BEYOND THE FFA: UNDERSTANDING FACE REPRESENTATION
WITHIN THE ANTERIOR TEMPORAL LOBES

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ABSTRACT

Extensive research has supported the existence of a specialized face-processing network that is distinct from the visual processing areas used for general object recognition. The majority of this work has been aimed at characterizing the response properties of the fusiform face area (FFA) and the occipital face area (OFA), which together are thought to constitute the core network of brain areas responsible for facial identification. Although accruing evidence has shown that face-selective patches in the ventral anterior temporal lobes (vATLs), within perirhinal cortex, play a necessary role in facial identification, the relative contribution of these brain areas to the core face-processing network has remained unarticulated. The current study assessed the relative sensitivity of the anterior face patch, the OFA, and the FFA, to different aspects of person information. Participants learned to associate a name and occupation label, or a name only, with different facial identities. The sensitivity of the face processing areas to facial identity, occupation, and the amount of information associated with a face was then assessed. The results of a multivoxel pattern analysis (MVPA) revealed that distributed activity patterns in the anterior face patch contained information about facial identity, occupation, and the amount of information associated with a face, with the sensitivity of the anterior face patch to occupation and amount of information being greater than the more posterior face processing regions. When a similar analysis was conducted that included all voxels in the perirhinal cortex, sensitivity to every aspect of person information increased. These results suggest that the human ventral anterior temporal lobes may be critically involved in representing social, categorical, information about individual identities.

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CHAPTER 1

INTRODUCTION

The neural basis of face perception has been the focus of extensive research as it offers insights into both the computational architecture of visual recognition, and the functional organization of the brain (Kanwisher, 2010). Results from clinical (Moscovitch, Winocur, & Behrmann, 1997) and psychophysical (for a review see Farah, Wilson, Drain, & Tanaka, 1998; Hole, George, & Dunsmore, 1999) studies suggest that specialized processes are used for recognizing faces that are distinct from those used for general object recognition. These findings have been corroborated by a large body of neuroimaging work suggesting that specialized cortical areas exist that preferentially respond to faces, relative to other visual objects (Haxby, Hoffman, & Gobbini, 2000; Kanwisher & Yovel, 2006).

Of the regions that respond to faces more than other objects, the fusiform face area (FFA), occipital face area (OFA), and posterior superior temporal sulcus (STS) are proposed to constitute the "core" face recognition system, whereas the ventral anterior temporal lobe (vATL) and the amygdala are part of the "extended network" for face recognition (Haxby, Hoffman, & Gobbini, 2000; Rossion, Schiltz, & Crommelinck, 2003). This proposal has lead to the presumption that the vATLs play a non-critical role in face processing. However several lines of evidence strongly suggest that the vATLs are highly interconnected with the FFA and OFA and play a *necessary* role in normal face perception and identification. Indeed, face-processing deficits have been more reliably observed following damage to the vATLs than more posterior portions of the face-processing network (Heywood & Cowey, 1992).

Despite their importance for accurate facial identification, the vATLs have been largely ignored within the face perception literature. Early imaging studies of face perception likely missed anterior activations because they used a restricted field-of-view that excluded the inferior temporal lobe from image acquisition, or because they suffered from the well known problem of imaging the ATLs: susceptibility artifacts and signal distortion due to the proximity of these regions to the nasal sinuses and ear canals (Devlin et al., 2000; Visser, Jefferies, & Lambon Ralph, 2010). However, recent findings of face-selective cortical areas - "face patches" - in the vATLs of monkeys have spurred fMRI researchers to optimize signal detection in the vATLs, resulting in several recent studies supporting the existence of functionally homologous face-processing areas in the vATLs of humans (see Figure 1a) (Avidan et al., 2013; Pinsk et al., 2012; Rajimehr, Young, & Tootell, 2009; Tsao, Moeller, & Freiwald, 2008).
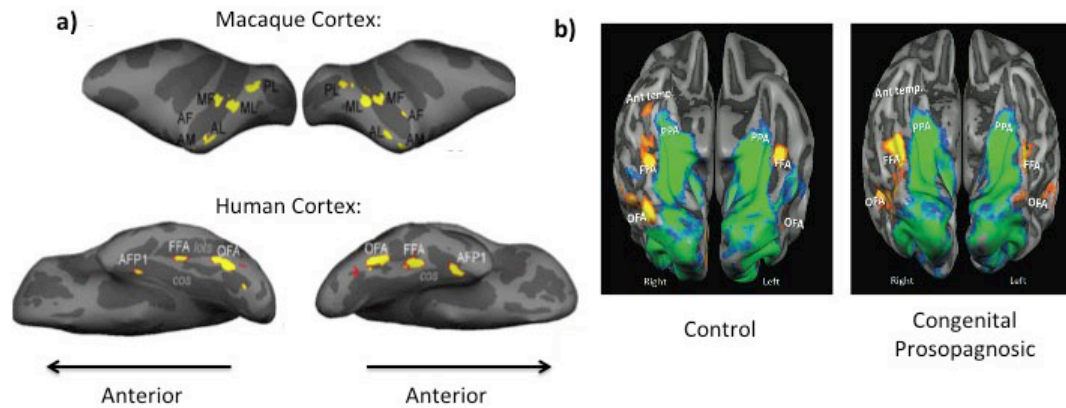
Figure 1. The Face-Processing Network (a) Face selective regions in a macaque (top) and human (bottom) have been superimposed on a lateral (top) and ventral (bottom) view of the inflated hemispheres with sulci shown in in dark gray. Top: PL, posterior face patch; MF, middle face patch in the STS fundus; ML, middle face patch on the STS lip, AF, anterior face patch in the STS fundus; AL, anterior face patch on the STS lip; AM, anterior face patch on the ventral surface of IT just lateral and anterior to the AMTS. Bottom: OFA, occipital face area; FFA, fusiform face area; AFP1, anterior face patch; cos, collateral; lots, lateral occipitotemporal. Taken with permission from Tsao, Moeller, & Freiwald, (2008). (b) Average activation maps for controls (left) and congenital prosopagnosics (right) for faces presented in a ventral view overlaid on a group-averaged folded cortical mesh of each group. The contrast faces > buildings is presented in red to yellow coloring, whereas the contrast buildings > faces is presented in blue to green coloring. Ant. Temp: anterior temporal cortex; PPA: Parahippocampal place area. Taken with permission from Avidan et al., (2013).

It is presently unclear how information is represented and processed within the face-processing network, and whether these face-processing regions are sensitive to perceptual, conceptual, or both perceptual and conceptual information about facial identity. Additionally, neuroimaging studies have shown that familiarity may produce a differential response to seen faces in several brain areas (George et al., 1999; Gorno-Tempini et al., 1998; Haxby et al., 2000; Henson, Shallice, & Dolan, 2000; Ishai, 2008; Nakamura et al., 2000) however the precise brain areas that code for face familiarity remain controversial. Here I will present a review of the literature aimed at addressing the following question: (1) What is the distinct contribution of the anterior face patch to face

perception and memory? I will first briefly review literature on the posterior face areas

(OFA and FFA; see Table 1) in order to place the role of the anterior face patch in

context.

TABLE 1. <u>Sensitivity of Face Processing Regions to Stimulus Manipulations.</u> This table presents a summary of similarities and differences between the known functionality of the OFA, FFA, and vATL face patches as assessed by fMRI.

	Contrast, luminance	Size	Position	Rotation	Identity	Emotional expression	Fame	Personal familiarity	Conceptual knowledge
OFA	Yes	No	Yes	Yes	Yes	Yes	No	No	No
FFA	No	No	No	Yes	Yes	Yes	?	?	?
vATL	?	?	?	?	Yes	?	Yes	Yes	Yes*

*One study reported that the ATL face patch was sensitive to conceptual knowledge that rendered a previously unfamiliar face salient and unique

The Fusiform Face Area

A large body research has focused on the fusiform face area (FFA), located in the

lateral middle fusiform gyrus (BA 37) which responds more strongly to faces than to

other objects (Allison, Puce, Spencer, & McCarthy, 1999; Bentin, Allison, Puce, Perez, &

McCarthy, 1996; Halgren, Raij, Marinkovic, Jousmäki, & Hari, 2000; Haxby et al., 1996;

Kanwisher, McDermott, & Chun, 1997; Sergent, Ohta, & MacDonald, 1992). Face

representations in the FFA are invariant to low-level stimulus manipulations such as

position (Kovács, Cziraki, Vidnyánszky, Schweinberger, & Greenlee, 2008), size

(Andrews & Ewbank, 2004; Grill-Spector et al., 1999; Kovács et al., 2008), spatial scale

(Eger, Schyns, & Kleinschmidt, 2004), and emotional expression (Winston, Henson,

Fine-Goulden, & Dolan, 2004); however they are sensitive to changes in the viewing

angle of faces (Andrews & Ewbank, 2004; Ewbank & Andrews, 2008; Fang & He, 2005;

Fang, Murray, & He, 2007; Pourtois, Schwartz, Seghier, Lazeyras, & Vuilleumier, 2005;

Xu, Yue, Lescroart, Biederman, & Kim, 2009) which is consistent with research in macaques (see Figure 2b).

The FFA is primarily implicated in the holistic processing of faces, and responds to the shape of facial features as well as the spacing between them (Liu, Harris, & Kanwisher, 2010; Schiltz, Dricot, Goebel, & Rossion, 2010; Yovel & Kanwisher, 2004). Another study using fMRI adaptation has shown that the FFA contains regions that exhibit both part-based and holistic neural tuning (Harris & Aguirre, 2010). Some (but not all) studies using fMRI repetition suppression have implicated the FFA in processing facial identity. Specifically, it has been shown that the repetition of two face images of the same individual reduces activity in the FFA relative to the repetition of the same individual (Andrews & Ewbank, 2004; Eger et al., 2004; Gauthier et al., 2000; Gilaie-Dotan & Malach, 2007; Loffler, Yourganov, Wilkinson, & Wilson, 2005; Winston et al., 2004), and that activation in the FFA correlates on a trial-by-trial basis with face identification accuracy (Grill-Spector, Knouf, & Kanwisher, 2004). These findings have been corroborated by studies utilizing multivoxel pattern analysis (MVPA) techniques (Anzellotti, Fairhall, & Caramazza, 2013; Goesaert & Op de Beeck, 2013; Nestor, Plaut, & Behrmann, 2011), but other groups using the same technique have failed to find this effect (Kriegeskorte, Formisano, Sorger, & Goebel, 2007; Natu et al., 2010).

Several neuroimaging studies have examined whether the FFA is sensitive to face familiarity, which is defined in the literature as faces for which there is conceptual or personal familiarity, such as the face of Barack Obama. A few studies reported increased activations in the FFA for faces made familiar through a laboratory training procedure (Lehmann et al., 2004; Verosky, Todorov, & Turk-Browne, 2013) whereas other studies

reported no difference in FFA activation for famous as compared to unfamiliar faces (Eger, Schweinberger, Dolan, & Henson, 2005; Gorno-Tempini & Price, 2001; Gorno-Tempini et al., 1998; Pourtois, Schwartz, Seghier, Lazeyras, & Vuilleumier, 2005) and one study showed *decreased* activation in the FFA for familiar relative to unfamiliar faces (Rossion, Kung, & Tarr, 2004). Thus the jury is still out as to whether the FFA is sensitive to conceptual familiarity.

<div align="center">The Occipital Face Area</div>

The OFA is located upstream from the FFA, on the inferior surface of the occipital gyrus (BA 19), and likely contributes to an earlier stage of face analysis than the FFA (Fairhall & Ishai, 2007). This region is primarily sensitive to low-level perceptual attributes of faces, such as spatial frequency (Eger et al., 2004), viewpoint (Ewbank & Andrews, 2008), and location (Kovács et al., 2008; Schwarzlose, Swisher, Dang, & Kanwisher, 2008). The results from several studies have suggested that the OFA is responsible for representing face parts, which are integrated into more complex representations at later processing stages, possibly by the FFA (Arcurio, Gold, & James, 2012; Liu et al., 2010; Pitcher, Charles, Devlin, Walsh, & Duchaine, 2009; Pitcher, Walsh, Yovel, & Duchaine, 2007; Schiltz et al., 2010).

Further supporting the role of the OFA in the low-level analysis of faces, Rothstein and colleagues (2005) showed that the OFA is sensitive to subtle perceptual differences between morphed faces, regardless of whether those faces are perceived as sharing an identity. This finding contrasts with the FFA, which is sensitive to the perceived identity, but not the physical similarity of faces (Rotshtein, Henson, Treves, Driver, & Dolan, 2005). Predictably, the OFA is largely insensitive to cognitive

manipulations such as conceptual familiarity (Davies-Thompson, Gouws, & Andrews, 2009; Rotshtein et al., 2005) or task requirements (Nasr & Tootell, 2012).

The Ventral Anterior Temporal Lobe Face Area

Evidence From Macaques

Single-unit recording studies have found face sensitive neurons on the inferior bank of the anterior STS, the anterior middle temporal gyrus (MTG), the temporal pole, and the inferior surface of the ATL (De Souza, Eifuku, Tamura, Nishijo, & Ono, 2005; Eifuku, De Souza, Tamura, Nishijo, & Ono, 2004; Hasselmo, Rolls, & Baylis, 1989; Ku, Tolias, Logothetis, & Goense, 2011a; Leopold, Bondar, & Giese, 2006). Using high-resolution fMRI it has been shown that these cells are organized into six face-selective cortical areas (face-patches) on the macaque temporal lobe, each with different functional specializations (see Figure 2a). Three face patches are located on the ATLs: AF, AL, and AM (Bell, Hadj-Bouziane, Frihauf, Tootell, & Ungerleider, 2009; Hadj-Bouziane, Bell, Knusten, Ungerleider, & Tootell, 2008; Ku, Tolias, Logothetis, & Goense, 2011; Moeller, Freiwald, & Tsao, 2008; Pinsk et al., 2012; Rajimehr, Young, & Tootell, 2009b; Tsao, Moeller, & Freiwald, 2008b).

The importance of the monkey ATLs in face identification has been supported by several sources of evidence. First, bilateral ablation of the monkey middle face patch does not impair face-identification if the ATLs are intact (Heywood & Cowey, 1992). Second, neuronal sensitivity to face identity is stronger in the anterior temporal regions than in other face sensitive regions (Hasselmo et al., 1989; Perrett, 1992; Rolls, Treves, Tovee, & Panzeri, 1997). Third, cells in the anterior most face patch demonstrate viewpoint-invariant identity tuning while cells in middle temporal regions (which appears

to be the homologue of the human FFA; Tsao, Freiwald, Knutsen, Mandeville, & Tootell, 2003) are tuned to specific views of a face (Freiwald & Tsao, 2010). Thus, the anterior most face patch appears to have the unique ability to represent facial identity in a viewpoint-invariant manner. Although the sensitivity of various face patches is distinct, there is evidence that they interact and modulate one another as a tightly interconnected network, such that electrical stimulation of the middle face patch activates the anterior face patches, and visa-versa (Moeller et al., 2008). It has been shown that the macaque middle face patch initially represents facial category, and after a delay, becomes slightly sensitive to facial-identity information (Tsao, Freiwald, Tootell, & Livingstone, 2006), potentially reflecting feedback from the anterior regions. Thus, the macaque face-processing network appears to be organized in a feed-forward hierarchy, with face representations becoming increasingly viewpoint-invariant and identity specific as they are fed forward in the temporal lobe (see Figure 2b), and activations in the anterior face patches feed back and influence sensitivity in more posterior regions.

The function of the anterior face patches appears to be both mnemonic and perceptual. In regards to memory there is evidence that neurons in the monkey ATLs have response profiles indicative of mnemonic activity: spike rates decrease rapidly with stimulus repetition, firing patterns are maintained over brief delay intervals, and neurons are sensitive to associations between faces and other stimuli (Nakamura & Kubota, 1996; Nakamura, Matsumoto, Mikami, & Kubota, 1994; Sakai & Miyashita, 1991). For instance, recently it was shown that cells in the ATLs of monkeys, but not in more posterior IT regions, can represent a trained associative pairing between faces and abstract patterns (Eifuku, Nakata, Sugimori, Ono, & Tamura, 2010). In regards to

perception, neurons in the ATLs are engaged during the passive viewing of faces (Freiwald & Tsao, 2010; Ku et al., 2011a) and are sensitive to the visual properties of individual faces (Leopold et al., 2006). Specifically, it has been shown that face-sensitive neurons the ATLs responded linearly to the perceptual deviation of morphed faces from an average template faces, thus demonstrating norm-based coding for individual face identities in this brain area (Leopold et al., 2006). Taken together, these findings suggest the intriguing possibility that the anterior face patches may bridge perception and memory, serving to link viewpoint invariant perceptual representations with person (or monkey) -specific identity information.

The relative homologies between the macaque face patches and the face processing regions in humans is not yet clear. Differences in the relative size of the macaque and human cortex, as well as differences in the number of cortical fields between the two species (Krubitzer, 2009) have made it difficult to make a one-to-one mapping across species. Moreover, while the OFA, FFA, and human anterior face patch all lay within ventral cortical areas, the macaque face-processing network is primarily located more superior, near or within the superior temporal sulcus (Tsao et al., 2008). However a functional overlap between the face processing networks of the two species is consistent with a ventral shift in visual areas from the macaque to the human cortex (Orban, Van Essen, & Vanduffel, 2004).

We can gain insight to the possible homologies of the human and macaque face processing network from the functional properties of the respective face-processing regions in both species. The shared mirror symmetric sensitivity of area AL in macaques (Freiwald & Tsao, 2010), and the FFA in humans (Axelrod & Yovel, 2012) suggests that

these regions may be functionally homologous. However another study also found mirror-symmetric face representations in the OFA, and distributed throughout higher-visual cortex (Kietzman et al., 2012). Notably, when the macaque and human brain are computationally morphed into the same space, the macaque middle face patch (ML) roughly corresponds to the human FFA (Rajimehr et al., 2009; Tsao, Freiwald, Knutsen, Mandeville, & Tootell, 2003) and area AM corresponds to the human anterior face patch (Rajimehr et al., 2009). The potential homology between area AM and the human anterior face patch is further supported by the shared invariance of these regions to transformations in viewpoint (Freiwald & Tsao, 2010; Anzellotti et al., 2013). Thus, although future work is needed to establish the functional homologies between the human and macaque face processing network, converging evidence suggests that the human anterior face patch may play a similar role in face processing as area AM in the macaque.

Evidence from Humans

Early PET studies by Justine Sergent and colleagues reported face-sensitive activations in the bilateral ATLs (Sergent et al., 1992). The right ATL is typically activated during the discrimination of familiar and unfamiliar faces (Nakamura et al., 2000) and face naming (Grabowski et al., 2001), and predicts face recognition performance (Kuskowski & Pardo, 1999; Sergent et al., 1992). Additionally, the bilateral ATLs exhibit an adaptation response for repeated presentations of familiar faces (Nakamura et al., 2000; Sugiura et al., 2001) suggesting an involvement in facial identification. These findings are consistent with three intracranial electrophysiological recording studies supporting the existence of an "anterior face area" in the human right vATL (Allison et al., 1999; McCarthy, Puce, Belger, & Allison, 1999; Puce, Allison, &

McCarthy, 1999). A face-specific late potential termed "AP350" potential originated from this brain area (Allison et al., 1999), following an earlier face-specific N200 originating from posterior ventral temporal cortex (Puce et al., 1999). The AP350 component, but not the N200, is reduced by the repetition of identical faces (Allison et al., 1999), further supporting the role of the vATLs in facial identification. Recent fMRI studies with optimized signal detection in the vATLs, have supported the existence of cortical areas in the human vATLs that respond more to faces than other visual object categories (see Figure 1a)(Avidan et al., 2013; Pinsk et al., 2009a; Rajimehr et al., 2009; Tsao et al., 2008).

These findings were preceded by several decades of research showing that focal lesions to the anterior temporal lobe cause face-processing deficits, which have been given the moniker "associative prosopagnosia". There have been several recent reviews of this literature (Gainotti & Marra, 2011; Olson, Mccoy, Klobusicky, & Ross, 2013) so I will simply summarize the most relevant findings. First, neuropsychological research consistently shows face memory, but not face perception, deficits after ATL resection. In other words, patients with lesions to the ATL, whether from epilepsy resection, head injury, or stroke, tend to have problems identifying individuals, not in differentiating individuals (Damasio, Tranel, & Damasio, 1990; Ellis, Young, & Critchley, 1989; Evans, Heggs, Antoun, & Hodges, 1995; Gainotti, 2003; Tranel, Damasio, & Damasio, 1997), whereas damage to the FFA or OFA often results in more global face discrimination impairments. Second, there are lateralized deficits with the left ATL being more closely associated with processing verbal information associated with individuals (e.g. proper names and other verbalizable semantic knowledge), and the right ATL being associated

with processing visual and biographical information related to faces, as well as feelings of familiarity (Gainotti, 2007). Finally, ATL lesions can lead to a deficit in forming new person-based associations. Whether these face identification deficits are due to gray matter damage or disconnection of the ATL from other face-processing regions due to destruction of association tracts (e.g. Fox, Iaria, & Barton, 2008) is not known.

The neuropsychological findings strongly suggest that the function of the anterior face patches is largely mnemonic, especially in regards to face identification. Indeed, the ATL shows heightened activations to famous and personally familiar faces as compared to unfamiliar faces (Gobbini & Haxby, 2007; Gobbini, Leibenluft, Santiago, & Haxby, 2004; Haxby et al., 2000; Haxby, Hoffman, & Gobbini, 2002; Sugiura et al., 2001), and responses in this area are up regulated by the presence of conceptual information about faces signifying semantic uniqueness (Barense, Henson, & Graham, 2011; Eifuku, De Souza, Nakata, Ono, & Tamura, 2011a; Ross & Olson, 2012; Tsukiura et al., 2010). Von der Heid and colleagues (Von Der Heide, Skipper, & Olson, 2013) conducted a meta-analysis of existing fMRI studies of famous and personally familiar face processing, as well as an empirical fMRI study using optimized imaging parameters to acquire signal from the ATLs. In both studies, the authors found left-lateralized ATL activations to personally familiar and famous individuals, while novel faces activated the right ATL (see Figure 2). Together these findings suggest that face memory-sensitive patches in the human ATL are in the ventral/polar ATL (Von der Heid et al., 2013). These findings are consistent with prior research showing greater fMRI adaptation to famous and personally familiar faces, relative to unfamiliar faces, in the ATL (Motoaki Sugiura, Mano, Sasaki,

& Sadato, 2011), and that selectivity for famous faces in the vATLs correlates with pre-
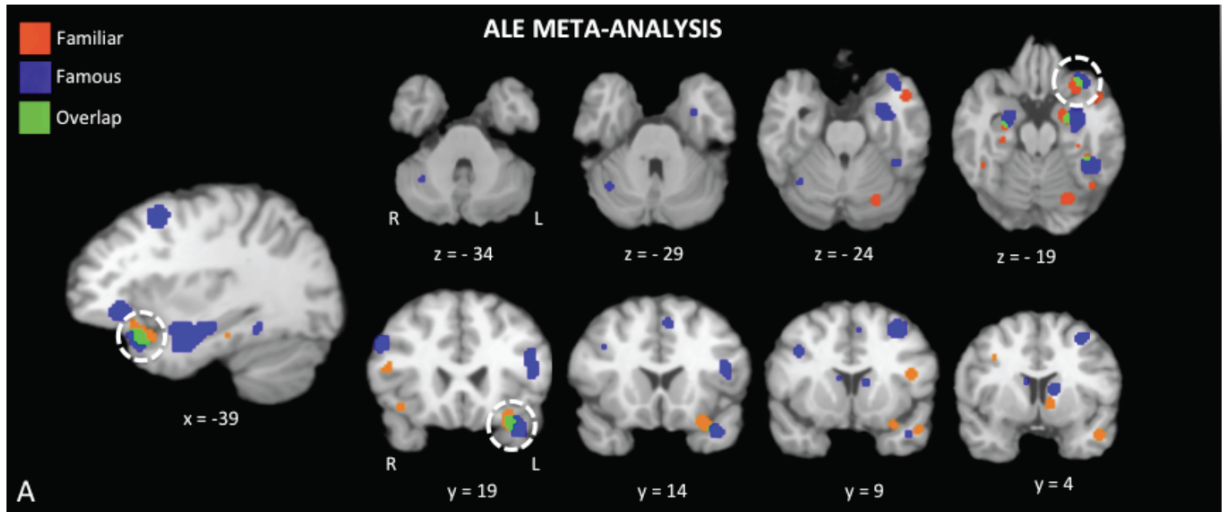
experimental familiarity (Rothstein et al., 2005).

Figure 2. Activations to famous and familiar faces from a random effects ALE meta-analysis. The white circle highlights activations to famous and familiar faces in the left anterior temporal lobe (Vonderheid et al., 2012).

However, other evidence paints a more nuanced and complex picture, with the

anterior face patch appearing to function at the intersection of high-level perception and

memory. There is clear evidence that activity in the anterior face patch is *insensitive* to

many low-level perceptual manipulations that leave facial identity intact such as

inversion, contrast reversal (Nasr & Tootell, 2012), or viewpoint (Anzellotti et al., 2013),

similar to what has been reported in the macaque (Friewald & Tsao, 2010). However, this

region is sensitive to the visual features of novel faces, discriminates between individual

(unknown) faces (Anzellotti et al., 2013), and BOLD activity in this region correlates

with face-recognition performance (Nasr & Tootell, 2012). Earlier studies demonstrated

that multivoxel activity patterns in the ATLs discriminated between facial identities,

however it was not clear whether the regions identified were selective for face stimuli

(Kriegeskorte et al., 2007; Nestor et al., 2011). Further, unilateral damage to the vATLs

impairs the ability to make fine-grained perceptual discriminations between morphed face stimuli, even when there is no time delay (Busigny et al., 2014; Fox, Hanif, Iaria, Duchaine, & Barton, 2011; Olson, Ezzyat, Plotzker, & Chatterjee, in press). Thus, as in monkeys, the evidence from humans indicates that neurons in the human vATL may serve to bridge perception and memory.

<p align="center">Evidence from Congenital Prosopagnosia</p>

Congenital prosopagnosia (CP) is a lifelong inability to recognize people that arises in the absence of any obvious cortical lesions (Jones & Tranel, 2001; Kress & Daum, 2003). The perceptual deficits seen amongst CP patients are often (but not always) selective to faces, and occur despite intact visual, social, and intellectual functions (Behrmann, Avidan, Marotta, & Kimchi, 2005; Behrmann & Avidan, 2005; Bentin, Deouell, & Soroker, 1999; Yovel & Duchaine, 2006). Congenital prosopagnosia is assessed using a variety of tasks that tax face memory and face perception revealing a heterogeneous behavioral profile amongst individuals with this disorder (Behrmann et al., 2005; Duchaine & Nakayama, 2005). The behavioral face-processing impairments in CPs have been demonstrated using tasks that require matching sequentially presented facial stimuli across a delay (Yovel & Duchaine, 2006) and that require discrimination between simultaneously presented faces (Behrmann et al., 2005; Duchaine & Nakayama, 2005) and thus have no mnemonic component.

CP's face recognition deficits may be due to the use of a featural processing strategy, which is different than the configural processing strategy typically adopted in the normal population (Duchaine & Nakayama, 2005). This claim is supported by research showing that CPs do not show an inversion effect for faces, and that they show a

bias towards featural processing for non-face objects (Behrmann et al., 2005). Furthermore, it has been shown that CPs are impaired at facial discrimination when the stimuli used differ with respect to the spacing of individual features (i.e. the distance between two eyes), or the shape of individual features (how round the eyes are; Yovel & Duchaine, 2006; see also Garrido et al., 2007).

It is possible that the disorder we call congenital prosopagnosia may in fact simply constitute the lower end of the spectrum for face recognition abilities in the normal population, with other individuals exhibiting superior face-recognition abilities. Russell et al (2009) assessed face processing abilities in a group of CPs, and a group of individuals with superior face-recognition abilities called "super-recognizers" using a face memory test that required the matching of faces across a short delay (e.g. the Cambridge Face Memory Test, or CMFT) and a face perception test (e.g. the Cambridge Face Perception Test; or the CPFT) that requires sorting simultaneously presented facial images according to their similarity with a presented target face (Russell, Duchaine, & Nakayama, 2009). Performance on both tasks was poorer for CPs relative to controls, and better for super-recognizers relative to controls. Performance on the face memory and face perception tasks was highly correlated in an additional control group, suggesting that face memory and face perception rely to some degree on shared neural substrates and cannot be easily dissociated (Russell et al., 2009).

To understand the neural basis for the face recognition deficits in CP, researchers have used a variety of neuroimaging methods with mixed results. For instance, some fMRI studies of CPs have revealed abnormal response profiles for faces in the FFA (Duchaine, Yovel, Butterworth, & Nakayama, 2006; Hadjikhani & De Gelder, 2002)

whereas other studies have not (Avidan, Hasson, Malach, & Behrmann, 2005; Avidan & Behrmann, 2009; Hasson, Avidan, Deouell, Bentin, & Malach, 2003; Von Kriegstein, Kleinschmidt, & Giraud, 2006). More consistent are findings implicating the vATL in the face deficits associated with CP. One study of CPs and matched controls revealed a significant reduction in the size of the anterior fusiform gyrus (Behrmann, Avidan, Gao, & Black, 2007), a region contiguous with the temporal pole, and lying squarely within the vATL face sensitive region. Reduced volume in this vATL region predicted the behavioral face recognition impairment of the patient group, as assessed by a famous face recognition task (Behrmann et al., 2007). This finding is consistent with research on a different group of CPs demonstrating that face selectivity in the anterior temporal lobe was linearly related to behavioral face identification performance on a battery of tasks assessing face discrimination and memory (Furl, Garrido, Dolan, Driver, & Duchaine, 2011). Further supporting the role of anterior face patches in CP a recent functional imaging study demonstrated normal face-related activation patterns in the posterior face processing areas (OFA and FFA) and little or no activation for faces in the vATLs within the patient group (see Figure 2b; Avidan et al., 2013). Using resting state functional connectivity analysis, the authors further demonstrated that functional connectivity between the right vATL and the FFA and OFA was disrupted in congenital prosopagnosics relative to controls, suggesting that connectivity between the anterior face patches and the posterior face network is necessary for normal face identification.

Overlap with the Perirhinal Cortex

Although traditionally studied in the context two independent bodies of research, the perirhinal cortex (PrC; consisting of BA 35 and 36, see Figure 3) and ventral ATLs

are spatially contiguous, highly interconnected, and perform similar computations during visual object processing (see Graham, Barense, & Lee, 2010 for a review of the perirhinal cortex). Several imaging studies have suggested that the human homologue to the monkey anterior face patch is located in the anterior (rostral) collateral sulcus in an area consistent with the PrC (Nasr & Tootell, 2012; Rajimehr et al., 2009; Rossion, Hanseeuw, & Dricot, 2012; Tsao et al., 2008). In humans, PrC activations are enhanced for faces relative to other objects (Lee et al., 2005; Lee, Scahill, & Graham, 2008), and face-specific activity in the PrC closely mirrors other face-selective areas of the ventral stream (O'Neil, Barkley, & Köhler, 2013).
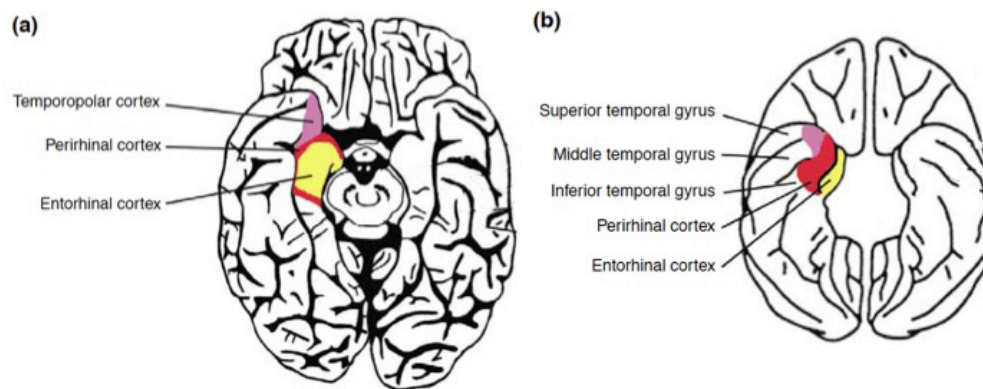
Figure 3. The Perirhinal Cortex. The location of the primate perirhinal cortex illustrated on the ventral view of a human brain (a) and the macaque brain (b). In humans the perirhinal cortex borders the temporopolar cortex rostrally and the entorhinal cortex caudally. The lateral boundary is located in the lateral bank of the collateral sulcus. The macaque perirhinal cortex is made up of Brodmann's areas 35 and 36 and is located in the lateral bank of the rhinal cortex and in the laterally adjacent cortex. Taken with permission from Buckley & Gaffan (2006).

The function traditionally ascribed to perirhinal cortex is declarative memory as part of the greater medial temporal lobe memory system (for a review see, Brown, Warburton, & Aggleton, 2010). However, the PrC is highly interconnected with the

ventral visual stream, and because of this, it has been argued that PrC may be involved in certain aspects of visual object processing (Bussey & Saksida, 2007; Bussey & Saksida, 2005; Saksida & Bussey, 2010). It should be noted that this view is highly controversial (Buffalo, Reber et al. 1998; Holdstock, Gutnikov et al. 2000; Stark and Squire 2000; Levy, Shrager et al. 2005). Nevertheless, data continues to accrue in support of the high-level visual functions of this region. Functional neuroimaging work in humans and lesion studies and non-human primates have supported this suggestion by showing that that the PrC is engaged during the visual discrimination of complex objects (Barense et al., 2011; Barense, Henson, Lee, & Graham, 2010; Baxter, 2009; Lee et al., 2008; Mundy, Downing, Dwyer, Honey, & Graham, 2013; O'Neil et al., 2013; Suzuki & Baxter, 2009), and may represent the conjunction of visual object features (Buckley & Gaffan, 2006; Cate & Köhler, 2006; Fang et al., 2007; Murray & Bussey, 1999; O'Neil, Cate, & Köhler, 2009).

The integration of multiple visual features into a durable representation is critical for face perception (as well as other discrimination tasks involving easily confusable stimuli) and memory. Thus, it is not surprising that damage to the PrC in humans impairs face recognition (Lee et al., 2005; Martin, McLean, O'Neil, & Kohler, 2013). Notably, the PrC is preferentially activated when face discrimination places a higher demand on feature integration (O'neil et al., 2013) due to changes in the viewpoint from which faces are presented (Barense et al., 2010), or the presentation of faces with many, as opposed to few, overlapping features (Mundy, Downing, & Graham, 2012). Thus the PrC appears to be critically involved in feature integration during the visual processing of highly similar faces.

However there is also evidence that the PrC has an important role in person memory. The PrC is preferentially sensitive to famous, as compared to unfamiliar faces (Barbeau et al., 2008; Barense et al., 2011; Martin et al., 2013) and damage to this region impairs one's ability to learn perceptual discriminations between highly similar faces (Mundy et al., 2013). Last, it has been reported that semantic memory deficits for concrete objects, most of which are defined by visual features, are associated with damage to the PrC (Mion et al., 2010). One explanation for the perception versus memory findings in this region is that the PrC is functionally coupled with different brain areas depending on task demands (O'Neil et al., 2009).

Together, these findings suggest that representational content, rather than task demands, may drive the functional specialization of the PrC, with the PrC being engaged to represent stimuli that require the integration of multiple visual features for individuation. Furthermore, PrC mechanisms are easily engaged during tasks involving face perception and memory. The representational capacity of the PrC appears well suited to perform the computational metrics attributed to the anterior face patch (Anzellotti et al., 2013; Nasr & Tootell, 2012), in which viewpoint-invariant identity representations are utilized for facial individuation, and possibly serve as an interface between perception and memory. It should be noted that I am not suggesting that the PrC as a whole is a face processing area. Rather, I believe that the representational affordances of the PrC are recruited during the discrimination of a variety of stimuli characterized by many overlapping visual features, and that a subpopulation of neurons within the human PrC may be optimally tuned for faces and thus may constitute the human homologue of one of the three macaque anterior face patches.

Summary of Face Findings

There are different levels of face representation across distinct regions of the brain (for a summary see Table 1). The OFA appears to be primarily involved in processing the low-level features of faces, and is relatively insensitive to modulations by conceptual knowledge and familiarity. The FFA is involved in the holistic processing of faces, and may encode the identity of individual faces; however it is currently unclear how familiarity impacts responding in the FFA.

Much less is known about face processing areas that are anterior to the FFA. It has been suggested that the ventral ATL face patch uses a population code to represent subtle differences between individual faces (Kriegeskorte et al., 2007), however the exact facial dimensions that the ATL uses to do this is not known. Convergent evidence from animal, neuropsychological, and neuroimaging studies suggest that the perirhinal cortex is critical for the perceptual discrimination of, and memory for, complex object and face representations. The BOLD signal in both the ventral ATL and the perirhinal cortex is sensitive to changes in facial identity but not other types of perceptual changes, such as color or rotation (Eifuku et al., 2011, 2010; Graham et al., 2010). These same ventral ATL regions are up-regulated by the presence of conceptual information about faces, such as personal familiarity, semantic uniqueness, or names (Barense et al., 2011; Eifuku et al., 2011; Ross & Olson, 2012).

Together, these findings suggest that cells in ventral ATL and perirhinal cortex may bridge perception and memory, and possibly serve to link high-level conceptual knowledge with complex object (or face) features necessary for social processing. Based on the extant literature, it is likely that there is a feed-forward flow of information, in

which facial representations become increasingly complex and diagnostic of identity as information is feed from more posterior (i.e. OFA and FFA) to anterior regions of the ventral temporal cortex. Furthermore, the perirhinal cortex and ventral ATLs may serve as the apex of this hierarchy, in which perceptual face information becomes ingratiated with conceptual information that is diagnostic of identity (Collins et al., submitted)

FMRI Measures of Representational Content

In traditional fMRI studies, the average BOLD response to multiple presentations of a stimulus is used to gauge the effects of stimulus variation on the amplitude of the neural response across a population of neurons in a voxel. Thus, the BOLD signal reflects the averaged response of a large number of neurons, and cannot be used to infer the response profiles of individual neurons within the imaged voxel (Malach, 2012). FMRI adaptation has been used to understand the stimulus dimensions across which neural responses in a given voxel are invariant, and thus provides insight into the types of representations coded by populations of neurons. FMRI adaptation refers to the reduction in the fMRI BOLD response that is seen when a population of neurons is stimulated twice, such as when two identical objects are presented in succession (Grill-Spector, Henson, & Martin, 2006). The more similar two visual stimuli are, the more the BOLD response for the second stimulus is reduced (Grill-Spector & Malach, 2001), thus making fMRI adaptation a useful tool for probing the dimensions across which neural populations gauge similarity.

Recently, studies have examined response patterns in clusters of voxels in order to further our understanding of the representational structure of various cortical areas. While signal from one voxel may be insufficient to represent behaviorally relevant stimulus

dimensions, the category of a stimulus might be sufficiently represented in the aggregate response across a population of voxels. Distributed pattern analysis (Haxby et al., 2001) examines stimulus representations that are distributed across multiple voxels; a change in the pattern of signal is taken to reflect a change in the underlying neural activity (Mur, Bandettini, & Kriegeskorte, 2009). It has been suggested that such multivariate methods are more successful at category discrimination than univariate tests and possibly more sensitive to sub-voxel information than adaptation techniques (Aguirre, 2007; Epstein & Morgan, 2012).

Although MVPA and fMRI adaptation both provide information about the representational content of cortical areas, they are infrequently used in the same study (for exceptions see Epstein & Morgan, 2012; Sapountzis, Schluppeck, Bowtell, & Peirce, 2010) and it is unclear how these distinctions are instantiated at the neuronal level. It has been suggested that fMRI adaptation reflects the tuning of individual neurons (or alternatively individual cortical columns) while MVPA reflects clustering at a coarser anatomical scale (Drucker, Kerr, & Aguirre, 2009). What we do know is that when fMRI adaptation and MVPA findings are consistent, and thus cross-validate each other, we can make strong claims about the representational content of various cortical areas. For example, findings from fMRI adaptation (Gilaie-Dotan, Gelbard-Sagiv, & Malach, 2010; Gilaie-Dotan & Malach, 2007) and MVPA (Nestor et al., 2011) have provided converging evidence for the existence of exemplar-level representations for faces within the FFA. When fMRI adaptation and MVPA findings contradict each other (for an example see Epstein & Morgan, 2012), they may provide insight into the distinct ways that different types of information are encoded in discrete cortical areas.

Continuous carry-over designs (Aguirre, 2007) were developed as a way to simultaneously acquire information about the relative contribution of different forms of neural coding to the representation of stimulus variation. Carry-over effects measure the influence of a previously presented stimulus on the neural response to a current stimulus, with neural adaptation being one type of continuous carry over effect. Carry-over effects can be contrasted with direct effects, which refer to the average amplitude of neural activity to a stimulus independent of its context (which is measured by traditional BOLD imaging). By paying careful attention to the order in which stimuli are presented, researchers can acquire unbiased and efficient estimation of both the direct effect of a stimulus on the amplitude of a neural response, and the carry-over effect of one stimulus on the neural responding to another. This thus enables researchers to analyze MVPs and fMRIa within the same dataset (Aguirre, 2007). Continuous carry-over designs necessitate the use of serially balanced sequences, in which the presentation of every stimulus follows every other stimulus. One type of serially balanced sequence, which will be used in this study, is a *type 1 index 1 sequence*. For these sequences, all *n* stimuli are presented in *n* "blocks" of different permutations of the ordering of stimuli, with the stimulus repeating at the termination of one block and the beginning of the next (Nonyane & Theobald, 2007). The efficiency of different *type 1 index 1 sequences* to reveal a direct effect of stimulus presentation on neural responding can be improved by increasing the time spent in the null trial condition (Aguirre, 2007). Additionally, longer stimulus durations improve the detectability of both the direct and linear adaptation effects (greater than 1 sec; Aguirre et al., 2007).

Study Objectives

Face patches in the human ATL have been identified however their sensitivity to different perceptual and conceptual information is poorly understood and their role in the greater face processing network has not been clearly articulated. It is clear that cells in this region are sensitive to relatively high-level person information - identity, personal familiarity, and conceptual uniqueness – and relatively insensitive to low-level visual information.

Although the anterior face patches neighbor perirhinal cortex and in some instances, appear to fall within perirhinal cortex (e.g. Nestor et al, 2011), the literature on the function of the ATL and perirhinal cortex have remained distinct. Similar to the anterior face patches, perirhinal cortex has been implicated in the identification of faces and other objects characterized by many overlapping visual features. However whether perirhinal cortex and the ventral ATL play distinct roles in face identification is unclear.

The goal of this dissertation research was to investigate the following question: What aspects of person knowledge are the anterior face patches sensitive to? This was assessed by training participants to associate different categories of knowledge with different faces (see Table 2). Although my questions were specifically about anterior face patches, I compared activations in this region to activations in the OFA and FFA to gain an understanding of the relative contributions of each region to the task at hand. I additionally investigated whether the PRC and anterior face patches perform similar or distinct functions during the identification of faces by comparing the dimensions across which each of these brain areas are sensitive. To investigate these questions I used both

fMRI adaption and MVPA techniques to probe the representational content of each of the

face-selective areas in the ventral visual processing stream.

CHAPTER 2

METHOD

Participants

Fifteen right-handed subjects (3-female) were recruited using flyers from Temple University. All participants were between the ages of 18 and 36 and were compensated monetarily for their time. One subject was excluded from future analysis because of insufficient activation levels in response to the functional localizer.

Training Methods

Stimuli

Sixteen full color male faces were used in the training paradigm. All faces lacked facial hair and glasses, and were forward facing. Stimulus images were provided by Michael J. Tarr (see http://www.tarrlab.org/).

Procedure

Participants learned to associate a name, and a semantically distinct occupation, with each of 8 faces, and a name only for another 8 faces (See Table 2 for the occupations and names that were used). Training was conducted over 2 days in a laboratory setting, with the first session lasting approximately 45 minutes, and the second session lasting 20 minutes.

Table 2. Labels Used in Training Procedure. An additional 8 facial identities were associated with names but no occupation. The names used were as follows: Evan, Dylan, Brayden, Issac, Caleb, Taylor, Gavin, Landon.

US Astronaut	Orchestra Conductor	NFL Quarterback	Ballerina
Joseph	*Jackson*	*Gabriel*	*Christina*
Samuel	*Nathan*	*Lucas*	*Ryan*

During the first training session, participants first completed "show" trials in which they viewed slides containing a face image, along with that face's associated biographical information. Each slide was presented four times (64 trials total) for 5 seconds in a random order, and participants were instructed to learn the information for each face. Next participants completed "response" trials, in which they viewed an image of a face, and were asked to type the first letter of that person's name. After responding, the correct biographical information for that individual was presented on the screen. For response trials each face was presented twice (32 trials total) in a random order. This procedure was repeated 3 times. The first training session terminated with a matching phase, in which participants were presented with trained biographical information for one of the faces, and asked to select the corresponding face identity from four faces presented below. The matching phase consisted of blocks of 64 trials, and accuracy was assessed at the end of each block. Participants completed the first training session when they correctly respond to 85% of trials within a block.

For the second training session participants first performed 32 show trials (each face was presented twice) followed by 32 response trials. This procedure was repeated twice. Afterwards participants completed a recall test. A number was presented on the computer screen with one of the 16 trained faces presented below. Participants were instructed to write down on a separate sheet of paper the information associated with each presented face. All participants correctly responded on at least 15 of the 16 faces.

Participants also completed a recall test for the trained facial identities immediately before their fMRI session. Participants were given a piece of paper with

images of the 16 trained faces and instructed to write next to each face their name and occupation information. All participants responded correctly to all facial identities.

Imaging Parameters

Neuroimaging sessions were conducted at the Temple University Hospital on a 3.0 T Siemens Verio scanner (Erlangen, Germany) using a twelve-channel Siemens head coil. The functional runs were preceded by a high-resolution anatomical scan that lasted 9 minutes. The T1-weighted images were acquired using a three-dimensional magnetization prepared rapid acquisition gradient echo pulse sequence. Imaging parameters were as follows: 144 contiguous slices of 0.9766 mm thickness; repetition time (TR) = 1900 ms; echo time (TE) = 2.94 ms; FOV = 188 x 250 mm; inversion time = 900 ms; voxel size = 1 x 0.9766 x 0.9766; matrix size = 188 x 256; flip angle = 9°.

Functional T2*-weighted images sensitive to blood oxygenation level-dependent contrasts were acquired using a gradient-echo echo-planar pulse sequence and automatic shimming. Imaging parameters were as follows: TR = 3 seconds; TE = 20ms; FOV = 240 x 240; voxel size = 3 x 3 x 2.5mm; matrix size = 80 x 80; flip angle = 90˚, GRAPPA=2. To ensure adequate sensitivity for signal detection in the anterior temporal lobes, the temporal signal-to-noise ratio (tSNR) for each participant was calculated using the first run of the functional localizer, by dividing the mean of the time series by the residual error SD after pre-processing. Visual inspection of a group tSNR map (Figure 4) confirmed signal coverage in the ATLs of all subjects that was above 40, which has been defined as a proper sensitivity range (Murphy, Bodurka, & Bandettini, 2007). Some signal loss in the medial orbitofrontal cortex was observed and varied between participants.
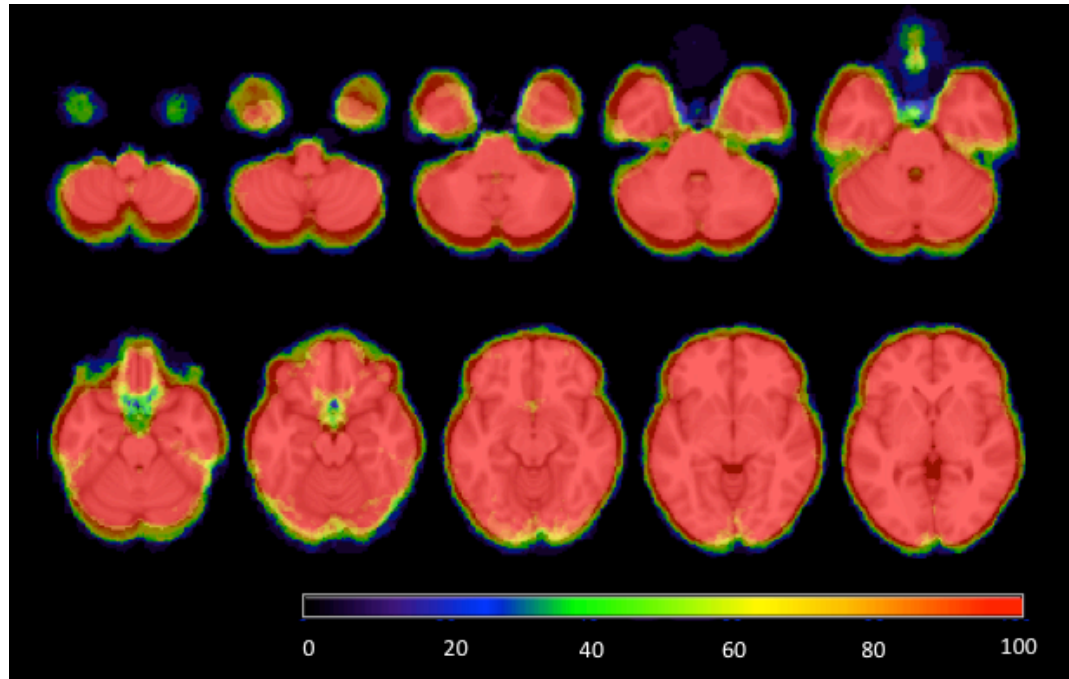
Figure 4. <u>Temporal Signal to Noise Map.</u> The percentage of participants with TSNRs above 40 at each voxel, superimposed on an average (MNI-152) brain. The tSNR for each participant was calculated using the first run of the functional localizer, by dividing the mean of the time series by the residual error SD after pre-processing.

Visual stimuli were shown using a rear mounted projection system. The stimulus delivery was controlled by E-Prime software (Psychology Software Tools Inc.; Pittsburg, PA) on a windows desktop located in the scanner control room. Responses were recorded using a four-button fiber optic response pad system.

Functional Localizer

Stimuli

A separate functional localizer was included to localize face sensitive and scene sensitive cortex using stimuli that were distinct from those used in the main experimental runs. Face stimuli consisted of 20 famous and 20 non-famous individuals taken from publically available sources on the Internet. The images of famous faces were pilot tested to ensure that they are highly familiar within the study cohort (see Ross & Olson, 2012).

To isolate scene-selective visual cortex and serve as a control for face-processing areas, 20 famous and 20 non-famous images of scenes were used. An additional null stimulus was used, consisting of a gray screen and central fixation cross.

Procedure

The functional localizer lasted two runs, with the first run containing all non-famous stimuli and the second run containing all famous stimuli. This run order was used to discourage participants from actively trying to name the non-famous faces. Each functional localizer run utilized a block-design, in which alternating blocks of face, place, or fixation stimuli were presented (see Figure 5). Each stimulus was presented for 800 ms followed by a 200 ms inter-stimulus interval. Each run contained 30 blocks (10 face, 10 place, and 10 fixation). For each face and place block 15 stimuli were presented, on each fixation block 9 stimuli were presented. Participants were instructed to pay attention to the images and respond whenever the same image was presented twice in a row (1-back). On each face and place block a randomly selected image was repeated.
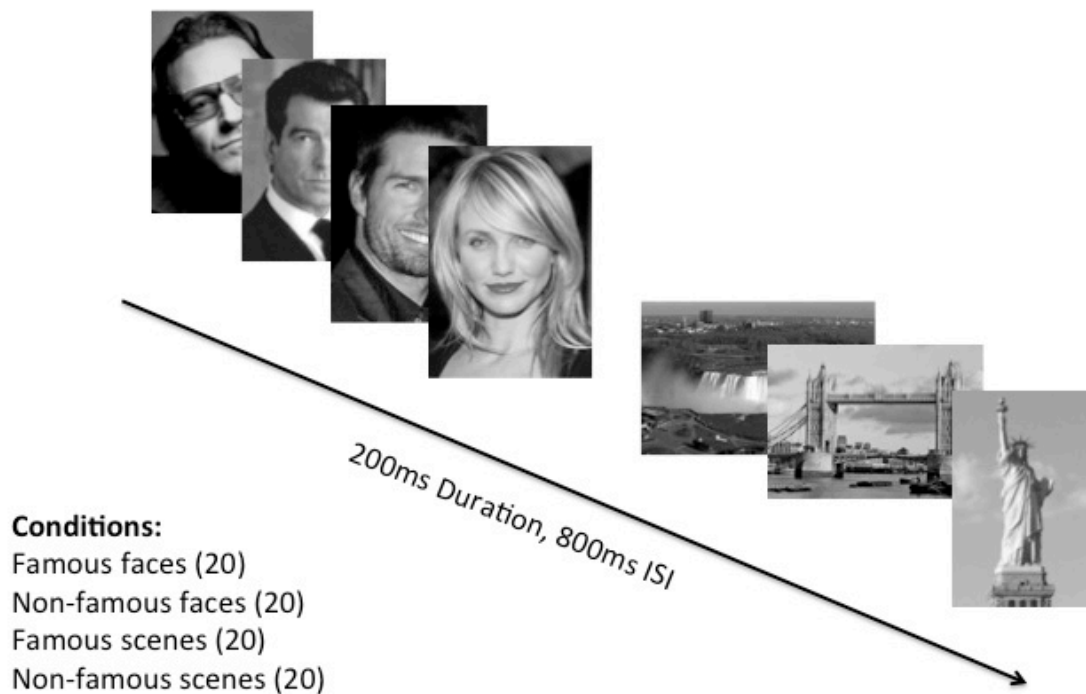
Figure 5. <u>Functional Localizer.</u> To functionally localize face-processing regions of interest, participants viewed blocks of alternating face and location stimuli. Participants performed a one-back task, responding whenever the same image was presented twice in a row. The functional localizer lasted two runs, one using famous stimuli and one using unfamiliar stimuli.

Main fMRI Experiment

Stimuli

The 16-trained facial stimuli were used in the main fMRI experiment. In addition, an untrained face that was rotated 30° to the left served as a target image. Null stimuli consisted of a grey screen with a central fixation cross.

Procedure

This main experiment utilized an event-related design in which participants performed a target-detection task by responding with a button-press whenever an untrained target-face was presented. A continuous-counterbalanced sequence was

used so that main effects were un-confounded from repetition effects, and so that

both multivoxel pattern classification and fMRI-repetition suppression data could be

analyzed. The 18 stimuli (each of the 16 facial identities, an untrained target

identity, plus a null stimulus consisting of a grey screen and a central fixation cross)

were presented continuously using two Type1-Index1 sequences broken into 4 equal

runs. Each stimulus was presented for 1 s followed by a 2 s inter-stimulus interval

(Figure 6). The length of the null stimuli was doubled to improve sensitivity to main

effects (Aguirre, 2007). Each run lasted approximately 9 minutes and was followed

by a 2-minute break. At the beginning of each run the last 5 images from the

preceding run (or the last 5 images from the last run in the case of Run 1) were

repeated. These trials were removed prior to analysis in order to allow the BOLD

signal to reach a steady state, and in order to maintain my counterbalancing scheme
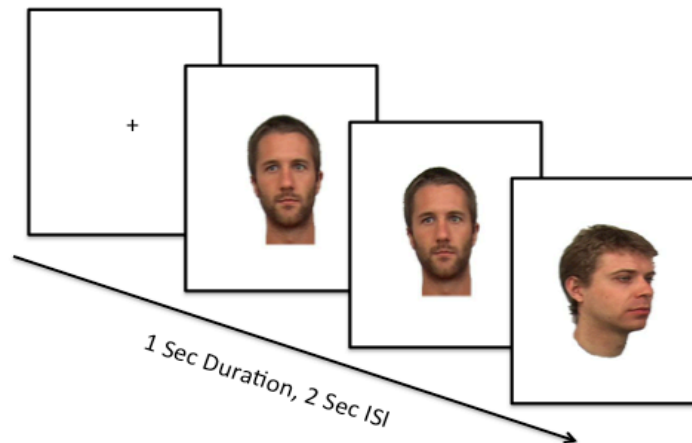
within the analyzed data.

Figure 6. <u>Primary fMRI Task.</u> For the main fMRI experiment participants viewed the 16 trained faces, plus one untrained target faces, presented continuously in two Type1-Index1 sequences.

CHAPTER 3

ANALYSIS

Data preprocessing and univariate analysis of fMRI data were performed using

FEAT (fMRI Expert Analysis Tool) version 6.0, part of the software library of the

Oxford Centre for Functional MRI of the Brain (fMRIB) (www.fmrib.ox.ac.uk/fsl).

MVPA analysis was carried out using the Princeton MVPA Toolbox version 0.7.1

running on MATLAB R2012b, and with custom MATLAB software.

Functional Localizer

The first 5 volumes of each run were discarded prior to any analyses. The

following pre-processing steps were applied to all functional localizer data: non-brain

removal using BET, motion correction using MCFLIRT, spatial smoothing using a 5mm

FWHM Gaussian kernel, high-pass temporal filtering with a 100 second cutoff, and un-

distorting of the EPI data to correct for magnetic field distortions by means of individual

field maps. EPI data was registered to each participant's T1-weighted anatomical scan

using BBR, and normalized to a standard Montreal Neurological institute (MNI-152)

template.

After preprocessing the functional localizer runs for each fMRI time-series for

each participant, the data were submitted to a fixed effects general linear model, with one

predictor that was convolved with a double-gamma model of the hemodynamic response

function (HRF) for each block type (face, places, fixation).

Regions of interest (ROIs) were identified in each study participant by choosing

peaks showing greater activity for faces than for places (uncorrected). Spheres of 9 mm

radius were generated, centered on the voxel with the highest activation within each peak.

Face-selective ROIs included bilateral FFA located in the mid fusiform gyrus, OFA, in the inferior occipital gyrus, and anterior face patch located on the ventral surface of the anterior temporal lobes (Figure 7).
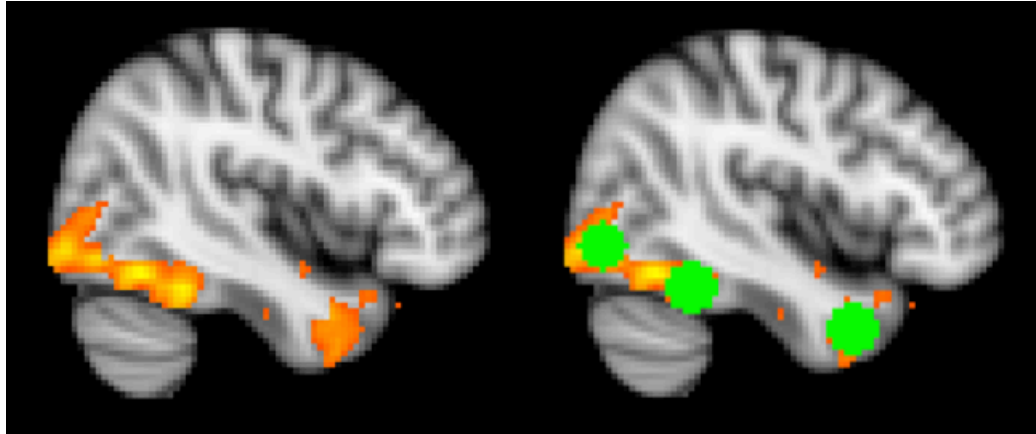

Figure 7. Regions of Interest. Face-sensitive regions of interest were identified for each participant individuating the peaks showing the highest response to the contrast faces > places. A 9mm spherical ROI was generated, centered on the voxel showing the highest activation within each peak.

Main fMRI Experiment

The first 5 volumes of each experimental run were discarded prior to any analyses. The following pre-processing steps were applied to all experimental data prior to the MVPA analysis: non-brain removal using BET, motion correction using MCFLIRT, high-pass temporal filtering with a 50 second cutoff, and un-distorting of the EPI data to correct for magnetic field distortions by means of individual field maps. EPI data was registered to each participant's T1-weighted anatomical scan using BBR.

I used MVPA to assess the sensitivity of the bilateral OFA, FFA, and anterior face patch to three types of person information: facial identity, facial occupation, and the presence or absence of a semantic representation (see Figure 8). For the first

analysis I defined 16 regressors, one for each identity. For the second analysis I defined four regressors, one for each occupation label. For the third analysis I defined two regressors, one for faces with a learned occupation and one for faces without a learned occupation. Trials in which a null stimulus or the target face were presented were excluded from all analyses. All other trials were included in the analysis of facial identity information, and the analysis of the sensitivity to the presence or absence of semantic information. For the analysis of facial occupation, only trials in which a face with a learned occupation was presented were included. Across all analyses data was z-scored within each run to control for baseline shifts in the magnetic resonant signal, and all regressors were convolved with a standard hemodynamic response function. I used a Gaussian Naïve Bayes (GNB) classifier and a leave-one-run-out cross validation scheme in which the classifier was trained on three runs of data and tested on the remaining un-trained run. This procedure was repeated 4 times, each time using a different test run, and the average classification accuracy was calculated for each ROI and compared to chance using a one-tailed t-test.
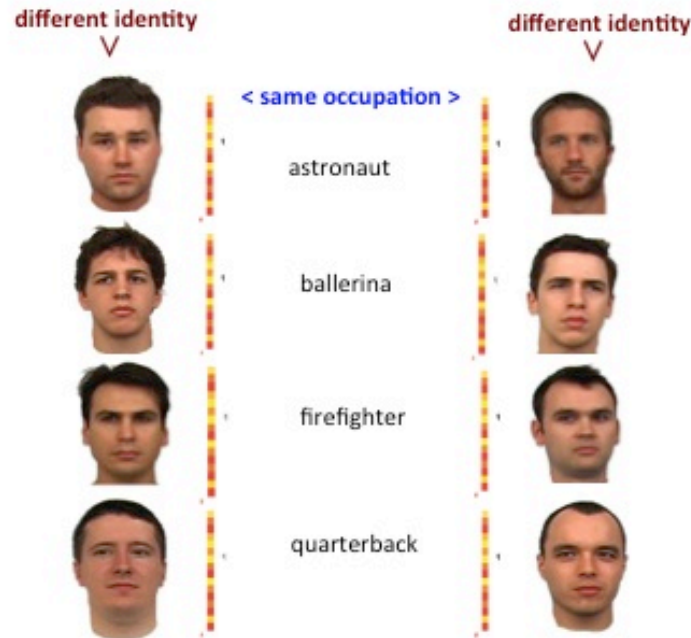
Figure 8. <u>Design for MVPA Analysis</u>. Information about facial identity was assessed by the classifier's ability to discriminate individual faces based on multivoxel activity patterns in each of the ROIs. Information about face occupation was assed by the classifier's ability to discriminate faces with different occupation labels, regardless of identity, using multivoxel activity patterns (represented here by the colored vectors next to each facial identity).

I additionally used fMRI adaptation (fMRIa) to assess the sensitivity of the bilateral OFA, FFA, and anterior face patch to facial identity and occupation. Pre-processing for the fMRIa analyses were the same as for the MVPA analysis, however data was also spatially smoothed using a 5mm FWHM Gaussian kernel. The data from each experimental run was then submitted to a fixed effects general linear model, with one predictor that was convolved with a standard model of the hemodynamic response function for the repetition of faces with the same identity and same occupation. Reponses to target stimuli were also included as a nuisance regressor in the model. Beta values were extracted at each ROI for every subject,

converted to percent signal change, averaged across subjects, and compared to zero using one-tailed t-tests. It has been suggested that fMRIa is less sensitive than MVPA to category distinctions instantiated at the neural level, and I thus expected person information to be more robustly represented in multivoxel patterns of activity in each of the ROIs than in the average adaptation response.

CHAPTER 4

RESULTS

Functional ROI Analysis

To test for conceptual face representations in the face-processing network, the ability of

each region to accurately classify different aspects of person information within its multivoxel

activity pattern (Figure 9) was assessed. Classification accuracy for facial identity was

significantly above chance in the anterior face patch [vATL, $t(12)=1.91$, $p=.04$], and in the OFA

[$t(13)=2.71$, $p=.01$], but not in the FFA ($p>.3$). Classification accuracy in the anterior face patch

for facial identity was not significantly greater than in the OFA or in the FFA ($ps>.05$). For

occupation, above chance classification accuracy was observed in the anterior face patch

[$t(12)=2.14$, $p=.03$) and in the OFA [$t(13)=1.99$, $p=.03$], but not in the FFA ($p>.05$). Importantly,

classification accuracy for occupation was significantly greater in the anterior face patch than in

the FFA [$t(11)=1.80$, $p=.05$] and the OFA [$t(12)=1.82$, $p=.05$], suggesting that this region may be

critically involved in representing social, categorical, information. Finally, we additionally

assessed the ability of each face-processing region to decode the amount of semantic information

associated with a face (i.e. to distinguish between faces with or without a trained occupation).

None of the face processing regions showed classification accuracy that was significantly above

chance for amount of information, though this effect was marginally significant in the vATL

[$t(12)=2.14$, $p=.054$]. Furthermore, classification accuracy for amount of information was

significantly greater in the vATL than in the FFA [$t(11)=1.80$, $p=.05$] and the OFA [$t(12)=1.82$,
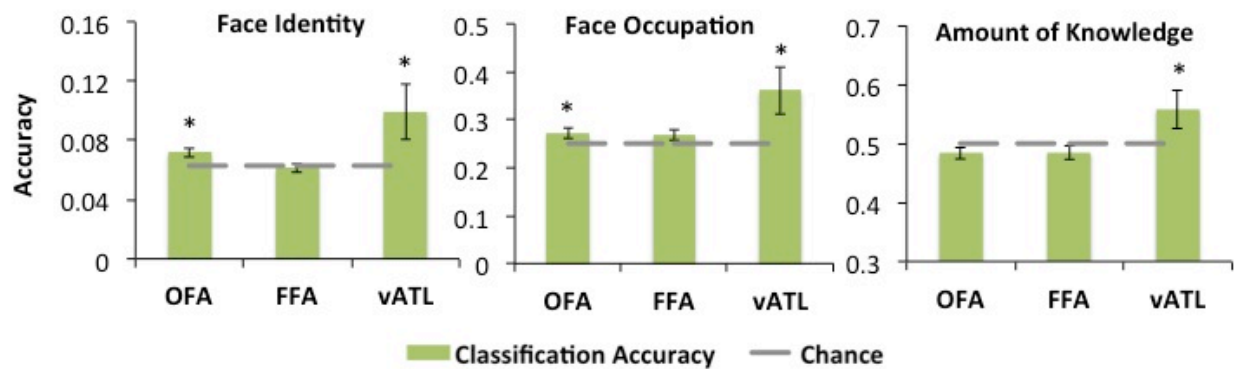
$p=.05$].

Figure 9. <u>Functional ROI Results.</u> The classification accuracy of each face-network ROI to facial identity, facial occupation, and the amount of knowledge associated with a facial identity in the MVPA analysis. The dashed line represents chance performance. Star indicates that above-chance classification accuracy significant ($p<.05$) or marginally significant ($p<.06$)

Perirhinal Cortex Analysis

As an exploratory analysis I used MVPA to investigate the sensitivity of the perirhinal cortex as a whole to different aspects of identity information. I included in my ROI voxels that had a 50% or greater chance of being located in perirhinal cortex, based on a probabilistic map published by Devlin & Price in 2007. It should be noted that the perirhinal ROI was much larger than the anterior face patch ROI, and in most of my subjects encompassed some or all of the anterior face patch (Figure 10). In my previous analysis I showed that activation patterns in the anterior face patches were sufficient to classify an individuals identify or social category, though optimal performance may be achieved through the redundant or diffuse representation of person information. If this is the case one should expect to see higher classification performance in the perirhinal cortex than in the anterior face patch. However if person-related information is represented compactly in the anterior face patch, then including non-informative voxels from the perirhinal cortex will cause a drop in classification accuracy.
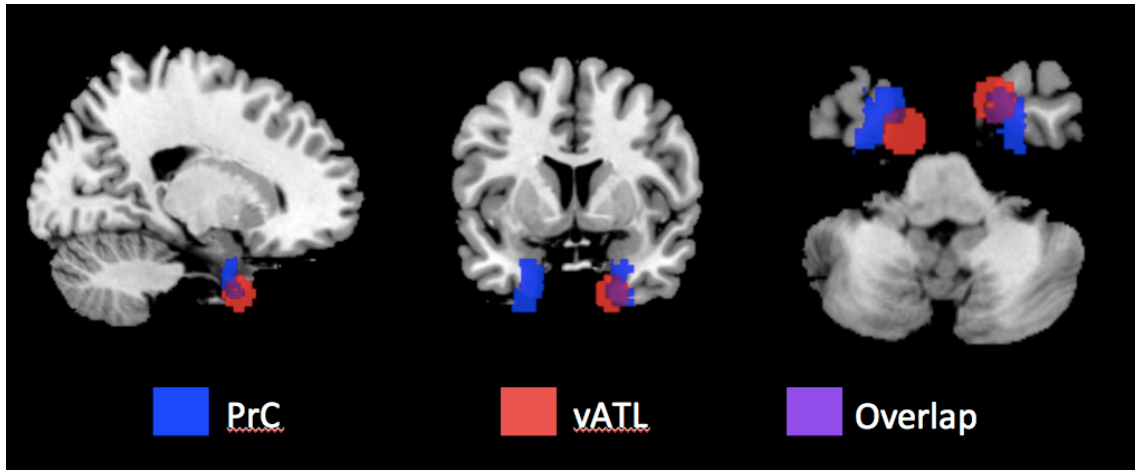
Figure 10. <u>Perirhinal Cortex ROI.</u> Overlap between the structural perirhinal cortex ROI (PrC) and the anterior face patch ROI (vATL) in a sample subject.

Classification accuracy in the perirhinal cortex was significantly above chance for identity [$t(13)=7.93$, $p<.001$], occupation [$t(13)=7.88$, $p<.001$], and the amount of information associated with a face [$t(13)=7.26$, $p<.001$]. Additionally, classification accuracy was significantly higher in the perirhinal cortex than in the anterior face patch (Figure 11) for identity [$t(12)=2.80$, $p=.016$], occupation [$t(12)=2.61$, $p=.023$], and the amount of information associated with a face [$t(12)=2.67$, $p= .02$]. Together these findings suggest that person-related information may be represented diffusely throughout the vATLs.

Figure 11. <u>Perirhinal Cortex Results.</u> The classification accuracy of the anterior face patch and perirhinal cortex to facial identity, facial occupation, and the amount of knowledge associated with a facial identity in the MVPA analysis. The dashed line represents chance performance. The star indicates a significant difference in the classification accuracy of the anterior face patch and the perirhinal cortex

Searchlight Analysis

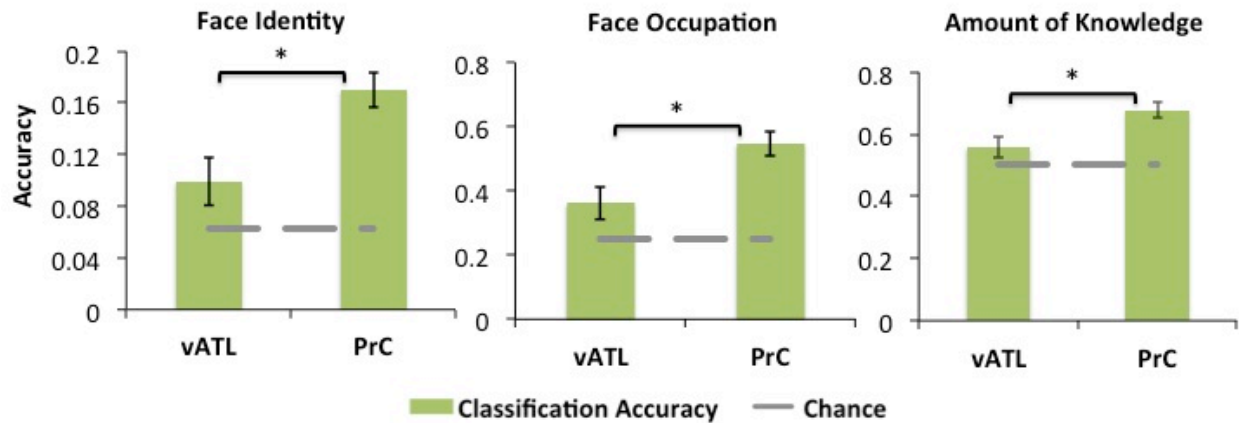I additionally used a spherical searchlight approach (Kriegeskorte et al., 2007) within each individual's temporal lobe to localize brain regions out-side of the face network that also represented person information in distributed patterns. I centered a spherical ROI (2-voxel radius) on each voxel in each individual's temporal lobe, and then used a GNB classifier and leave-one run cross validation to assess the sensitivity of voxels within each of these spheres to identity, occupation, and amount of semantic knowledge. The results of each classification test were assigned to the voxel at the center of the spherical ROI, and used to create an average voxel-wise information map for each participant. These average information-maps were then normalized to the MNI-152 template and subjected to a one-sample t-test. No significant clusters were observed significant at 0.05 FWE corrected, based on the threshold-free cluster-enhancement statistic image.

fMRI Adaptation Analysis

My fMRI adaptation analysis did not reveal sensitivity to facial identity, or occupation, in any of my face-processing regions of interest, that was significantly above chance (all ps > .05). This is not surprising given previous studies suggesting that MVPA is a more sensitive measure of the representational content of a cortical area than the adaptation response.

CHAPTER 5

DISCUSSION

Overview of Findings

The results of the current study show that a face-sensitive region in the ventral anterior temporal lobes carries information about an individual's identity, social category (occupation), and the amount of information associated with an individual. Information about facial identity and occupation was also observed in the OFA, however the FFA did not discriminate between different facial identities or between faces with different occupation labels. Additionally, neither the FFA nor the OFA discriminated between faces with different amounts of associated semantic knowledge. Sensitivity in the anterior face patch to occupation and the amount of information associated with a face was greater than in the more posterior face-processing regions. These findings are consistent with previous studies implicating the vATLs in representing facial identity (Anzellotti et al., 2013; Kriegeskorte et al., 2007; Nestor et al., 2011), and suggest that this region may possess the unique ability to represent abstract conceptual information about an individual.

I did not find that the FFA was sensitive to facial identity. Although two prior MVPA studies reported sensitivity to facial identity in this region (Anzellotti et al., 2013; Nestor et al., 2011), another MVPA study failed to find identity representations in the FFA (Kriegeskorte et al., 2007). Single unit recording studies in non-human primates have suggested that sensitivity to individual identity in the monkey homologue to the FFA only arises following feedback from more anterior face-processing regions (Moeller et al., 2008). Thus, these findings are consistent with the idea that the anterior face patch, more so than more posterior face processing regions, is critically involved in facial identification.

Identity representations in discrete face-processing areas are likely optimized for different functions, and may rely on different information. Single-cell recordings in non-human primates (Moeller et al., 2008) and diffusion-weighted imaging in humans (Pyles, Verstynen, Schneider, & Tarr, 2013) have shown that face-sensitive cortical areas in the vATLs are highly interconnected with the OFA and FFA. The disruption of structural connections between the vATLs and posterior face-processing areas has been implicated in the face-selective visual processing deficits seen in congenital prosopagnosics (Thomas et al., 2008). Thus the integration of the anterior face patches with the OFA and FFA appears to be necessary for normal facial identification. The interconnectedness of the anterior face patches with the OFA and FFA suggest a feed-forward architecture, with facial representations becoming increasingly complex and abstracted from low-level perceptual features as they move forward along this network. Consistent with this possibility, neurons in the macaque vATLs display identity tuning that is more viewpoint invariant than more posterior brain regions (Freiwald & Tsao, 2010); and viewpoint-invariant identity representations are latent in a more compact neural code in the human vATLs than in more posterior face-processing areas (Anzellotti et al., 2013).

Similarity Between our vATL Face Patch and that Reported in Prior Studies

In all subjects I identified 1 or 2 face-sensitive regions anterior to the FFA. The first anterior face patch (AP1), was located on the inferior temporal or fusiform gyrus, along the anterior collateral sulcus. The second anterior face patch (AP2) was located more anteriorly, on the inferior or middle temporal gyrus near the temporal pole. These regions showed no laterality bias. These locations are consistent with the location of anterior face-patches identified in earlier fMRI studies (Rajimehr et al., 2009; Tsao et al., 2008), and are also consistent with the facial identify area identified by Nestor and colleagues (2011). In the left hemisphere, 8 subjects had

both AP1 and AP2, 4 subjects had AP1 only, and 2 subjects had AP2 only. In the right

hemisphere 7 subjects had both AP1 and AP2, 5 subjects had AP1 only, and 1 subject had AP2

only. One subject had no face-specific activation in their right ATLs. In this sample face-

specific activations were also found in bilateral amygdala (8 participants had left amygdala

activations and 9 had right amygdala activations). This finding is consistent with previous

literature (Gobbini & Haxby, 2007; Rajimehr et al., 2009), and is likely driven in part by the

motivational relevance of the famous face stimuli used in my localizer.

Table 3. Description of Subject-Specific Anterior Face Patches. Each subject is listed along with whether reliable activation for the contrast faces > places was observed in each of the anterior face processing regions. Abbreviations: lAP1 = left anterior face patch 1; lAP2 = left anterior face patch 2; rAP1 = right anterior face patch 1; rAP2 = right anterior face patch 2

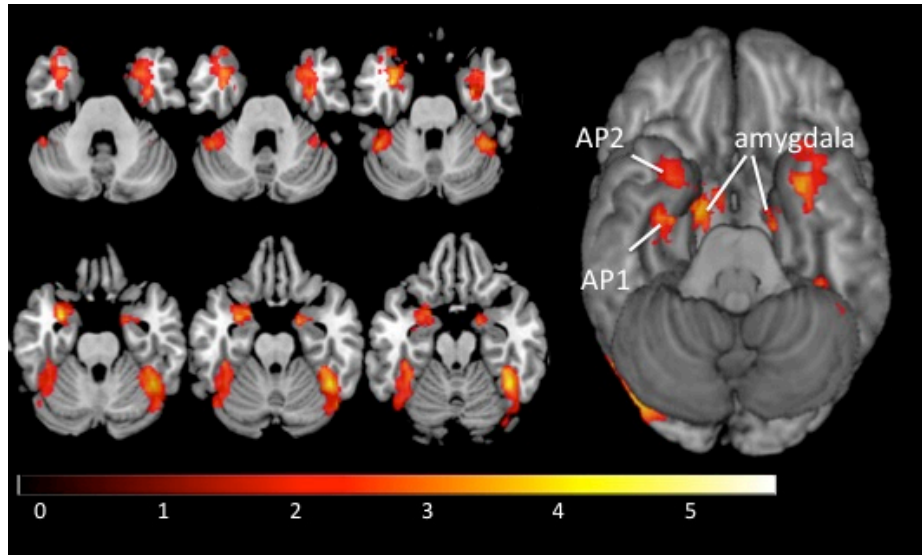| Subject	lAP1	lAP2	rAP1	rAP2
1		✔	✔	
2		✔		
3	✔		✔	✔
4	✔	✔	✔	
5	✔	✔	✔	✔
6	✔			✔
7	✔		✔	
8	✔	✔	✔	✔
9	✔	✔	✔	✔
10	✔	✔	✔	
11	✔	✔	✔	✔
12	✔	✔	✔	✔
13	✔	✔	✔	✔
14	✔		✔	

Figure 12. <u>Group Map of Anterior Face Patches.</u> Average activations for the contrast faces > places (*p*<.05 cluster corrected) superimposed on axial slices, and a ventral view of the inferior surface of the brain. Anterior faces patches 1 and 2 are labeled as AP1 and AP2 respectively. Amygdala activations are also labeled.

The vATLs in Face Memory vs. Face Perception

Psychologists like to divide the world cleanly into perceptual processes and mnemonic processes, a dichotomization that has carried over into our mapping of functional neuroanatomy. This dichotomy may be a hindrance when trying to understand psychological processes that require a fusion memory and perception, like face identification. I believe that the anterior patch is critically involved in the integration of perception and memory for the end goal of person identification. This can occur due to several special properties of this region.

First, the anterior face patch is sensitive to perceptual attributes of faces but in a highly restricted manner. It appears to represent faces in a perceptually abstracted form that is largely view, lighting, age, and expression-invariant. For instance, a recent study tested two humans with unilateral ATL resections across a range of face discrimination tasks using carefully controlled morphed face stimuli. The patients performed normally on many difficult face discrimination tasks involving facial gender or age, but performed abnormally low when performing facial

identity tasks (Olson et al., accepted pending revisions). This result mimics findings in macaques

and humans showing that cells in the vATL are only sensitive to perceptual manipulations that

alter facial identity, but are *insensitive* to many low-level perceptual manipulations that leave

facial identity intact such as inversion, contrast reversal, and viewpoint (Anzellotti et al., 2013;

Freiwald & Tsao, 2010; Nasr & Tootell, 2012). This region may even be insensitive to higher-

level perceptual changes that leave identity intact such as changes in facial expression (Nestor et

al., 2011).

Second, the anterior temporal lobe is sensitive to a wide range of mnemonic

manipulations (reviewed in the Introduction). Cells in the vATL are acutely sensitive to different

types of familiarity manipulations: responsiveness is enhanced by knowledge-base familiarity in

the form of semantic knowledge (Nieuwenhuis et al., 2012; Ross & Olson, 2012) but decreased

by perceptual familiarity in the form of stimulus repetition (Sugiura et al., 2001; Motoaki

Sugiura et al., 2011). The strong repetition suppression effect may underlie the familiarity signal

reportedly lost after ATL damage (Bowles et al., 2007; Gainotti, 2007b). Research from my lab

has noted before (Von Der Heide et al., 2013) that some of these memory effects appear

discordant but in fact, may be essential for how we encode our conspecifics. When an individual

is important to you, such as your boss, you acquire a great deal of conceptual knowledge about

them such as their name, their title, and their personality characteristics. On the other hand, there

are individuals who you may frequently see but you stop noticing because they hold no personal

significance.

Cells in this region also have the ability to represent associative pairings (Brambati,

Benoit, Monetta, Belleville, & Joubert, 2010; Eifuku et al., 2010; Nieuwenhuis et al., 2012). One

recent study showed that face-place associations were initially represented in the human

hippocampus but later were found to reside in the ATL (Nieuwenhuis et al., 2012). It has often

been suggested that the hippocampus is responsible for the initial consolidation of associations

but that a short time later, these representations are shipped out to various parts of the cortex, a

notion supported by these findings. The tight structural interconnectivity of the vATL, amygdala,

and anterior hippocampus via short-range fiber pathways may facilitate this process (Blaizot et

al., 2010; Insausti, Amaral, & Cowan, 1987; Morán, Mufson, & Mesulam, 1987; Suzuki &

Amaral, 1994). Thus cells in this region appear to bridge perception and memory. Indeed, both

components are required for accurate and rapid identification and there is a wealth of behavioral

data showing that person identification is facilitated by knowledge (Bruce, 1986; Burton, Bruce,

& Hancock, 1990; Buttle & Raymond, 2003; Jackson & Raymond, 2006; Klatzky & Forrest,

1984).

The anterior face patch's role in processing face identity could help explain findings by

my laboratory (Von der Heide, et al. 2013, accepted pending revisions) and others (Kanai et al.

2012), implicating this region in social network size. It was shown across measures of gray

matter density and BOLD response that individual differences in social network size were

consistently related to structural and functional differences in three regions: the left and right

amygdala and medial aspects of the right vATL, similar to the portion of the vATL found to be

sensitive to novel face identification (Nestor et al., 2011). It is possible that volumetric changes

observed in the vATL reflect one's ability to discriminate and identify a large number of

different individuals.

Relationship Between the vATL Face Patch and Perirhinal Cortex

Several imaging studies have suggested that the human homologue to the monkey

anterior face patch is located in the anterior (rostral) collateral sulcus in an area consistent with

the perirhinal cortex (PrC; Nasr & Tootell, 2012; Rajimehr et al., 2009; Rossion, Hanseeuw, & Dricot, 2012; Tsao et al., 2008). In my sample, the anterior face patch overlapped partially or completely with the perirhinal cortex in all subjects. Face-sensitive vATL cortex was smaller than the perirhinal cortex proper and differed in size and location between individuals. When I re-ran my analysis using an anatomically defined PrC ROI (Devlin & Price, 2007) rather than a functional anterior face patch ROI, the direction of my effects remained unchanged although some effects became stronger. In light of this finding, I briefly review what is known about the functionality of the PrC.

Recent studies of the PrC have focused on three functions: high level vision, episodic/associative memory, and semantic memory (for a review see Brown et al., 2010; Ranganath & Ritchey, 2012). Its role in high level vision originates in findings showing that the PrC is highly interconnected with the ventral visual stream (Barense et al., 2011; Barense, Henson, Lee, & Graham, 2010; Baxter, 2009; Lee et al., 2008; Mundy, Downing, Dwyer, Honey, & Graham, 2013; O'Neil et al., 2013; Suzuki & Baxter, 2009). In humans, PrC activations are enhanced for faces relative to other objects (Lee et al., 2005, 2008), damage to the PrC impairs face recognition (Lee et al., 2005; Martin et al., 2013), and face-specific activity in the PrC closely mirrors other face-selective areas of the ventral stream (O'Neil et al., 2013). Furthermore, the PrC is preferentially sensitive to famous, as compared to unfamiliar faces (Barbeau et al., 2008; Barense et al., 2011; Martin et al., 2013).

In a separate literature, the PrC has been linked to episodic and semantic memory. Perirhinal cortex activations during encoding predict item familiarity and successful retrieval (Davachi, Mitchell, & Wagner, 2003; Ranganath et al., 2004), and damage to the PrC severely impairs recognition memory (Baxter & Murray, 2001; Nemanic, Alvarado, & Bachevalier,

2004). Patients with semantic dementia, a progressive neurodegenerative illness that results in the loss of semantic knowledge about concrete objects, typically experience cell loss in the frontal and temporal lobes, but most dramatically in portions of their anterior temporal lobe (Hodges et al., 1992; Hodges et al., 2000; Mummery et al., 2000; Nestor et al., 2006). Recent evidence has linked the semantic memory impairment most closely with cell loss in PrC (Mion et al., 2010). A recent study by Peelen & Caramazza (2012) has corroborated these findings in healthy individuals by demonstrating that multivoxel patterns in the vATLs represent conceptual properties of every day objects, such as how they are used and where they are typically located.

Based on the reviewed literature, it is clear that the PrC supports aspects of visual perception as well as possessing important mnemonic properties that likely facilitate perceptual identification (Collins & Olson, Submitted). We do not yet know if the PrC can be parcellated into face and object-specific regions. We also do not have a good understanding of whether the same cells perform perceptual and mnemonic functions or if these cell types are distinct but neighboring. Last, we have only a poor grasp of the relationship between the anterior face patch and perirhinal cortex more generally. We would advise future researchers to consider this relationship more closely.

Optimizing Signal in the vATLs

Early imaging studies of face perception likely missed anterior activations because they used a restricted field-of-view that excluded the inferior temporal lobe from image acquisition, or because they suffered from the well known problem of imaging the ATLs: susceptibility artifacts and signal distortion due to the proximity of these regions to the nasal sinuses and ear canals (Devlin et al., 2000; Visser et al., 2010). I was thoughtful about this problem in designing this study and made several adjustments that I believe optimized my signal to noise. My acquisition

sequence used small slice-thickness (2.5mm) which has been shown to reduce signal drop-out caused by variations in the static magnetic field within a voxel (Carlin, Rowe, Kriegeskorte, Thompson, & Calder, 2012; Farzaneh, Riederer, & Pelc, 1990; Olman, Davachi, & Inati, 2009). I also used a short echo time (TE, 20ms), which has also been shown to reduce signal drop-out (Farzaneh et al., 1990; Olman et al., 2009). Finally, my lab previously found that the anterior face patch is very sensitive to semantic uniqueness (Ross and Olson, 2012) so my face stimuli were with distinctive occupations.

Conclusions

To conclude, the present study shows that conceptual knowledge about an individual's identity and social category is represented in multivoxel activity patterns in the anterior face patch. Activity patterns in the more posterior face-processing regions (the OFA and FFA) were less sensitive to an individual's social category, suggesting that sensitivity to conceptual social information is a unique property of this anterior face region. These results are consistent with a recent model of face processing in which a hierarchically organized system of face patches extends bilaterally from the inferior occipital gyri to the vATLs, with facial representations becoming increasingly complex and abstracted from low-level perceptual features as they move forward along this network (Collins et al., Submitted). These results further suggest that the anterior face patch may serve as an interface between face perception and face memory, linking perceptual representations of individual identity with person-specific semantic knowledge.

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