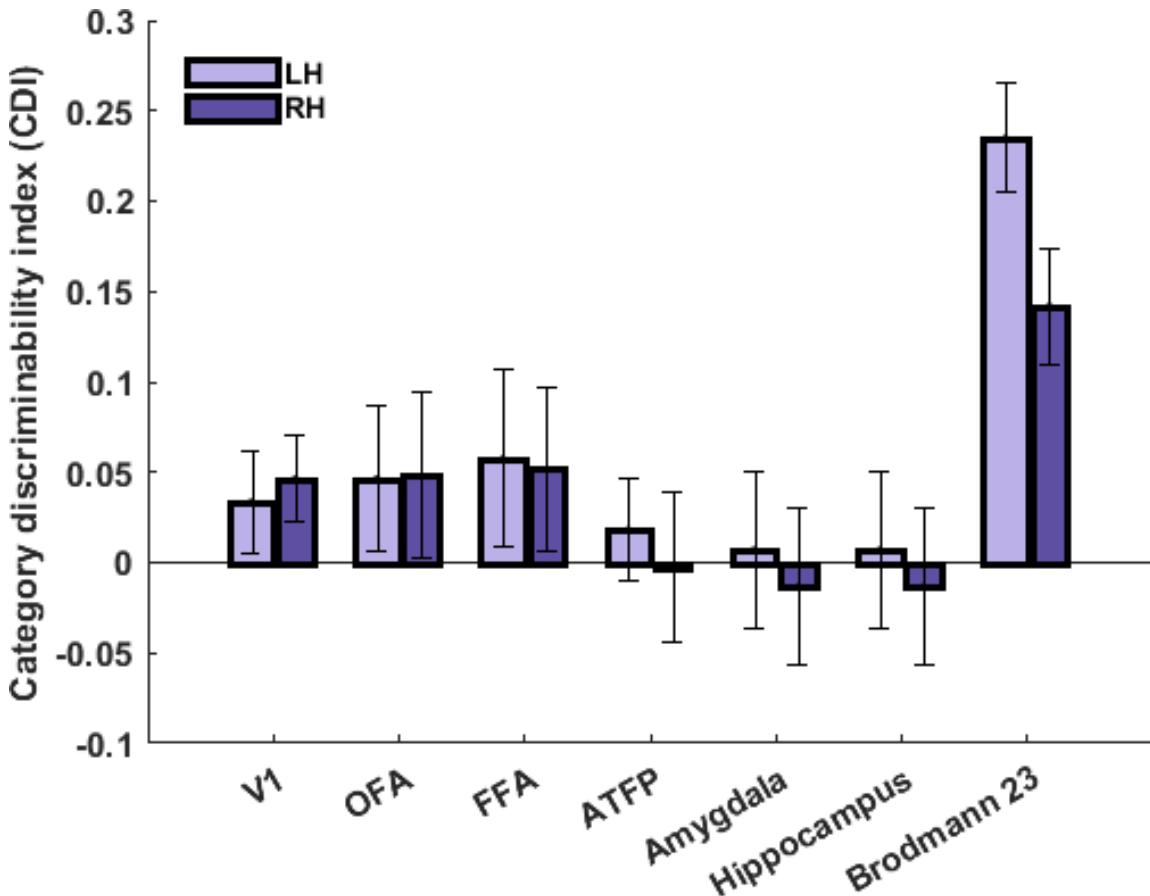


Figure 4.7: CDI for familiar face subcategories in selected ROIs. The bar plot shows CDI (a metric for encoding categorical information of familiar faces) in V1, OFA, FFA, ATFP, Amygdala, Hippocampus, and Brodmann area 23. Light purple and dark purple bars show CDI in left and right hemispheres, respectively. CDI was significantly greater than zero ($p < 0.05$, t-test, FDR-corrected) only in Brodmann area 23. Error bars denote the standard error of the mean calculated across subjects.

4.3.5 Cortical representations of familiar face identities

To localize regions containing information for familiar face identities, we did a surface-based searchlight analysis (Figure 4.8A). For each region on the cortical surface, sdRSM with the size was computed. Rows and columns of the matrix corresponded to 32 individual examples of familiar faces. Neural sdRSM was correlated with identity matrix of the same size using rank correlation, then the correlation coefficient values were mapped on the cortical surface. The searchlight maps from

group analysis are shown on the inflated surfaces of both hemispheres in Figure 4.8B-G. Different identities of familiar faces could be decoded significantly in PCC of left hemisphere, in a region that was located immediately superior to Brodmann area 23. Information for familiar face identities was also represented in discrete regions within LPFC of both hemispheres. In the searchlight analysis for familiar face identities, the correlation values were low possibly due to a high number of conditions used in this analysis. Nonetheless, the searchlight maps revealed localized regions which had significant information for familiar face identities. Similar to the result of searchlight analysis for familiar face subcategories, no significant cluster was found in ventral temporal cortex.

4.3.6 Topographic organization of semantic face representations in PCC

A consistent feature of our univariate and multivariate analyses was an activation in PCC/Precuneus of left hemisphere. However, the peaks of activations for different levels of semantic face processing appeared to be located in different spots within PCC. In the next analysis, we aimed to investigate the topographic relationship between representations for familiar faces, familiar face subcategories, and familiar face identities in left PCC. In this analysis, we also included a map from the HCP database, which showed visual activations for faces in left PCC. This map was obtained by comparing faces versus other categories (places, objects, and body parts). Figure 4.9A-D show unthresholded maps from four analyses: (i) univariate comparison between faces vs. other categories, (ii) univariate comparison between familiar faces vs. unfamiliar faces, (iii) multivariate searchlight analysis for familiar face subcategories, and (iv) multivariate searchlight analysis for familiar face identities. In each map, the hot spot area, which was located in left PCC, was delineated. These hot spot areas overlapped with each other though there was also a systematic shift in the location of areas (Figure 4.9E). The area distinguishing faces from other categories was located in the posterior-superior subdivision of left PCC. The area dis-

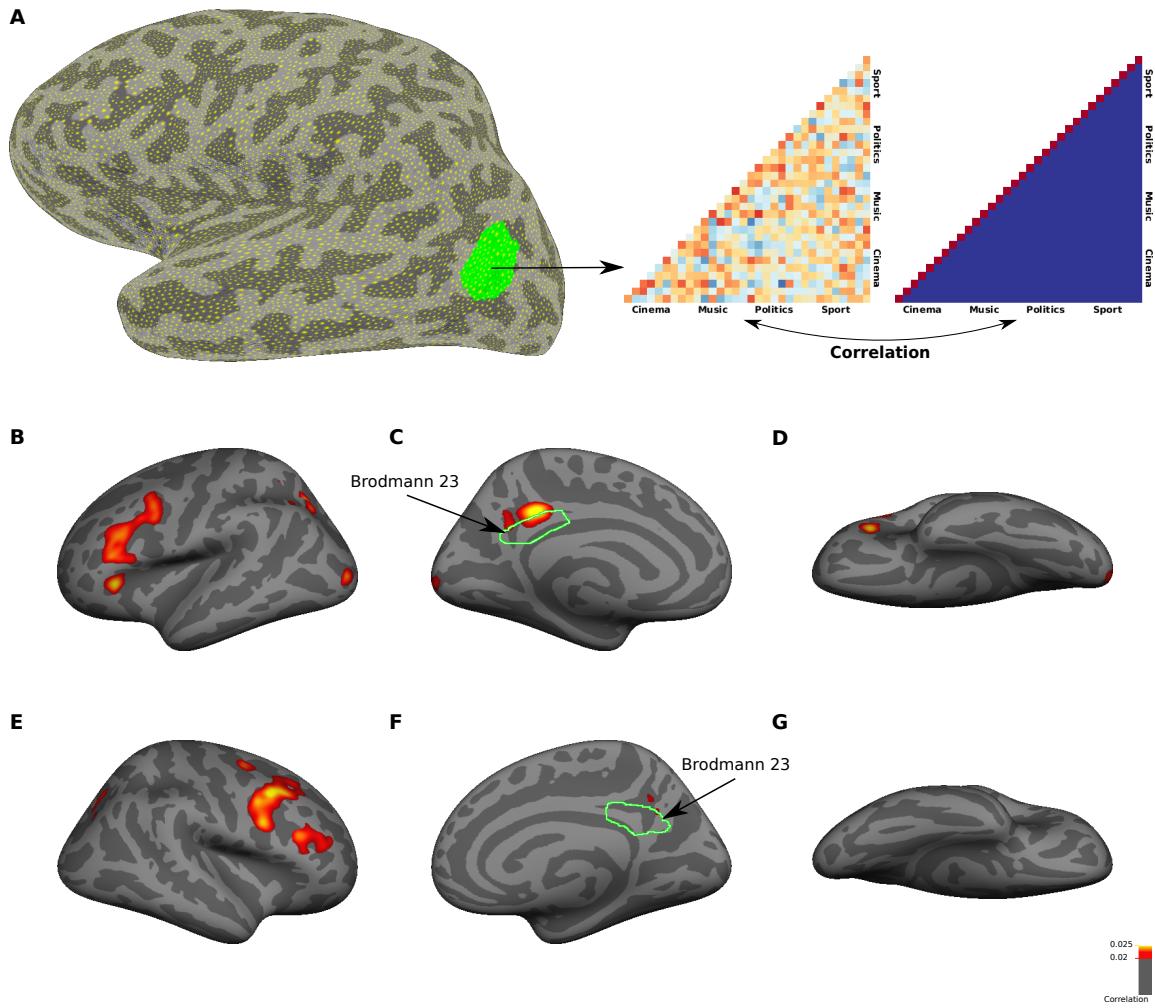


Figure 4.8: Whole-brain searchlight analysis for identifying regions that encode familiar face identities. A, The procedure for surface-based searchlight analysis was similar to the one described in Figure 4.5A, except that here we used a model to test pattern information for familiar face identities. B-G, The maps show averaged correlation coefficient values (Kendalls tau correlation) from 16 subjects in left (B-D) and right (E-G) hemispheres. Only vertices with a significant ($p < 0.05$, t-test, uncorrected) correlation are included in the maps. The correlation maps are displayed on lateral (B,E), medial (C,F), and ventral (D,G) views of inflated fsaverage surface.

tinguishing familiar faces from unfamiliar faces was located in the posterior-inferior subdivision of left PCC. Finally, the area distinguishing different subcategories and identities of familiar faces was located more anteriorly in left PCC.

To evaluate the topographic relationship between representations for familiar faces and familiar face subcategories at the individual subject level, we obtained the

peak activations for univariate analysis (the highest significant response to familiar than unfamiliar faces) and the peak activations for multivariate searchlight analysis (the highest correlation between response pattern and categorical model) in each subject. The peak-finding was confined to the ROI of Brodmann area 23 in the left hemisphere. As shown in Figure 4.9F, the peak activations for multivariate searchlight analysis were clearly shifted anteriorly in half of the subjects.

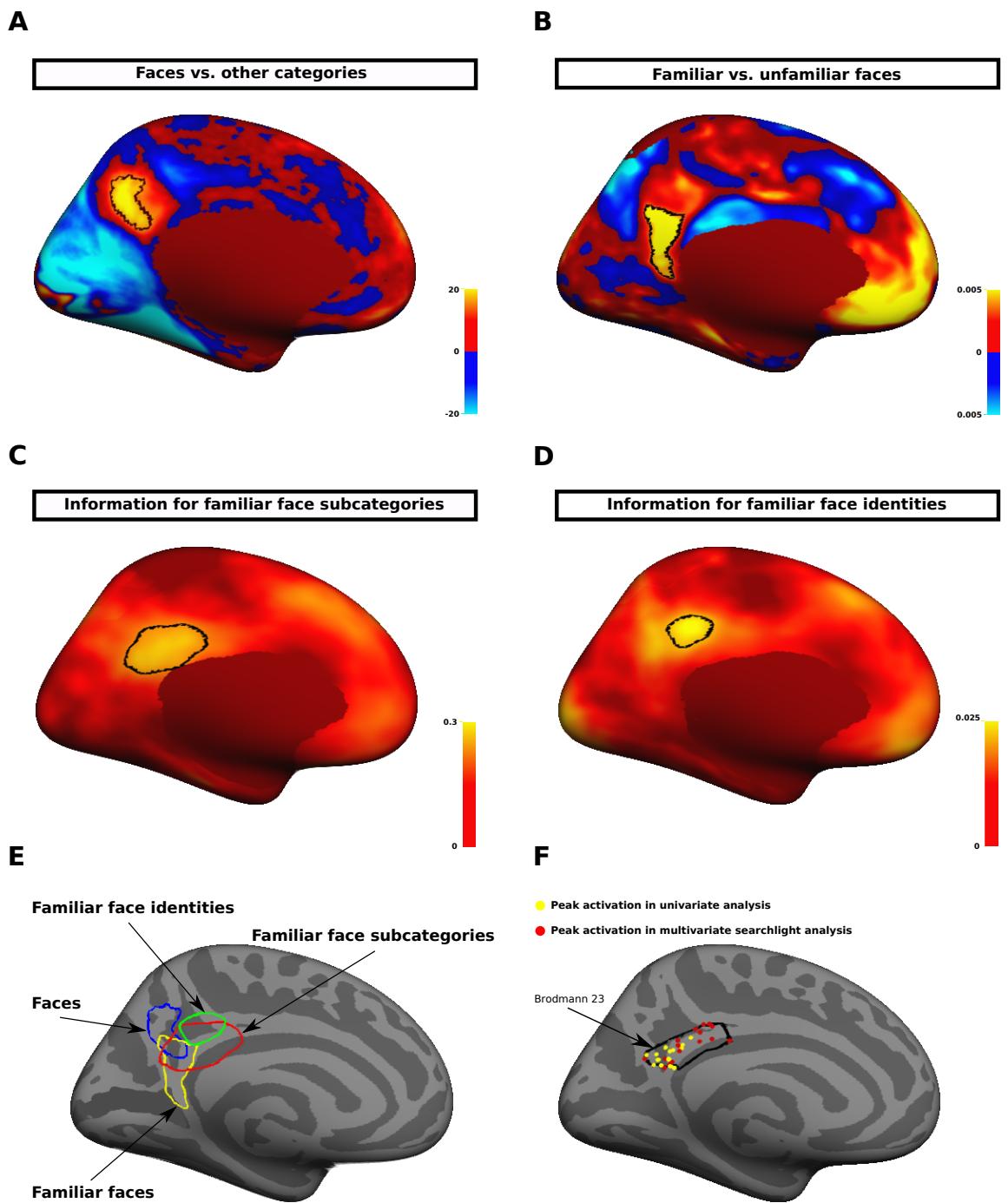


Figure 4.9: Caption next page.

Figure 4.9: Topographic organization of semantic face representations in PCC. A, Unthresholded map of group-average ($N = 787$ subjects) activation for the contrast of faces (red/yellow) versus other categories (blue/cyan). The most significant face-selective vertices (the top 1% of vertices with the highest z-values) are indicated with a black border. The color scale bar represents z-values. B, Unthresholded map of group-average activation for the contrast of familiar (red/yellow) versus unfamiliar (blue/cyan) faces. The significant vertices ($p < 0.05$, t-test, FDR-corrected) are indicated with a black border. The color scale bar represents p-values. C, Unthresholded map of searchlight analysis for subcategories of familiar faces. The area within the black border indicates the thresholded vertices (Kendalls tau correlation > 0.2 , $p < 0.05$, t-test, FDR-corrected) shown in Figure 4.5C. The color scale bar is truncated to show positive correlation values. D, Unthresholded map of searchlight analysis for identities of familiar faces. The area within the black border indicates the thresholded vertices (Kendalls tau correlation > 0.02 , $p < 0.05$, t-test, uncorrected) shown in Figure 4.8C. The color scale bar is truncated to show positive correlation values. E, Topological organization of areas representing information of faces (blue), familiar faces (yellow), subcategories of familiar faces (red), and identities of familiar faces (green) in left PCC. F, The locations of the peak activations for univariate analysis (yellow dots) and multivariate searchlight analysis (red dots) within Brodmann area 23 in the left hemisphere. Each colored dot corresponds to one subject. All maps in this figure are displayed on medial view of the left hemisphere in fsaverage space.

Chapter 5

Discussion

In this study, we investigated how different levels of semantic information for familiar faces were represented in the brain. To address this question, we tested the brain responses to the images of familiar and unfamiliar faces. Familiar faces were selected from four categories of famous people, each with specific social information and semantic associations. To discover cortical areas encoding semantic information of faces, we gradually increased the specificity of our fMRI analysis from univariate analysis to different levels of multivariate analysis. The result of univariate analysis showed that information about familiarity of faces was represented in PCC, ACC, ATL, and TPJ. This result was consistent with previous neuroimaging findings ([Gobbini et al., 2004]). The result of multivariate searchlight analysis for familiar face subcategories revealed that information about different subcategories could be decoded from neural patterns in PCC and also regions within the frontoparietal network. The result of multivariate searchlight analysis for familiar face identities revealed that information about different identities could be decoded from neural patterns in PCC and also areas in the frontal cortex. Identification of individual faces of familiar face category could be considered the most specific level of semantic face processing. To include a more general level of semantic face processing, we used the HCP database with a large sample of subjects to localize neural structures that were more sensitive to faces than other semantic categories such as places, objects, and body parts. As expected, these structures included face patches

within ventral temporal cortex plus a relatively new area within PCC/Precuneus. The activations in PCC/Precuneus from all levels of analyses had some overlap with each other. However, the peak activations were spatially distinct. Overall, these results demonstrated that different subdivisions within PCC/Precuneus may have a central role in processing the face-related semantic information. Moreover, semantic information of faces appeared to be progressively disentangled/abstracted by a hierarchically organized network of areas in PCC/Precuneus. Semantic processing of faces in this network could be complimentary to perceptual processing of faces, which is mainly mediated by the face-selective network in ventral temporal cortex.

5.1 Representation of information for familiar faces

In humans, PCC/Precuneus (as part of the posterior medial cortex) plays an important role in representing face-related semantic information. Neuroimaging studies have reported that PCC/Precuneus is well activated by familiar faces including one's own face ([Kircher et al., 2000, Platek et al., 2008, Sugiura, 2015]), personally familiar faces ([Sugiura et al., 2009a, Leibenluft et al., 2004, Pierce et al., 2004, Gobbini et al., 2004, Lee et al., 2013, Blank et al., 2014b]), and famous faces ([Leveroni et al., 2000, Eger et al., 2005, Bernard et al., 2004]). Neuropsychological evidence also provides support for the role of PCC/Precuneus in familiar face processing. One study implicated that failure of familiar/famous face recognition in congenital prosopagnosic patients could be attributed to abnormal functioning of PCC/Precuneus in the extended face network ([Pierce et al., 2004]). Another study showed that abnormal behavior of autistic subjects in recognizing familiar faces was correlated to the lower extent of activity in this area ([Pierce et al., 2004]).

While successful recognition of familiar faces entails both visual component and personal knowledge, the activity within PCC/Precuneus was mostly attached to person knowledge. The role of this area in person knowledge retrieval was corroborated by studies that experimentally associated faces with fictional knowledge ([Todorov

et al., 2007, Cloutier et al., 2011]) and studies that attributed the higher extent of activities for personally familiar than famous faces to the higher amount of associated person knowledge either episodic ([Gobbini et al., 2004]) or semantic ([Fairhall et al., 2014]) knowledge. Other studies showed that the higher sensitivity to personally familiar than famous faces in PCC/Precuneus was mediated by the caudal part of this area, and the activation relevant to famous faces was located more rostrally ([Sugiura et al., 2009b, Blank et al., 2014b]). In the present study, the location of familiarity-selective area in PCC/Precuneus was consistent with the location that was reported to be selective for famous faces (i.e. posterior to corpus callosum).

PCC was not the only region that revealed higher activity to familiar faces. Consistent with previous findings ([Leveroni et al., 2000, Gobbini and Haxby, 2007, Visconti Di Oleggio Castello et al., 2017b]), other areas in ACC, ATL, and TPJ also revealed sensitivity to familiar stimuli. It has been suggested that these areas are recruited in processes such as person perception and person knowledge. Here, while these areas showed a strong activity with respect to the familiarity attribute, they did not show any representation of categorical information for subcategories of familiar faces. Thus, the observed activity in these areas was less likely to be related to contextual, social, and semantic information of faces. The activity in ACC may have been driven by information about traits of familiar faces, which could have been retrieved automatically by subjects. Activation in ACC has been reported in tasks requiring participants to form impressions about others, make inferences about psychological traits of others ([Denny et al., 2012, Wagner et al., 2018, Jenkins et al., 2008]), make inferences about mental states of others ([Frith and Frith, 1999]), and unconsciously process emotional/affective information of faces ([Killgore and Yurgelun-Todd, 2004]). The activity in TPJ could also reflect covert retrieval of distinct names associated with familiar faces (Gesierich et al., 2012).

5.2 Representation of information for subcategories of familiar faces

In the multivariate analysis, we found an area within PCC, which contained reliable and decodable information for familiar face subcategories. Functionally, PCC/Precuneus is typically involved in high-level cognitive processes including episodic and semantic memory. The posterior neural structures within PCC/Precuneus were reported to be sensitive to autobiographical retrieval and episodic memory, whereas the anterior neural structures within this area were more responsive to semantic information ([Cavanna and Trimble, 2006, Binder et al., 2009]). What we know about the function of PCC is largely based on the cognitive tasks which differentiate neural activities during episodic versus semantic information processing. However, it is not clear how various types of episodic or semantic information are represented in PCC. One possibility is that this area has only a modulatory role in encoding these information, which happens through an enhanced activity during episodic/semantic functional tasks. Alternatively, information of different episodic/semantic attributes may be represented in the patterns of activity in this area. Our analysis showed that information of four categories of famous faces could be decoded from the patterns of activity in PCC. Since knowledge about famous people is usually acquired through semantic information (not through direct social relationships and episodic events), we can suggest that PCC plays an important role in encoding different attributes of semantic information.

In our analysis to define regions representing information for subcategories of familiar faces, we also found activities in a network of areas within PPC and LPFC. Although activity in these areas has been reported invariably during tasks involving semantic processing ([Fletcher, 2001]) or maintenance of semantic information ([Gabrieli et al., 1998]), recruitment of these areas might be less bound to long-term neural representation of semantic information. There are numerous evidence showing that a distributed network of areas in parietal and prefrontal cortex, located

at the interface of sensory and motor systems, gradually transforms stimulus-related information to an appropriate behavioral response ([Christophel et al., 2017]). PPC has been reported to be involved in short-term memory representation of task-related visual features (like color and shape) ([Marois and Todd, 2004, Xu and Chun, 2006, Bettencourt and Xu, 2015]) and behaviorally relevant object identity information (like famous faces and well-known cars) ([Jeong and Xu, 2016]). Prefrontal regions are also engaged in encoding short-term memories of sensory stimuli in an amodal format for the guidance of upcoming behavioral actions ([Spitzer et al., 2014]). In our experiment, subjects were asked to attend to the category of the presented face stimulus, and after a delay (1 second), compare it with a letter stimulus and report a match/non-match response. It is possible that semantic information of face categories is initially processed in PCC, then the categorical information is sent to the network of parietofrontal areas where the attended information is temporarily maintained in a short-term memory buffer for an upcoming comparison with the letter stimulus.

5.3 Representation of information for familiar face identities

In the multivariate analysis, we found a distinct area within PCC, which contained reliable and decodable information for familiar face identities. The information in this area was weak; however, the result was consistent with the finding of a recent study which reported decodable information for familiar face identities in the dorsal part of PCC ([Tsantani et al., 2019, Visconti Di Oleggio Castello et al., 2017a]). Several factors may have contributed to weak identity-specific information. As mentioned in the Results section, the searchlight analysis for familiar face identities had a high number of conditions and consequently a low statistical power. There was also a low demand for identification in our task, as subjects were required to attend to semantic subcategories (not specific identities) of familiar face stimuli (e.g. a politician face instead of Barak Obamas face). An fMRI study with an optimized

design for familiar face identification may show strong activities in PCC for different face identities.

In addition to PCC, we found that regions within LPFC also contained information for familiar face identities. These prefrontal representations were slightly stronger in the right hemisphere. A recent study has reported an area in a similar location in the right inferior frontal cortex for decoding visually-familiar individual faces invariant of head view ([Guntupalli et al., 2017]). View-invariant representation of face identities in this area might be critical for engaging PCC and other parts of the extended face network in the successful recognition of familiar individuals.

5.4 Representation of perceptual information for faces in PCC

In the comparison between faces versus other object categories (a more general level of face processing), we localized a face-selective area in the posterior part of PCC. Given the fact that stimuli used in this level of analysis were all unfamiliar and did not contain any predetermined personal knowledge, face representation in this area would not be related to attributes such as familiarity or knowledge about each identity. Rather, the area may encode some aspects of perceptual information for faces. This idea is supported by studies which showed the role of this area in perceptual learning of faces and also in the conditions of increased perceptual demands when participants had to access to the information of specific identities. Neuroimaging studies reported that this area was face-responsive using perceptual learning paradigm ([Leveroni et al., 2000, Gobbini et al., 2004, Maguire et al., 2001, Katanoda et al., 2000, Kosaka et al., 2003, Natu and O'Toole, 2015, Cloutier et al., 2011, Anzellotti and Caramazza, 2016]), fMRI-adaptation paradigm ([Weibert et al., 2016, Pourtois et al., 2005]), visual imagery ([Ishai et al., 2000]), functional localizers with dynamic facial stimuli ([Fox et al., 2009]), and functional localizers with a working memory task ([Anzellotti and Caramazza, 2017]). A recent EEG-fMRI study also showed that activation in PCC/Precuneus covaried with early ERP markers of face

processing ([Bayer et al., 2018]). In our analysis, we used category localizer data from the HCP database. A large sample size and presence of a working memory task in this dataset enabled us to detect a robust and localized activity for faces in PCC.

5.5 Hierarchical organization of semantic face representations in PCC

Within PCC, the peak activations for different semantic face representations were spatially distinct though the extent of activations showed some overlap. Areas representing faces and familiarity were located in the posterior part of PCC, whereas areas representing subcategories and identities of familiar faces were located in the anterior part of PCC. This posterior to anterior gradient/hierarchy of face representations in medial parietal cortex is analogous to the posterior-anterior organization of face-selective areas in ventral temporal cortex (i.e. OFA –> FFA –> ATFP). The ventral pathway and medial pathway of face processing may serve as two parallel pathways with complementary functions: the ventral pathway for perceptual processing of faces (analysis of facial features, configuration, viewpoint, and identity) and the medial pathway for semantic processing of faces (detailed analysis of familiar faces). Although, using fMRI, we did not (and perhaps we could not) investigate the connectivity between different subdivisions of PCC, we speculate that there is a flow of face-related information from posterior to anterior PCC, in which semantic information is processed at multiple levels from general to more specific levels. Such posterior-anterior distinction has been also proposed for a nearby region in retrosplenial complex (RSC) which is involved in scene perception and spatial navigation (Silson et al., 2016). It has been shown that the posterior part of RSC processes scene-related visual information, whereas the anterior part of RSC processes mnemonic information to reconstruct scenes from memory (Silson et al., 2019a). In medial parietal cortex, the area recruited during memory recall of specific places is located posterior and ventral to the area recruited during memory recall of familiar

people (Silson et al., 2019b).

5.6 The role of OFA and FFA in semantic face processing

There has been a considerable controversy surrounding sensitivity of core face-selective areas (OFA and FFA) to semantic information of familiar faces. Some studies reported no significant modulation of activity for the familiarity attribute ([Dubois et al., 1999, Leveroni et al., 2000, Gorno-Tempini and Price, 2001, Eger et al., 2005, Ramon et al., 2015]), while others found weak results ([Sergent et al., 1992, Rossion et al., 2003, Kosaka et al., 2003, Gobbini and Haxby, 2006]). One potential caveat of the studies, which reported high-level abstract information of faces in core face-selective areas, was that the stimuli used in those studies were not carefully matched based on low-level visual features. To control for this confound, one study compared semantic component of faces when the visual information of faces was absent ([Van Den Hurk et al., 2011]). The results revealed weak selectivity to semantic information in FFA. Our univariate analysis showed no sensitivity to familiarity in OFA and FFA. Additionally, our multivariate analysis showed that these areas could not discriminate between patterns of activities for different subcategories of familiar faces. Overall, these findings support the idea that core face-selective areas are not particularly involved in processing the semantic information of faces.

5.7 The role of ATL in semantic face processing

While PCC was sensitive to different levels of semantic information of faces, no such sensitivity was observed in ATL. It is generally accepted that ATL plays a critical role in semantic processing ([Skipper et al., 2011]), and its ventral subdivision contains view-invariant information of face identities ([Anzellotti et al.,

2014, Kriegeskorte et al., 2007, Nestor et al., 2011]). It has been suggested that face-selective areas in ATL might link invariant perceptual information of faces with person-specific semantic information ([Collins and Olson, 2014]). A recent fMRI study in monkeys also reported two face patches in macaques ATL, which selectively responded to faces of familiar monkeys ([Landi and Freiwald, 2017]). In our study, we used famous faces which clearly contained semantic information; however, we could not observe any categorical information for famous faces in face-selective areas of ATL. Similarly another fMRI study failed to find successful decoding of the identity of famous faces in ATL ([Axelrod and Yovel, 2015]). ATL is located in a region which is prone to susceptibility artifacts ([Devlin et al., 2000, Gorno-Tempini et al., 2002]). Thus, the lack of pattern information in this region could potentially be due to insufficient signal-to-noise ratio of fMRI signal. It is also possible that neural representations of semantic information in ATL are based on a sparse code which may not be resolvable at current imaging resolutions. As shown previously, sparsely distributed neurons in anterior medial temporal cortex could encode abstract information of faces (e.g. a neuron that responded selectively and invariantly to pictures and word of a famous celebrity like Jennifer Aniston) ([QuijanQuiroga et al., 2005]). Further research using optimized imaging techniques could shed light on whether face-selective areas within ATL contain categorical information for familiar faces.

Collectively, we found distinct areas within PCC/Precuneus, which represented semantic information of faces in different levels of abstraction. The functional segregation of neural structures within PCC suggests that semantic information of familiar faces could be progressively disentangled by a network of hierarchically organized areas a network which is dissociable from the network of classic face-selective areas in ventral temporal cortex. In our study, we used a limited number of face subcategories and individual faces. fMRI responses in the PCC areas could be tested for other social classes of face stimuli and also for a larger number of face identities. Furthermore, it would be interesting to evaluate cortical representations for subcategories of familiar faces, familiar scenes/buildings, and familiar objects in one experimental setup. Such study could provide a more comprehensive view of functional organization in medial

parietal cortex.

Acknowledgments: We thank Shaghayegh Karimi, Mojtaba Barzegar, and other members of the MRI team in National Brain Mapping Laboratory (Tehran, Iran) for designing MR pulse sequences and providing data acquisition service. We also thank Hossein Esteky, Hossein Vahabi, Elahe Yargholi, Grace Rice, and Rocco Chiou for helpful discussions. This research was supported by a funding from Institute for Research in Fundamental Sciences (Tehran, Iran). The authors declare no competing interests.

Chapter 6

Appendix Figures

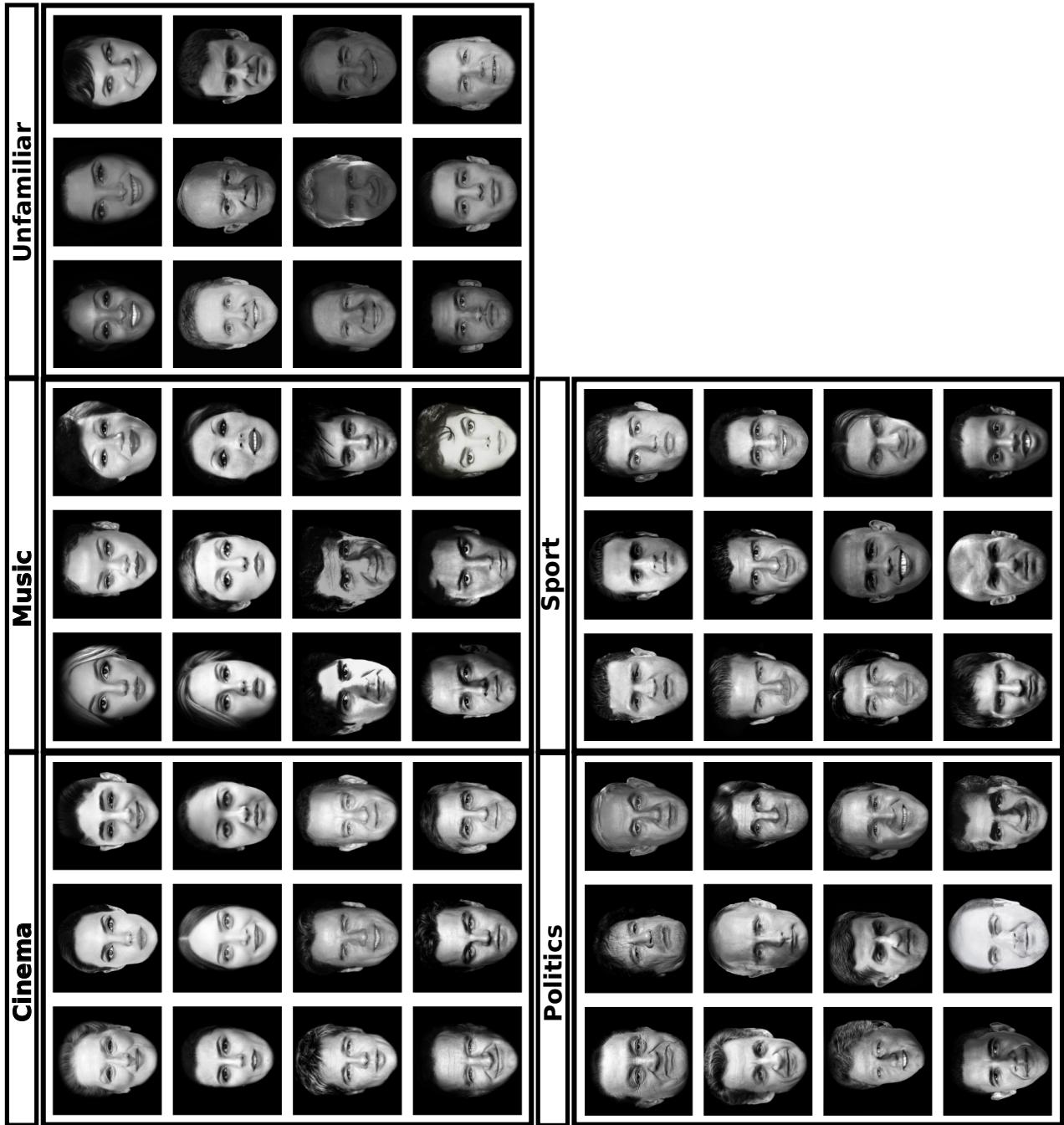


Figure 6.1: All samples of face stimuli used in the fMRI experiment 1.

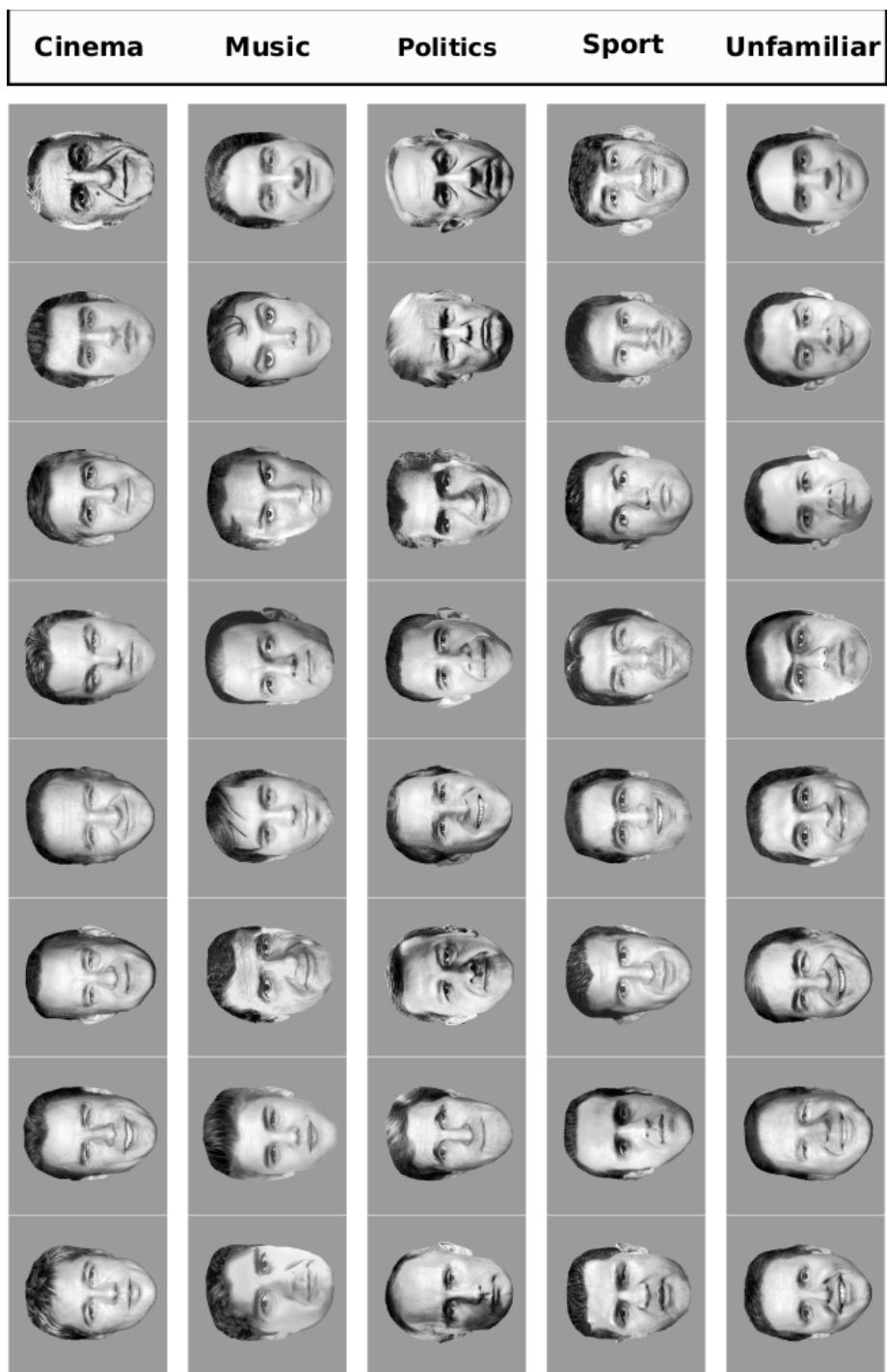


Figure 6.2: All samples of face stimuli used in the fMRI experiment 2.

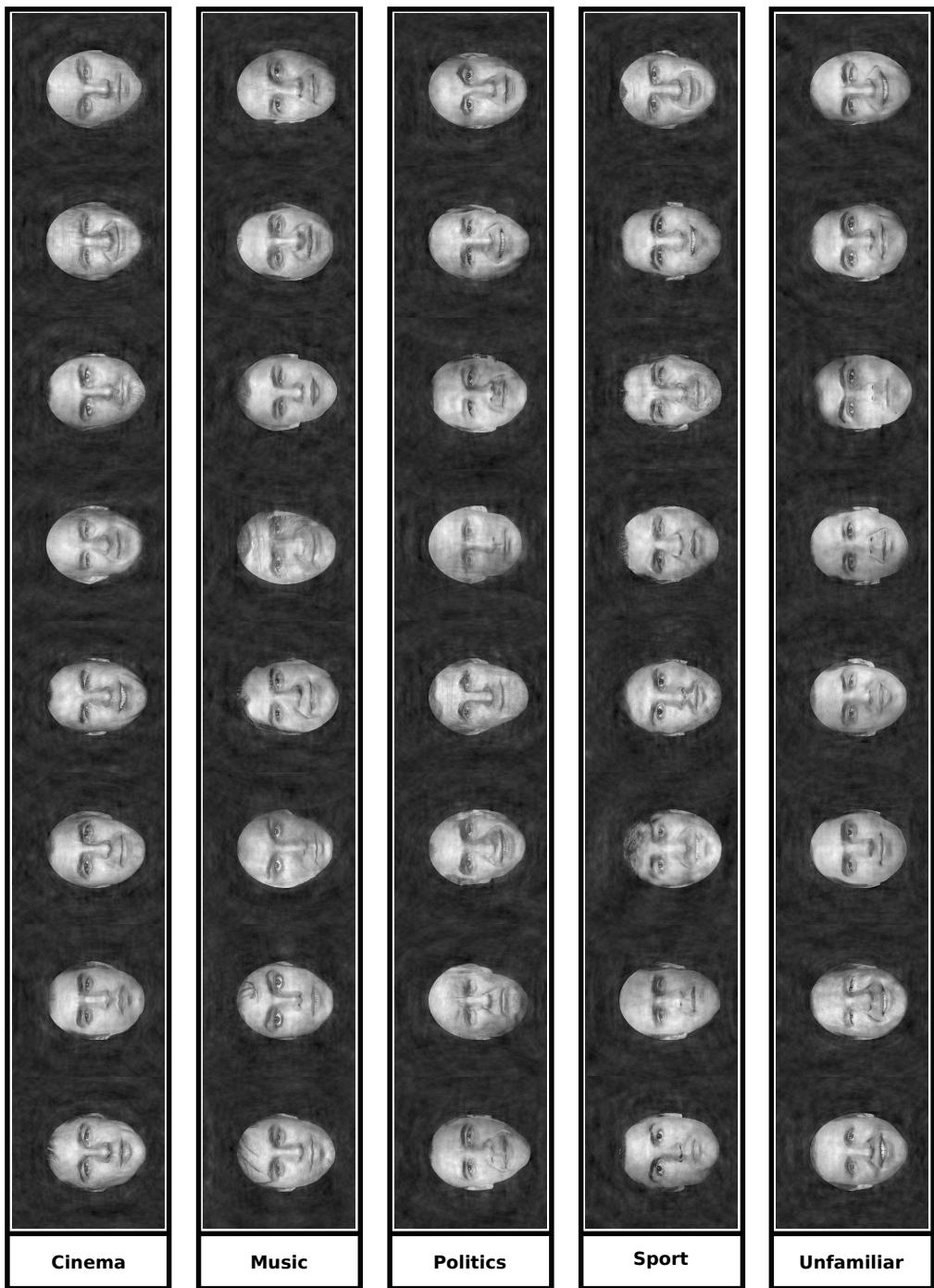


Figure 6.3: (Caption next page.)

Figure 6.3: All samples of face stimuli used in the fMRI experiment 3. The stimulus set contained faces of famous actors (cinema category), famous singers (music category), famous politicians (politics category), famous football players (sport category), and unfamiliar persons (unfamiliar category). There were eight images in each category. Images of all identities did not differ by any distinctive features such as gender, visual view, gaze direction, or facial expression. Also the images did not include characteristic features such as beard, mustache, or glasses. All images were transformed to grayscale format, masked with an oval-shaped aperture, and equalized with respect to low level visual features such as size, brightness, contrast, luminance histogram, and power spectrum.

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