The neural processing of familiar and unfamiliar faces: A review and synopsis

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Familiar faces are represented with rich visual, semantic, and emotional codes that support nearly effortless perception and recognition of these faces. Unfamiliar faces pose a greater challenge to human perception and memory systems. The established behavioural disparities for familiar and unfamiliar faces undoubtedly stem from differences in the quality and nature of their underlying neural representations. In this review, our goal is to characterize what is known about the neural pathways that respond to familiar and unfamiliar faces using data from functional neuroimaging studies. We divide our presentation by type of familiarity (famous, personal, and visual familiarity) to consider the distinct neural underpinnings of each. We conclude with a description of a recent model of person information proposed by Gobbini and Haxby (2007) and a list of open questions and promising directions for future research.

People recognize familiar faces in poor viewing conditions, with low-quality images, and from variable viewpoints (Burton, Bruce, & Hancock, 1999; Johnston & Edmonds, 2009). The robust skills we show for familiar face recognition contrast sharply with our ability to recognize relatively unfamiliar faces (Hancock, Bruce, & Burton, 2000). Unfamiliar face recognition is easily disrupted in poor lighting conditions (e.g., Hill & Bruce, 1996, Johnston, Hill, & Carman, 1992), across changes in viewpoint (e.g., Bruce et al., 1999; Hill, Schyns, & Akamatsu, 1997; O’Toole, Edelman, & Bültthoff, 1998; Troje & Bültthoff, 1996), and when image/video quality is poor (e.g., Burton, Wilson, Cowan, & Bruce, 1999; O’Toole et al., 2010). Decades of literature point to the conclusion that familiarity with a face increases identification accuracy and facilitates generalization of the recognition process under a variety of suboptimal recognition conditions. Presumably, our superior recognition ability for familiar faces stems from differences in the quality and richness of our neural representations of these faces.

In addition to enhanced visual coding, familiar faces also activate brain regions associated with representations of semantic, episodic, and emotional information about a person. This can include a name, profession, hobbies, memories of previous encounters, and a host of emotional judgements about a person’s character. When we see the

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face of a familiar person, we activate these ‘other’ representations and use them to
guide us through our social interactions with the person. These richly interconnected
representations can influence the ease of retrieving visually derived semantic (e.g.,
gender, Bruce & Young, 1986) and identity information from faces (Balas, Cox, &
Conwell, 2007).

Much is known about the neural underpinnings of face processing from functional
neuroimaging studies (Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999; Grill-Spector,
Sayres, & Rees, 2006; Haxby et al., 2001; Haxby, Hoffman, & Gobbini, 2000; Kanwisher,
McDermott, & Chun 1997). In most of these studies, pictures of unfamiliar faces served
as stimuli. This controls for, or at least limits, the activation of brain regions that process
semantic, episodic, and emotional knowledge about a person (Gobbini & Haxby, 2007).
Although this process has simplified the functional neuroimaging endeavour in ways that
make sense for a newly developing field, it has perhaps left us with limited knowledge
of how the system works in the real world with faces we know, faces we do not know,
and faces we are getting to know.

Our goal here is to characterize what is known about differences in the neural
pathways that respond to familiar versus unfamiliar faces, based on data from functional
neuroimaging studies (Burton and Schweinberger, this issue). As noted, although most
functional neuroimaging studies of face processing have used unfamiliar faces as stimuli,
there are exceptions. In recent years, there has been a growing interest in understanding
the effects of familiarity on the neural processing of faces. Moreover, the use of familiar
faces in functional neuroimaging studies, in a limited way, spans the entire history of
the endeavour. Some studies have compared the neural activations elicited in response
to familiar and unfamiliar faces. Others studies have simply used familiar faces as stimuli
for a variety of unrelated reasons. Both kinds of studies are relevant to our goal of
characterizing differences in the neural representations of familiar and unfamiliar faces.

This review is organized as follows. First, we begin with a brief overview of
the neural areas activated during unfamiliar face perception. Second, we present
positron emission tomography (PET) studies that have addressed questions about
familiar face processing. We organize the studies based on the type of face familiarity
considered: famous, personal, and visual. We treat the PET studies separately from
the functional Magnetic Resonance Imaging (fMRI) studies, because most were carried
out before there was strong agreement about the location of face-selective brain
areas. Third, we review fMRI studies, again organizing by type of face familiarity.
The results of the PET and fMRI studies are summarized in three tables (Table 1:
Famous faces, Table 2: Personally familiar faces, and Table 3: Visually familiar faces).
At the outset, we note that there is an excellent, recent paper proposing a model of
the neural systems that underlie the activation of ‘person knowledge’ with familiar face
recognition (Gobbini & Haxby, 2007). We consider that model in the fourth section of
the paper. Finally, we sum up and conclude briefly with open questions, unresolved
issues, and a sketch of promising future research directions.

Overview of neural regions implicated in unfamiliar face perception

Functional neuroimaging studies on unfamiliar face perception have identified brain
regions in the occipital and temporal areas that respond more strongly to faces than
to objects. Anatomically, this network of brain areas includes the fusiform gyrus (FG)
(Halgren et al., 1999; Hoffman & Haxby, 2000; Kanwisher et al., 1997; McCarthy,
Puce, Gore, & Allison, 1997), inferior occipital gyrus (e.g., Halgren et al., 1999), and
superior temporal sulcus (STS; e.g., Allison, Puce, & McCarthy, 2000; Haxby et al., 2000).
Table 1. Summary of functional neuroimaging results for famous faces.

<table>
<thead>
<tr>
<th>Famous familiar</th>
<th>Result type</th>
<th>Regions</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sergent et al., 1992 (PET)</td>
<td>Famous &gt; unfamiliar</td>
<td>-B fusiform gyrus</td>
</tr>
<tr>
<td></td>
<td></td>
<td>-B medial anterior temporal gyrus</td>
</tr>
<tr>
<td></td>
<td></td>
<td>-B temporal poles</td>
</tr>
<tr>
<td></td>
<td></td>
<td>-R parahippocampal gyrus</td>
</tr>
<tr>
<td></td>
<td></td>
<td>-R lingual gyrus</td>
</tr>
<tr>
<td></td>
<td></td>
<td>-L medial temporal gyrus</td>
</tr>
<tr>
<td>Gorno-Tempini &amp; Price, 2001 (PET)</td>
<td>Famous &gt; unfamiliar</td>
<td>-R anterior middle temporal gyrus</td>
</tr>
<tr>
<td></td>
<td></td>
<td>-fusiform, no difference</td>
</tr>
<tr>
<td></td>
<td></td>
<td>-parahippocampal, no difference</td>
</tr>
<tr>
<td>Leveroni et al. (2000) (fMRI preference)</td>
<td>Famous &gt; unfamiliar</td>
<td>-B middle temporal</td>
</tr>
<tr>
<td></td>
<td></td>
<td>-R superior temporal</td>
</tr>
<tr>
<td></td>
<td></td>
<td>-R hippocampus</td>
</tr>
<tr>
<td></td>
<td></td>
<td>-B superior frontal</td>
</tr>
<tr>
<td></td>
<td></td>
<td>-L medial frontal</td>
</tr>
<tr>
<td>Elfgren et al. (2006) (fMRI preference)</td>
<td>Task and face comparisons</td>
<td>&gt; 25 regions for (famous &gt; unfamiliar)</td>
</tr>
<tr>
<td>Ishai et al. (2002) (fMRI preference)</td>
<td>Only famous faces tested</td>
<td>-famous activated core face regions (inferior occipital gyri, FG, STS)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>-amygdala</td>
</tr>
<tr>
<td></td>
<td></td>
<td>-no activation in anterior or middle temporal areas</td>
</tr>
<tr>
<td>Henson et al. (2000) (fMR-A)</td>
<td>Adaptation pattern</td>
<td>-adaptation in fusiform to familiar faces</td>
</tr>
<tr>
<td></td>
<td></td>
<td>-response enhancement in fusiform to unfamiliar faces</td>
</tr>
<tr>
<td>Eger et al. (2005) (fMR-A)</td>
<td>Famous &gt; unfamiliar adaptation</td>
<td>-familiar face image independence anterior rather than middle fusiform</td>
</tr>
<tr>
<td>Pourtois et al. (2005) (fMR-A)</td>
<td>Adaptation pattern overview change</td>
<td>-view specificity for familiar and unfamiliar faces</td>
</tr>
<tr>
<td></td>
<td>Famous &gt; unfamiliar adaptation</td>
<td>-L anterior fusiform gyrus</td>
</tr>
<tr>
<td></td>
<td></td>
<td>-R temporal lobe</td>
</tr>
<tr>
<td></td>
<td></td>
<td>-R anterior parahippocampal gyrus</td>
</tr>
<tr>
<td>Ewbank and Andrews (2008) (fMR-A)</td>
<td>Adaptation pattern overview change</td>
<td>-adaptation across view change to familiar faces in FFA (only small view changes tested)</td>
</tr>
<tr>
<td>Thompson et al. (2009) (fMR-A)</td>
<td>Adaptation pattern over image (but not view) change</td>
<td>-image-dependent adaptation in FFA, OFA but not STS for famous and unfamiliar faces</td>
</tr>
<tr>
<td></td>
<td>Famous faces &lt; unfamiliar faces</td>
<td>-R amygdala</td>
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<tr>
<td></td>
<td></td>
<td>-L fusiform</td>
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</tbody>
</table>

PET, positron emission tomography; FG, fusiform gyrus; STS, superior temporal sulcus; fMR-A, functional Magnetic Resonance-Adaptation; FFA, fusiform face area; OFA, occipital face area.
Table 2. Summary of functional neuroimaging results for personally familiar faces.

<table>
<thead>
<tr>
<th>Personal familiarity</th>
<th>Result type</th>
<th>Regions</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sugiura et al., 2001 (PET)</td>
<td>Personally familiar adaptation decrease in rCBF</td>
<td>B anterior middle temporal gyrus -left medial temporal -amygdala -hypothalamus -medial frontal cortex -posterior cingulate cortex</td>
</tr>
<tr>
<td>Shah et al. (2001) fMRI</td>
<td>Familiarity for face and voice</td>
<td>-paracingulate including retrosplenic cortex</td>
</tr>
<tr>
<td></td>
<td>Personally familiar &gt; famous familiarity</td>
<td>-anterior paracingulate , -posterior cingulate -precuneus -posterior STS fusiform gyrus</td>
</tr>
<tr>
<td></td>
<td>Mother’s child versus familiar child</td>
<td></td>
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</tbody>
</table>

RCBF, regional cerebral blood flow.

The functional definition of a face-selective area is computed commonly using a contrast between the neural activation elicited by passively viewing faces versus objects (e.g., houses, chairs, and tools), (i.e., faces > objects) or by passively viewing faces versus scrambled faces (faces > scrambled faces). Based on this contrast, a face-selective neural region in the middle part of FG, known as the fusiform ‘face’ area (FFA; Kanwisher et al., 1997) (see Figure 1a) and a face-selective neural region in the inferior occipital gyrus, known as the occipital ‘face’ area (OFA; Halgren et al., 1999) (see Figure 1b, are consistently found (e.g., Haxby et al., 1999; Kanwisher et al., 1997; Kanwisher & Yovel, 2006; McCarthy et al., 1997; Puce, Allison, Asgari, Gore, & McCarthy, 1996). Several studies also report face-selective neural responses in the STS (e.g., Hoffman & Haxby, 2000) (see Figure 1c, though localization of this area is less consistent across individuals than the FFA and OFA). A recent study by Fox, Iaria, and Barton (2009) suggests that the use of dynamic stimuli (moving faces > moving objects) localizes face-selective areas in the STS more consistently than the standard (static face > static object) localization.
Figure 1. Coronal slices showing the core visual areas in the ventral temporal cortex. (a) Right fusiform face area (FFA). (b) Right occipital face area (OFA). (c) Right posterior superior temporal sulcus (pSTS) (all figures used are from Fox, Moon, Iaria, & Barton, 2009).
Table 3. Summary of functional neuroimaging results for visually familiar faces.

<table>
<thead>
<tr>
<th>Visually familiar</th>
<th>Result type</th>
<th>Regions</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dubois et al. (1999) (PET)</td>
<td>Visually familiar versus unfamiliar</td>
<td>-no difference in fusiform activity</td>
</tr>
<tr>
<td></td>
<td></td>
<td>-weaker activity in early visual areas for familiar</td>
</tr>
<tr>
<td></td>
<td></td>
<td>-amygdala stronger for unfamiliar faces</td>
</tr>
<tr>
<td>Rossion et al. (2001) (PET)</td>
<td>Visually familiar versus unfamiliar</td>
<td>-no difference in fusiform activity</td>
</tr>
<tr>
<td></td>
<td></td>
<td>-weaker activity in early R visual areas for familiar</td>
</tr>
<tr>
<td></td>
<td></td>
<td>-posterior fusiform near OFA</td>
</tr>
<tr>
<td>Rossion et al. (2003), re-analysis of Rossion et al. (2001) with functional areas</td>
<td>Visually familiar &gt; unfamiliar</td>
<td>-R FFA</td>
</tr>
<tr>
<td></td>
<td></td>
<td>-R OFA</td>
</tr>
<tr>
<td>Leveroni et al. (2000) (fMRI preference)</td>
<td>Visually familiar &gt; unfamiliar</td>
<td>-widespread frontal regions</td>
</tr>
<tr>
<td></td>
<td></td>
<td>-R fusiform</td>
</tr>
<tr>
<td>Katanoda et al. (2000) (fMRI preference)</td>
<td>Visually familiar &gt; (familiar and unfamiliar)</td>
<td>-bilateral fusiform gyrus</td>
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<tr>
<td></td>
<td></td>
<td>-superior and inferior parietal lobe</td>
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<tr>
<td></td>
<td></td>
<td>multiple regions in R frontal lobe</td>
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<tr>
<td></td>
<td></td>
<td>-L medial frontal/anterior cingulate cortex</td>
</tr>
<tr>
<td>Schwartz et al. (2003) (fMRI preference)</td>
<td>Unfamiliar &gt; visually familiar</td>
<td>-R amygdala</td>
</tr>
<tr>
<td></td>
<td></td>
<td>-R middle occipital gyrus</td>
</tr>
<tr>
<td>Kosaka et al. (2003) (fMRI learning)</td>
<td>Habituation</td>
<td>-amygdala to familiar and unfamiliar faces</td>
</tr>
<tr>
<td></td>
<td></td>
<td>-bilateral posterior cingulate cortex</td>
</tr>
<tr>
<td>Gobbini &amp; Haxby (2006)</td>
<td>Visually learned &gt; highly repeated</td>
<td>-amygdala</td>
</tr>
<tr>
<td></td>
<td></td>
<td>-precuneus</td>
</tr>
<tr>
<td></td>
<td>Highly repeated &gt; visually learned</td>
<td>-fusiform gyrus</td>
</tr>
<tr>
<td></td>
<td></td>
<td>-intra-parietal sulcus</td>
</tr>
<tr>
<td></td>
<td></td>
<td>-multiple additional areas</td>
</tr>
</tbody>
</table>

In the distributed neural model proposed by Haxby et al. (2000) (see Figure 2a), the lateral FG, inferior occipital gyri, and the STS are the core face-selective regions in the ventral temporal (VT) cortex. This framework posits a representation of the invariant aspects of faces (for face identification) in the fusiform and inferior occipital gyri and the changeable aspects of faces (expression, gaze, and facial speech) in the posterior (pSTS). Haxby et al. (2000) also proposed an extended neural system linking the core visual areas to regions that are functionally dedicated to more complete face processing.

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1 Haxby et al. (2000) describe the location of the core face-processing areas anatomically. The lateral FG, for example, is the gyrus along which the FFA can be functionally localized. The inferior occipital gyrus is the anatomical structure along which the OFA can be functionally localized.
Figure 2. (a) The distributed neural model of Haxby et al. (2000) separates the processing of the invariant and changeable information in faces. (b) The familiar face recognition model, including brain regions involved in the retrieval of person knowledge (Gobbini & Haxby, 2007).

Specifically, they posit a connection from the lateral FG to anterior temporal regions involved in coding personal identity, name, and biographical information. From the STS, the extended system includes connections to the intra-parietal sulcus (IPS) (for spatially directed attention, e.g., from gaze), the auditory cortex (for the processing of facial speech), and the amygdala, insula, and limbic system (for the processing of emotional...
information from faces). This set of extender regions gives an initial ‘blueprint’ for understanding the neural processing of familiar faces.

**Neural systems for processing familiar versus unfamiliar faces**

*Positron emission tomography (PET) studies of familiar and unfamiliar faces*

The earliest work on functional neuroimaging of face processing was conducted using PET. Many of these studies were done prior to the definition, or at least common use, of functionally defined regions of interest (ROI) that are face selective. When available, these regions serve as landmarks to make comparisons across subjects and studies. For the PET studies, region comparisons must be made anatomically.

**Famous familiar faces**

Familiarity with famous faces (e.g., celebrities, politicians) is acquired, not in person, but through the media. We see famous faces on television, read about them in magazines, and associate them with rich pictorial, semantic, and episodic information. This kind of familiarity has both a visual component to it (i.e., allowing for robust recognition across viewpoint, illumination, etc.) and a semantic long-term memory component.

Sergent, Ohta, and MacDonald (1992) measured regional cerebral blood flow (rCBF) in a PET study comparing several conditions. We focus on their comparison of a ‘face identity’ and a ‘gender categorization’ condition. In the face identity condition, participants made ‘actor versus non-actor’ judgements about *famous* faces (actors, athletes, singers, etc.). For the gender-categorization task, participants made male/female judgements about *unfamiliar* faces. Although these definitions confound task type with face type, the results foreshadow those of subsequent studies. The primary finding Sergent *et al.* (1992) report is that all of the areas specifically activated in the famous face identity task were anterior to those activated in the unfamiliar face gender categorization task. In comparing the familiar and unfamiliar face tasks, Sergent *et al.* (1992) found areas in the FG bilaterally (roughly analogous to FFA) to be more active for the face identification condition than for the gender categorization. The anatomically based coordinates for the fusiform area given are close to those now commonly reported for the functionally defined FFA (e.g., Kanwisher *et al.*, 1997). Sergent *et al.* (1992) also showed differential activation of the medial anterior temporal gyrus and temporal poles bilaterally, the parahippocampal and lingual gyri in the right hemisphere, and the medial temporal gyrus on the left in response to the famous identity versus an unfamiliar gender classification test.

Several other PET studies have considered ‘familiarity’ in a broader context of objects, names, and faces. Gorno-Tempini *et al.* (1998) examined the neural processing of famous/non-famous faces and names. For the perceptual processing of faces, combining data from both famous and unfamiliar stimuli, they found face-specific activity in the bilateral FG and right lingual gyrus. Combining data from faces and names, the famous versus non-famous contrast highlighted more anterior regions in the left temporal gyrus. Gorno-Tempini and Price (2001) examined the neural response to famous and non-famous, faces, and buildings. A direct comparison between famous and non-famous face responses did not show differences in activity in the FG (near coordinates typical of the FFA) or in the parahippocampal/lingual areas. However, a small region in the right anterior middle temporal gyrus was more active for famous versus unfamiliar faces (see Figure 3a). Gorno-Tempini and Price (2001) also found a region in the left anterior middle temporal gyrus that showed a common effect of fame for faces and buildings.
Figure 3. Examples of brain slices showing areas activated during familiar face perception: (a) an axial slice showing the anterior temporal area (from Gorno-Tempini & Price, 2001); (b) an axial slice showing the amygdala (figure used from Ishai et al., 2002); and (c) a sagittal slice showing the anterior paracingulate gyrus (1) and the posterior cingulate/precuneus (2) (figure used from Gobbini et al., 2004)

**Brief summary.** These early studies using famous faces as stimuli establish the fusiform and anterior and middle temporal cortex as brain regions potentially modulated by face familiarity.

**Personally familiar faces**

Behavioural studies have shown that *real-world* experiences with faces offer an advantage for the recognition of identity, gender, and head orientation (e.g., Balas *et al*., 2007; Young, McWeeny, Hay, & Ellis, 1986). The faces we see most often are those of our parents, children, and friends. Personal familiarity with these faces differs from famous face familiarity on factors such as the amount of exposure, knowledge about personal traits, and emotional and semantic associations (e.g., Gobbini, Leibenluft, Santiago, & Haxby 2004). This implies that personal familiarity is related, not only to the appearance of a face, but also to representations of the person’s mental state, personality, and the emotions an observer experiences on seeing the face (Gobbini & Haxby, 2007).
In an early PET study, Sugiura et al. (2001) examined ‘neural repetition priming’ effects for personally familiar faces (colleagues) versus unfamiliar faces. The rationale behind this work builds on behavioural experiments that show semantic repetition priming effects with repeated presentations of the face of a familiar person (Bruce & Valentine, 1985). The repeated presentation of personally familiar faces across multiple sessions allowed Sugiura et al. (2001) to measure the change in rCBF in various brain areas across time. The central finding of this study was a decrease in rCBF in the bilateral anterior temporal cortices – areas thought to be involved with access to long-term memories about people. Sugiura et al. (2001) also found consistent activation of the bilateral amygdala, hypothalamus, and medial frontal cortices during the face tasks. The comparison between the personally familiar and unfamiliar/control conditions, implicated the left medial temporal regions, amygdala, hypothalamus, medial frontal cortex, and the posterior cingulate cortex. The bilateral occipitotemporal regions, FG, and the right medial temporal regions were active during face perception.

**Brief summary.** The use of personally familiar faces in PET studies suggested the importance of the amygdala (see Figure 3b) and medial frontal cortex in the processing of familiar faces.

**Visually familiar faces**

Dubois et al. (1999) were the first to test directly for differences in the neural activity elicited in response to *visually familiar* and unfamiliar faces. Participants learned faces outside the scanner. In a PET study, Dubois et al. (1999) examined neural activity during a gender-categorization task (with familiar and unfamiliar faces) and a face-recognition task (‘familiar’ or ‘unfamiliar’?). The bilateral FG, again close to the stereotactic coordinates now associated with the functionally defined FFA, showed no difference in response activation to unfamiliar and visually familiar faces. Dubois et al. (1999) suggest this region as a part of the ‘common’ face-processing network proposed by Bruce and Young (1986).

For differentiating familiar and unfamiliar faces, Dubois et al. (1999) found stronger neural activations in the left amygdala for unfamiliar faces. This was an unexpected result, but one that we will see (partially) replicated in later fMRI studies. Dubois et al. (1999) suggest that unfamiliar faces may appear more threatening than familiar faces, resulting in larger activations in the amygdala. Finally, Dubois et al. (1999) reported weaker activity in early visual processing areas for the familiar faces versus unfamiliar faces. This suggests that familiar faces may be processed with ‘less neural effort’ in early visual areas than unfamiliar faces.

Next, Rossion, Schiltz, Robaye, Pirenne, and Crommelinck (2001) used morphed stimuli that varied between a familiar and unfamiliar face to examine the neural areas that differentially process visually based face familiarity. The stimuli consisted of morphs between a newly learned face and an unfamiliar face. The 0%, 20%, and 40% morph-levels were perceived as unfamiliar faces and the 60%, 80%, and 100% morph-levels were perceived as familiar faces. Familiar faces showed less activity in right ventral visual areas. There was less activity for more familiar faces in an area in the posterior FG (near what might be considered OFA or part of the lateral occipital areas, important for object processing). The authors conclude cautiously about the role of this area in face familiarity because of the possibility that this response may not be face specific.

The literature turns sharply at this point to focus on the importance of functional localization for achieving some stability in the functional neuroimaging results. To digress
briefly, the anatomical localizations in most of the PET studies rely strongly on stereotactic coordinates extracted from Talairach-aligned brains. This procedure creates anatomically uniform brain regions to assess functional activity differences. Functional localization procedures allow for individual subject variation in the location of a brain region, with some minimal anatomical constraints (e.g., the FFA is a functionally face-selective area found along the FG).

In a pivotal paper, Rossion, Schiltz, and Crommelinck (2003) present a reanalysis of Rossion et al. (2001) by using a second PET study to localize face-selective areas (Rossion et al., 2000). The latter study tested faces and objects, thereby providing functional localization data for a set of participants common to both studies. Rossion et al. (2003) report that the functionally defined face areas (FFA and OFA) in the right hemisphere show larger neural activations for unfamiliar faces than visually familiar faces. Finally, it is worth noting that, unlike Dubois et al. (1999) (cf., Table 3), neither Rossion et al. (2001) nor Rossion et al. (2003) report a differential activation of the amygdala for familiar versus unfamiliar faces.

**Brief Summary.** These studies suggest that it may be difficult to establish a clear role for face-selective visual areas in processing face familiarity. Of note also, stronger amygdala response to unfamiliar faces (Dubois et al., 1999) is noteworthy, given the limited emotional associations we have with both unfamiliar and visually familiar faces.

**Functional magnetic resonance imaging studies of familiar and unfamiliar faces**

We organize the studies by type of familiarity, further subdividing the section on famous face familiarity by the type of fMRI method: *subtraction* or *adaptation*.

In the subtraction method, inferences about the importance of a voxel/ROI for coding familiar versus unfamiliar faces are made based on a measure of the magnitude of the neural activity elicited in response to an experimental condition minus a control condition. Adaptation methods make use of the ubiquitous finding that the initial neural response to a stimulus habituates with repeated presentations of the ‘same’ stimulus (or more precisely, stimuli that are treated the same by the brain area). Different versions of this method have been called variously functional Magnetic Resonance-Adaptation (fMR-A, Grill-Spector et al., 1999), repetition priming and/or repetition suppression, (e.g., Henson, Shallice, & Dolan, 2000). Adaptation can offer information about the nature of the neural representations in a brain region. This is done by measuring whether a habituated neural response (e.g., to a face presented from a frontal view) recovers when a stimulus property (e.g., the viewpoint of the face) is altered. Response recovery suggests that the brain area is sensitive to (i.e., differentiates) the dimension in question (e.g., codes faces in a view-specific format).

**Famous faces versus unfamiliar faces: fMRI studies**

*Subtraction method.* Leveroni et al. (2000) examined neural activation in brain areas during the recognition of famous versus unfamiliar faces using fMRI. Famous faces elicited neural activity in a widespread network of brain areas including the bilateral middle temporal, right superior temporal, right hippocampus, bilateral superior, and left medial frontal cortex. No difference in neural activity for famous versus unfamiliar faces

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2Leveroni et al. (2000) also compared visually familiar and unfamiliar faces. We return to this condition comparison in the section on visually familiar faces.
was observed in the FG. The activations in the temporal areas and hippocampus were interpreted in terms of the long-term memories associated with processing famous faces.

Elfgren et al. (2006) focused on the role of medial temporal lobe (MTL), including the hippocampus and perirhinal cortex, during the intentional and incidental recognition of famous faces. Participants were scanned while performing two tasks: an incidental task (gender categorization of faces) and an intentional task (judging whether a face is famous or not and try to generate the name). The contrast between famous and non-famous revealed no less than 25 regions (cortical in all four brain lobes and subcortical) that responded differently to famous and non-famous faces.

For the task effects, both the incidental and intentional tasks for famous faces produced significant activation of the MTLs. The intentional task revealed larger neural activations for famous faces than for unfamiliar faces in the antero-lateral hippocampus, a region close to the amygdala. The incidental task revealed stronger activation in the perirhinal cortex and right parahippocampus for famous faces than for unfamiliar faces. Elfgren et al. (2006) proposed the involvement of the hippocampus in the intentional recall of semantic information about faces and the regions surrounding the hippocampus (the perirhinal cortex and parahippocampus) for the incidental recognition of semantic information.

An interesting effort to investigate whether similar neural areas are activated during visual perception and visual imagery of famous faces was conducted by Ishai, Haxby, and Ungerleider (2002). They examined the neural mechanisms underlying visual imagery for famous faces during a short-term (STM) and long-term memory (LTM) task. Ishai et al. (2002) found that the visual perception condition evoked bilateral responses in inferior occipital gyri, FG, STS, and the amygdala. Imagery of famous faces also activated the hippocampus, precuneus, early visual areas, inferior frontal gyrus (IFG), and IPS and less distributed areas of the FG, STS, and amygdala. Ishai et al. (2002) reported that the stored representations evoked by imagery are weaker than representations evoked by visual stimuli.

**Brief summary.** The complexity of the task type (perceptual versus memory) complicates the interpretation of results in these studies. All but one of the studies (Leveroni et al., 2000) is focused on understanding different tasks (e.g., incidental vs. intentional memory, imagination vs. perception), rather than on understanding face processing. Simple interpretations of a stimulus-processing system (e.g., for faces) may not be possible when the task constraints differ significantly.

**Adaptation methods (repetition-suppression and fMRI-A)**

It is now well known that the FFA adapts to repeated presentations of the same unfamiliar identity, but recovers when the viewpoint of the face is changed (Andrews & Ewbank, 2004; Ewbank & Andrews, 2008; Pourtois, Schwartz, Seghier, Lazeyras, & Vuilleumier, 2005a, 2005b). This finding has been used to argue for a viewpoint-specific representation of unfamiliar faces in the FFA.

An early face-adaptation study by Henson et al. (2000), however, did not find even the basic face-adaptation effect for unfamiliar faces (i.e., decreased neural response with repetition). Instead, Henson et al. (2000) found a decreased response to the repeated presentation of familiar faces in the right fusiform region, but response enhancement (i.e., increased neural response with repeated presentations) to unfamiliar faces. Henson et al. (2000) suggest that the response enhancement reflects the limited efficiency of processing unfamiliar stimuli relative to familiar stimuli. Henson et al. ’s (2000) finding of
response enhancement for unfamiliar face repetition has not (to our knowledge) been replicated. This results discrepancy is likely due to differences in adaptation methods between Henson et al. and more recent studies. Specifically, Henson et al. (2000) tested adaptation with repetitions of identical images.

The remaining studies we review in this section use adaptation as a method for testing the dependency of face representations on viewpoint as a function of familiarity. These studies consider whether (and where in the brain) famous and unfamiliar face representations are view-(in)dependent (Eger, Schweinberger, Henson, & Dolan, 2005; Pourtois et al., 2005b; Ewbank & Andrews, 2008). These studies stem from the behavioural findings we discussed at the outset of this review. Namely, recognition of unfamiliar faces is disrupted with viewpoint change, whereas recognition of familiar faces is not.

In Eger et al. (2005) study, participants viewed repeated presentations of the same image, different images of the same identity, and faces of two different (dissimilar) identities and made gender judgements. In the different image conditions, there was no explicit control placed on how the images varied (e.g., view, illumination, expression, hairstyle, etc). Eger et al. (2005) found identity priming for famous and unfamiliar faces in the bilateral mid- to anterior fusiform areas and in the orbitofrontal cortex. Further, the medial anterior right fusiform elicited stronger habituation for famous faces than for unfamiliar faces - although this was mainly due to the same-image condition. Consistent with more 'abstract' processing, Eger et al. (2005) found greater image independence for familiar face priming effects in the anterior versus middle fusiform cortex. They suggest that image-independent face representations are anterior to image-dependent representations along the FG.

In a related study, Pourtois et al. (2005b) measured the effect of familiarity (using famous and unfamiliar faces) and repetition on neural responses in several brain areas. Participants viewed two presentations of famous and unfamiliar face identities. Each identity was followed by an image of the same identity taken from a distinctly different viewpoint angle. Pourtois et al. (2005b) found no priming-related reductions in the neural responses to faces across view change for either familiar or unfamiliar faces in the FFA. They conclude that the FFA is involved in the view-dependent processing of faces, regardless of familiarity.

Pourtois et al. (2005b) also observed significantly greater responses for famous faces than for unfamiliar faces in the left anterior FG, right temporal lobe, and the anterior right parahippocampal gyrus. And, they report a priming-related repetition decrease in neural response to unfamiliar faces in the posterior visual areas and the right medial FG. Priming-related repetition reductions for famous faces, however, were observed in the lateral–temporal and inferior–frontal regions. Pourtois et al. conclude that view-invariant famous face representations involve non-face-selective areas in the temporal and frontal cortex.

Ewbank and Andrews (2008) used fMR adaptation to examine the view invariance for famous and unfamiliar faces in face-selective areas. They measured the neural responses in the FFA, OFA, and the STS across three conditions: repetition of the exact same image, same identity over parametrically varied small changes in viewpoint (rotation in the left- and right-side views from 0° to 8° in steps of 2°), and different identities. Note that the viewpoint variations here are quite small (e.g., 2–8°) relative to the other studies (e.g., Pourtois et al. (2005b), e.g., 45°). The FFA response adapted to both familiar and unfamiliar faces. The adaptation level was constant across all changes in viewpoint for familiar faces. Although these results appear to contradict previous findings, the small
degrees of viewpoint change tested here almost certainly accounts for the apparent inconsistency. For unfamiliar faces, adaptation in the FFA depended on the viewpoint change with larger adaptation to smaller viewpoint disparities. For the OFA, Ewbank and Andrews (2008) found view-dependent adaptation for unfamiliar faces, but no adaptation for familiar faces. They found no adaptation for any condition in the STS.

The final study in this section looked more generally at adaptation when the viewpoint remains constant but the appearance and illumination of a face change. Davies-Thompson, Gouws, and Andrews (2009) used three repetition conditions: same image, different image-same identity, and different identities. They found adaptation to repeated images of the same famous and unfamiliar faces in the FFA, OFA, but not STS. Contrary to expectation, FFA and OFA showed release from adaptation in response to both 'same-person/different-image' and 'different identities' conditions for familiar and unfamiliar faces. Davies-Thompson et al. (2009) conclude that both known and unknown faces are represented in FFA in an image-dependent fashion. Moreover, they report one additional intriguing finding. They show that large swaths of ventral visual areas adapt to repetitions of the same image.

**Brief Summary.** The adaptation-based studies demonstrate that face-selective areas in the FG code faces in a view-dependent way. This makes the FFA an unlikely candidate for supporting the recognition generalization we see for familiar faces (cf., also Natu et al., 2010). These studies bring into question whether traditional definitions of functional face selectivity are too narrow to capture the robust nature of the visual codes underlying familiar faces.

**Personally familiar faces versus unfamiliar faces**

In an early study aimed at understanding 'familiarity' at a general level, Shah et al. (2001) compared neural activations for personally familiar and unfamiliar faces and voices. Faces activated areas in the bilateral fusiform, whereas voices activated areas in the superior temporal gyrus, Heschl’s gyrus, and the IFG. Familiarity, regardless of modality (face or voice), activated areas in the paracingulate gyrus including the retrosplinal cortex. Shah et al. (2001) suggest this region as a multimodal ‘familiarity-checking’ processor.

Pierce, Haist, Sedaghat, and Courchesne (2004) compared neural responses to personally familiar (mother or colleague) and unfamiliar faces in autistic and normal adults. In both groups, the FFA was active in response to familiar and unfamiliar faces and showed a stronger FFA response to familiar faces. The main differences between the normal and autistic participants involved the extent of the semantic and emotional network of brain areas activated. For normal participants, the posterior cingulate, medial frontal lobe, and amygdala activated more strongly to familiar faces. For autistic participants, a similar but more restricted network was identified.

Gobbini et al. (2004) dissociated the role of familiarity with famous faces from the social and emotional factors involved in recognizing personally familiar faces (family and close friends) and famous faces. This is the first study to compare the neural processing of unfamiliar faces with the processing of famous and personally familiar faces. In comparing personally familiar and unfamiliar faces, Gobbini et al. (2004) found larger neural activations to personally familiar faces in the anterior paracingulate cortex and left posterior cingulate gyrus (see Figure 3a). These results are in agreement with the results reported by Frith and colleagues (‘theory of mind’ areas; Frith & Frith, 1999; Gallagher & Frith, 2003) indicating that the anterior paracingulate cortex, posterior cingulate gyrus, and the precuneus are linked with representations of personal knowledge and traits.
In comparing famous faces and unfamiliar faces, Gobbini et al. (2004) found stronger neural responses in the left anterior paracingulate cortex to famous faces. The right amygdala and left fusiform responded more to unfamiliar faces. Gobbini et al. (2004) tentatively interpreted the increased neural responses in the amygdala for unfamiliar faces to increased vigilance when we see unknown people, suggesting the amygdala as a social brake in the appraisal of novel individuals.

In comparing personally familiar and famous faces, the personally familiar faces evoked stronger neural responses in the bilateral anterior paracingulate cortex, posterior cingulate gyrus, precuneus, pSTS, and FG. A weaker right amygdala response was found for personally familiar faces than for famous faces.

Leibenluft, Gobbini, Harrison, and Haxby (2004) took personal familiarity one step further and tested the neural correlates of maternal attachment, using images of a mother’s own child and other personally familiar children. Mothers viewed images of their own children, personally familiar children, unfamiliar children, and unfamiliar adults. The contrast between the face of a mother’s own child and a familiar child localized areas in the anterior paracingulate, pre-frontal cortex, left insula, left FG, left STS, right posterior cingulate-precuneus. There was also an unexpected increase in amygdala activation for a mother’s own child versus a personally familiar child. They interpret this difference as a reflection of the intense attachment and vigilant protectiveness of maternal attachment. Consistent with previous studies (e.g., Gobbini et al., 2004), Leibenluft et al. (2004) found a weaker neural response in the amygdala for personally familiar children versus unfamiliar children.

Brief Summary. These studies re-emphasize and refine the role of the amygdala in signalling familiarity.

Visually familiar faces versus unfamiliar faces

In this final review section, we return to the study of Leveroni et al. (2000). They compared neural activation for newly learned faces versus unfamiliar faces. This revealed greater activation for newly learned faces in the left medial frontal, left inferior parietal, and left precuneus, with a notable absence of temporal lobe differences. Of note, there was widespread frontal lobe activation in response to unfamiliar faces as compared to newly learned faces and greater activation of the right fusiform cortex.

Using a face-recognition memory task paradigm, Katanoda, Yoshikawa, and Sugishita (2000) examined neural activation as participants viewed sequences of newly learned faces (all-target) and sequences of faces made up of an equal number of visually familiar and unfamiliar faces (half-target). Because they used a fixation point as a control, the effects of visual familiarity are best indicated by the contrasts they report between the all- and half-target conditions. The results showed that the bilateral FG was more active for the all-target condition. The superior and inferior parietal lobe and several regions in the right frontal lobe were more active for the half-target condition.

In a similar study with analogous results, Leube, Erb, Grodd, Bartels, and Kircher (2003) examined the neural regions involved in the recognition of visually learned faces. They compared neural activation during correct recognition of newly learned faces with that observed during correct rejection of unfamiliar faces. This contrast showed activation in the left inferior parietal lobe and left medial frontal/anterior cingulate cortex. Leube et al. (2003) suggested that these regions are implicated in the detection of novel faces and in the elicitation of a feeling of familiarity.
In an effort to develop a neural technique to study the behaviour of socially anxious children, Schwartz et al. (2003) examined the neural response of the amygdala to visually familiar and unfamiliar faces. Participants viewed four alternate blocks of visually familiar faces and unfamiliar faces. Schwartz et al. (2003) found larger neural activation in the right amygdala and right middle occipital gyrus for unfamiliar faces relative to visually familiar faces. Schwartz et al. (2003) also reported a continuous decrease in the overall magnitude of neural activation of the amygdala from Block 1 through Block 4 for both unfamiliar and familiar faces. No such decrease was found in the right occipital gyrus. These results suggest that the amygdala, a region known to respond to both happy and fearful faces (Morris et al., 1996), responds differentially as a function of the amount of visual familiarity with faces.

A unique effort to study the underlying representations of visually familiar faces was conducted by Kosaka et al. (2003). They examined changes in neural activation during the acquisition of familiarity. Kosaka et al. (2003) scanned participants as they viewed initially unfamiliar faces repeated over the course of nine sessions. They measured (dis)habituation of the neural signal as participants became familiar with these faces. The response in the bilateral posterior cingulate cortex increased over the nine sessions, whereas the amygdala and left medial FG response decreased. Kosaka et al. (2003) attributed the increasing activity in the bilateral posterior cingulate gyrus signals to increased familiarity with the faces. The decreased neural response is interpreted in terms of diminished threat as previously unfamiliar faces become familiar.

Gobbini and Haxby (2006) induced visual familiarity using laboratory training. In an unusual method, they compared ‘learned faces’ to highly repeated faces that were not learned explicitly. Relative to the highly repeated faces, learned faces showed stronger activation of the precuneus (posterior cingulate) and less activity in the FG and intra-parietal sulcus. There was also weaker activity to unfamiliar faces in the amygdala and in a host of other brain regions, too numerous to list here. Gobbini and Haxby (2006) conclude primarily that (visually induced) familiarity is tagged most clearly by the precuneus, with most other face-processing areas responding less actively (perhaps due to sparse coding or more efficient processing).

Brief Summary. These studies include the first attempts to track face learning over multiple scan sessions or within the scanner itself. They add valuable information about the neural correlates of familiarity, confirming a role for the posterior cingulate (cf., also precuneus, an area close to the posterior cingulate gyrus) as a brain region that mediates visual familiarity with faces, in addition to personal familiarity.

Model of neural systems for familiar face recognition (Gobbini & Haxby, 2007)

The model proposed by Gobbini and Haxby (2007) (see Figure 2b) is the first to consider the diverse and potentially distinct nature of semantic, episodic, and emotional associations with familiar faces. Their theory is based strongly on the results of two fMRI experiments that compared different types of familiarity (Gobbini et al., 2004; Leibenluft et al., 2004). Both studies included a condition that examined the neural processing of the faces we know best – faces of family and friends (Gobbini et al., 2004) and the faces of our own children (Leibenluft et al., 2004). The model is aimed explicitly at understanding familiar person recognition, eliminating generic components of face processing that support social communication functions for all faces, regardless of
familiarity. At the outset, Gobbini and Haxby (2007) define person knowledge to include distinct components of personal traits, intentions, transient mental states, biographical information, and episodic memory.

Taking the model components step-by-step, Gobbini and Haxby (2007) consider the combination of personal trait knowledge, mental state knowledge, and the assessment of intention as ‘theory of mind’ processing. Retrieving what you know about a person’s traits and mental state sets a context for the evaluation of the person’s intent. In their model, personal trait knowledge and mental state evaluation are attributed to the anterior paracingulate cortex. Intent judgements are assigned to pSTS/the temporal parietal junction (TPJ), consistent with what is generally known about the role of these areas in social cognition (cf. Haxby et al., 2000; Puce et al., 1996).

Distinct from theory of mind processing, the retrieval of biographical knowledge and related semantic knowledge activate areas in the anterior temporal cortex. Episodic memory retrieval is attributed to the precuneus/posterior cingulate areas.

The emotional component of the extended face system includes the amygdala, insula, and the striatum. Gobbini and Haxby (2007) note the paradoxical role of the amygdala in responding to familiar faces. Although there is consistent evidence for deactivation to familiar versus unfamiliar faces, there is also evidence for increased amygdala activation, perhaps related to vigilance, for mothers viewing the faces of their children.

The comprehensive model of Gobbini and Haxby (2007) forms a useful framework for putting the past literature on the neural processing of faces into a broader social and cognitive context. The model considers not only what we know about individuals, but also how we interact with them personally and socially. It further enables the formulation and testing of hypotheses about the posited model components.

Summary, conclusions, and pressing open questions

Open questions

More effort? Less effort?
Implicit in most theoretical accounts of familiar face processing is the assumption that we process familiar faces in many more complex ways than we process unfamiliar faces. Indeed, the literature offers evidence for this claim in the form of a list of brain regions that respond to familiar, but not unfamiliar faces. There is evidence also that familiar face processing may require less neural effort and computation than unfamiliar face processing – particularly in early and high-level visual areas. This is reasonable given the complex processing required to learn new faces (e.g., attention, effort, and the construction of robust representations). Thus, familiar face processing, in visual terms, may be more automatic than unfamiliar face processing. There is likewise evidence to suggest that familiar faces may, in some cases, require less emotional effort than unfamiliar faces.

Future studies should consider hypotheses about which parts of the neural system are expected to incur increased versus decreased processing load as a face becomes familiar in different ways.

Precision in defining brain areas and comparing across studies
The functional neuroimaging literature on faces spans nearly two decades from the classic study of Sergent et al. (1992) to the present. The location of the core high-level visual areas involved in face processing can now be localized in functionally precise, but anatomically flexible, ways that facilitate comparisons across studies. Although some of
these definitions are rather narrow, on the whole the technique of functional localization has been a positive development in the study of the neural substrates of face processing.

Functional localization methods have not been developed for brain regions involved in semantic, episodic, social, and emotional face processing. These regions are unlikely to have face-specific responses, but may be activated by faces in reliable ways. A normative task that can activate semantic information (e.g., name recall) from a visual presentation of a face, in a repeatable way, might allow for the development of functionally defined semantic landmarks. These areas could be constrained roughly by anatomically identifiable brain structures and compared across subjects. Whether or not this is the case, remains to be seen. If this kind of method is successful, it would help to establish more firmly a network of face processing areas that could be characterized in terms of types of face familiarity.

Unresolved brain areas and task types
A number of brain regions re-appear across multiple studies, but have not been considered in a model-based or functional context. The activation of these regions in individual studies may be due to the constraints of particular tasks, rather than types of information used in specific tasks. The unresolved areas include regions across the frontal cortex and in medial temporal structures, such as the hippocampus and parahippocampal area. The existing literature in functional neuroimaging of memory can be used to inform hypotheses about the expected neural correlates of particular task types. The gap between passive viewing of faces and complex learning, imagination, or memory-based judgements about faces is perhaps too large to bridge in any one study. We should be cautious, therefore, about over-interpreting studies with highly complex tasks.

A promising direction might be to look for normative task paradigms that can be replicated across multiple studies for comparison with simpler visual perception tasks.

Famous faces, personally familiar faces, and visually familiar faces
The stratification of studies into these three categories highlights the fact that we become familiar with faces in different ways. These categories add unavoidable complexity to overall picture. A large obstacle to clarifying the picture is that, to date, there are still limited data comparing different types of familiarity (though see, Gobbini et al., 2004; Leveroni et al., 2000). Moreover, although visual familiarity is the ‘least common denominator’ of familiarity, it is difficult to argue for pure visual familiarity as a real-world phenomenon. We freely make personality and social judgements about unfamiliar faces, and these judgements can effectively change the quality of our memory for faces (Bower & Karlin, 1974). Although visual familiarity may be largely a laboratory phenomenon, it is still at the core of understanding human expertise at recognizing faces. Progress in this area, however, will need to understand how visual familiarity interfaces with other types of familiarity.

Summary
We have presented a detailed account of functional neuroimaging studies that provide data on the neural processing of familiar and unfamiliar faces. Despite the extended time span of the literature, only recently has the work become sufficiently focused to extract the basics of the neural system. Readers may find the many open questions remain unsettling, but the studies we review here, offer more than a good ‘first start’
to filling in the neural boxes we are still attaching to Bruce and Young’s (1986) model. The place-holders for these boxes, set out 25 years ago, have guided the development of neural models like those proposed by Haxby et al. (2000) and more recently by Gobbini and Haxby (2007). They also set an agenda for behavioural studies that were readily linked into neural systems. Both sides of the research equation have made impressive gains over this time period. The broader and more complete understanding we have of human face recognition owes much to the Bruce and Young (1986) foundations on which it stands.

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References


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