



Research report

An image-invariant neural response to familiar faces in the human medial temporal lobe



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ABSTRACT

The ability to recognise familiar faces with ease across different viewing conditions contrasts with the inherent difficulty in the perception of unfamiliar faces across similar image manipulations. Models of face processing suggest that this difference is based on the neural representation for familiar faces being more invariant to changes in the image, than it is for unfamiliar faces. Here, we used an fMR-adaptation paradigm to investigate neural correlates of image-invariant face recognition in face-selective regions of the human brain. Participants viewed faces presented in a blocked design. Each block contained different images of the same identity or different images from different identities. Faces in each block were either familiar or unfamiliar to the participants. First, we defined face-selective regions by comparing the response to faces with the response to scenes and scrambled faces. Next, we asked whether any of these face-selective regions showed image-invariant adaptation to the identity of a face. The core face-selective regions showed image-invariant adaptation to familiar and unfamiliar faces. However, there was no difference in the adaptation to familiar compared to unfamiliar faces. In contrast, image-invariant adaptation for familiar faces, but not for unfamiliar faces, was found in face-selective regions of the medial temporal lobe (MTL). Taken together, our results suggest that the marked differences in the perception of familiar and unfamiliar faces may depend critically on neural processes in the medial temporal lobe.

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1. Introduction

As members of a highly social primate species, our everyday lives depend critically on being able to recognise people we know, so that we can interact with them appropriately based on our knowledge of their characteristics and personal

histories. Recognising the faces of familiar individuals is often central to this process, and this has led to a great deal of interest in the neural underpinnings of face recognition.

The distinction between often seen familiar faces and unfamiliar faces that have not been previously encountered is central to understanding face recognition. While photographs of unfamiliar faces can be remembered and later recognised

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remarkably well, recognition performance with unfamiliar faces breaks down as soon as any changes are made between studied and test images (Bruce, 1982; Longmore, Liu, & Young, 2008). Remarkably, the same problems arise in perceiving unfamiliar faces, where the perceptual matching of unfamiliar faces is severely hampered by image changes (Hancock, Bruce, & Burton, 2000; Kemp, Towell, & Pike, 1997). In striking contrast, the behavioural hallmark of familiar face recognition is that it is remarkably successful across substantial changes in expression, viewing angle, and lighting conditions (Bruce, 1994; Bruce & Young, 2012; Burton, 2013).

These findings have been incorporated into cognitive models of face processing which propose that familiar faces are represented differently from unfamiliar faces (Bruce & Young, 1986; Burton, Bruce, & Hancock, 1999). These models propose that all faces are initially encoded in an image-dependent representation, which is sufficient to recognise identical images of faces. However, our ability to recognise familiar faces across changes relies on representations that are relatively invariant to changes in the image, which are often referred to as face recognition units (FRUs) in models of face processing (Bruce & Young, 1986). These FRUs interact with person identity nodes (PINs), which are involved in the retrieval of names, and other semantic information associated with the face (Bruce & Young, 1986).

In terms of how faces are represented in the brain, many studies have followed Kanwisher et al. (1997) procedure of localising face-selective regions by contrasting neural responses to faces and other visual stimuli. These have revealed a network of posterior regions now usually designated the occipital face area (OFA), the fusiform face area (FFA) and the posterior superior temporal sulcus (STS) which form a core system for the visual analysis of faces in the widely used neural model proposed by Haxby, Hoffman, and Gobbini (2000). Within this core system of face-selective regions, the FFA is thought to be particularly important to the representation of invariant facial characteristics necessary for face recognition (Grill-Spector, Knouf, & Kanwisher, 2004; Haxby et al., 2000; Ishai, 2008). The Haxby et al. model explicitly acknowledges that other brain regions will contribute to the recognition of faces. One of these regions is the anterior temporal lobe which is suggested to represent biographical semantic knowledge associated with a face, e.g., the name of the person (Collins & Olson, 2014).

Although functional localisers can be used to identify face-selective brain regions, this in itself gives only limited information about what such regions do. A powerful complementary method for understanding the functional properties of a region is fMR-adaptation, as it offers insight into the underlying neural mechanisms (Grill-Spector, Henson, & Martin, 2006). Consistent with Haxby et al.'s (2000) idea of FFA involvement in processing invariant aspects of faces (such as identity), fMRI studies have shown a reduced response (adaptation) to repeated images of the same face in the FFA (Andrews & Ewbank, 2004; Grill-Spector et al., 1999; Harris, Rice, Young, & Andrews, 2015; Loffler, Yourganov, Wilkinson, & Wilson, 2005; Rotshtein, Henson, Treves, Driver, & Dolan, 2004; Yovel & Kanwisher, 2005). Such findings imply that the identity of the face is represented at some level in the FFA and it is being adapted by repeated presentations. However, given our discussion of the behavioural evidence, a much stronger

test for a link between neural activity and the recognition of facial identity is needed to determine whether this adaptation is still evident when different images of the same identity are shown (i.e., image-invariant adaptation). It turns out that fMR-adaptation studies that have used different images of the same identity have shown mixed results. Some studies show a complete absence of adaptation to different images in the FFA (Andrews & Ewbank, 2004; Grill-Spector et al., 1999; Pourtois, Schwartz, Seghier, Lazeyras, & Vuilleumier, 2005a; Xu, Yue, Lescroart, Biederman, & Kim, 2009), whereas other studies show continued adaptation (Loffler et al., 2005; Winston, Henson, Fine-Goulden, & Dolan, 2004).

A limitation of previous studies using fMR-adaptation to probe the neural correlates of face recognition is that they often fail to provide a direct comparison of familiar and unfamiliar faces (Johnston & Edmonds, 2009; Natu & O'Toole, 2011). This is a key limitation since, as we have noted, cognitive models only propose an image-invariant representation for familiar and not for unfamiliar faces (Bruce & Young, 1986; Burton et al., 1999). However, studies that have compared familiar and unfamiliar faces also report mixed results. Some studies have found image-invariant identity adaptation in the FFA for familiar but not unfamiliar faces (Eger, Schweinberger, Dolan, & Henson, 2005; Ewbank & Andrews, 2008), whereas other studies fail to find any difference in adaptation to familiar and unfamiliar faces (Davies-Thompson, Gouws, & Andrews, 2009; Pourtois, Schwartz, Seghier, Lazeyras, & Vuilleumier, 2005b). Together, these findings show at best limited evidence that the marked behavioural differences in the perception of familiar and unfamiliar faces are linked to differences in the way faces are represented in core face-selective regions of the human brain. One problem with identifying image-invariant responses to faces is that the representation of identity may involve a sparse code (Quiroga, Reddy, Kreiman, Koch, & Fried, 2005) involving only a limited number of neurons and thus require substantial power to be detected in fMRI. To address this issue, we performed an fMR-adaptation experiment with a large sample of participants ($N = 80$). Our aim was to use the combination of the sensitive adaptation method and the statistical power of a large participant sample to reveal regions in either the core or extended face processing network that show an image-invariant response to familiar faces.

2. Methods

2.1. Participants

Eighty right-handed participants with normal or corrected to normal vision participated in the experiment (45 females; mean age: 23.8 years, SD: 4.24 years). All participants gave their written informed consent. The study was approved by the York Neuroimaging Centre Ethics Committee.

2.2. fMRI experiment

Face stimuli were taken from previous studies (Davies-Thompson, Newling, & Andrews, 2013; Weibert & Andrews, 2015) and included male and female identities. All images

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