Face recognition during naturalistic viewing

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Abstract

The ability to recognize familiar individuals is essential for guiding social interactions, yet the cognitive and neural mechanisms underlying familiar face processing remain incompletely understood. While prior research has emphasized the role of perceptual information in generating image-invariant visual representations for recognizing familiar faces, the influence of conceptual information—naturally associated with faces in real-world contexts—has received less attention. This thesis aims to investigate the neural correlates of familiar face perception under naturalistic conditions and to understand the role of conceptual information in the recognition process. A series of empirical studies employing natural viewing paradigms in combination with behavioural, computational and neural measures were conducted. First, fMRI was used to identify neural correlates of familiar face processing (Chapter 2). Results revealed differential activation patterns for familiar versus unfamiliar faces across a distributed brain network extending beyond the visual face regions. These findings were further examined in individuals with developmental prosopagnosia and in a case study of hyperfamiliarity for faces, highlighting the critical role of non-visual brain regions in face recognition (Chapter 3). Building on this, Chapters 4 and 5 explored the contribution of conceptual information to face familiarization during natural viewing. Findings demonstrated that faces are more accurately recognized when learned alongside contextual conceptual information, which also modulates neural responses in non-visual brain regions. In Chapter 6, individuals with developmental prosopagnosia exhibited reduced conceptual understanding during face processing, reinforcing the relationship between conceptual information and familiar face recognition. Collectively, this thesis underscores the importance of non-visual brain regions in familiar face processing and establishes conceptual information as a pivotal component of face familiarization and recognition. These findings challenge traditional models that attribute familiar face recognition solely to image-invariant visual representations within visual brain regions. By integrating perceptual and conceptual processes, this work offers novel insights into theoretical models of face recognition and advances our understanding of the interplay between visual and conceptual information in social cognition.

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Author's Declaration

This thesis is a presentation of original work carried out by the sole author, Kira Noad, under the supervision of Professor Timothy Andrews. This work has not been previously presented for a degree or other qualification at this University or elsewhere. All sources are acknowledged as references. The empirical work presented in this thesis has been published in the following journals:

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Chapter 1

The cognitive and neural basis of familiar face recognition during naturalistic viewing

1.1 Introduction

Recognising familiar people is essential for effective social interactions in daily life. A significant challenge in face recognition is that substantial visual changes occur during natural viewing, such as changes in lighting, visual angle, expression and hairstyle. Despite this challenge, recognition of familiar others is highly accurate and fast across these visual transformations (Bruce, 1982). In contrast, recognition of unfamiliar faces is much more sensitive to changes in the image, breaking down under even small changes in viewing conditions (Hancock et al., 2000). These differences imply distinct cognitive mechanisms underlie the representation of familiar and unfamiliar faces.

This literature review will begin by describing influential cognitive models of face processing. These models focus on the role of visual information in generating an image invariant representation that is used for familiar face recognition. The review will then examine how these processes are instantiated in neural models of face processing. Consistent with the cognitive models, neural models focus on the processing of visual information within the core face-selective regions of the visual brain in order to generate an image invariant representation of familiar faces. However, despite the clear differences in the perception of familiar and unfamiliar faces, current research shows only modest differences in the neural response to familiar and unfamiliar faces in core face-selective regions. Neural models also propose that the core face-selective regions access a distributed network of regions that represent information about the person. This review will discuss evidence for the role of these extended regions in face processing, and argue that non-visual, conceptual information associated with a face may play a critical role in the recognition of familiar individuals. Finally, this review will provide an overview of how natural viewing paradigms can be used to understand real-world cognition, and how these could be applied specifically to understand familiar face processing.

1.2 Cognitive models of face processing

1.2.1 Bruce & Young's cognitive model

Bruce and Young's (1986) influential cognitive model of face processing begins with structural encoding of the physical components of a face (Figure 1.1). This initial representation is an image-dependent, structural representation that allows matching of identical images of the same face, but fails to account for within-person changes in the image. For a familiar face to be recognised across changes in the image, an image-invariant representation is necessary. According to the model, this is achieved with face recognition units (FRUs). Activation of these FRUs lead to the recognition of the person as being familiar, but not recognition of the identity. In order for identity to be recognised, person identity nodes (PINs) need to be accessed. These PINs hold identity-specific semantic codes (conceptual information), such as their name or biographical details. This stage is when a person is recognised. The key distinction in the model is that a FRU will respond to any view of a familiar face, while PINs can respond more abstractly to the face, voice or name of a person (or anything distinctly characteristic of a familiar individual). Overall, this model suggests that over successive stages the representation of the face becomes more related to the identity of face and less dependent on the image. At its core, the model emphasizes the critical role of an image-invariant visual representation for the recognition of familiar faces.

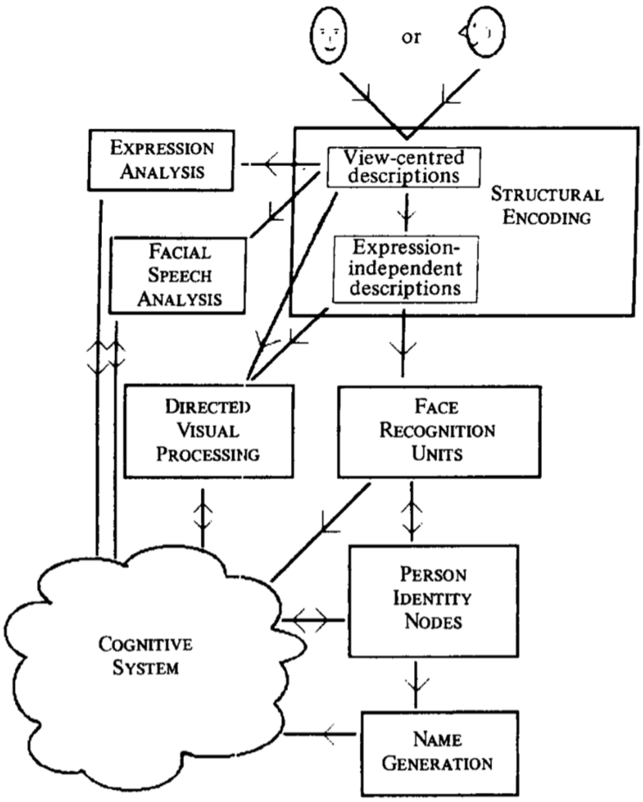


Figure 1.1. Cognitive model of face processing taken from Bruce & Young (1986), demonstrating the proposed successive stages of face representations in the recognition of a face.

1.2.2 IAC model of face recognition

The interactive activation and competition (IAC) model of person recognition (Burton, 1994; Burton, Bruce, et al., 1999; Burton et al., 1990) is a computational framework that integrates perceptual processes with the conceptual knowledge associated with an identity. Building on the Bruce and Young model, the IAC model incorporates similar components such as FRUs and PINs, while extending the functionality through an interconnected network of processing units. These units are organised into pools, with inhibitory links between units within a pool and excitatory links between units across pools (Fig. 1.2). One pool of units are FRUs, with one unit for each known face, enabling image-invariant recognition. The PIN pool classifies the person rather than face, and again has one unit for each known person. It is posited that at this stage familiarity is signalled. Following PINs, there are Semantic Information Units (SIUs) which code information about known individuals and have connections to an individual's PIN. As conceptual information is often shared between individuals, many SIUs will be shared across identities. The model also includes recognition routes for domains other than faces, such as Word Recognition Units (WRUs), with links directly to Name Recognition Units (NRUs) which are in turn linked to PINs.

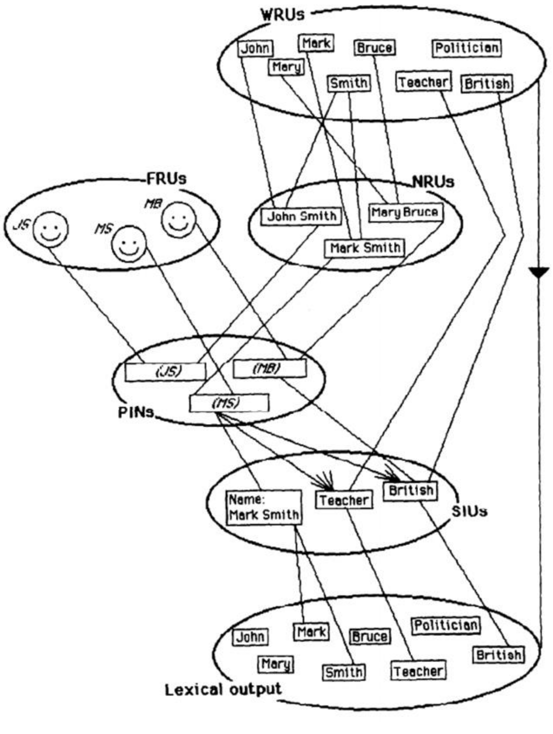


Figure 1.2. IAC model of face processing taken from Burton, Bruce & Hancock (1999).

An advantage of the IAC model over Bruce and Young's model is that it provides a clear framework for the role of non-visual, conceptual information in familiar face recognition. For instance, priming studies have demonstrated that faces are better recognised when preceded by an associated face (Bruce & Valentine, 1986). While a purely perceptually driven model has no explanation for such a phenomenon, the feedback activations in the IAC model lower the threshold needed to activate conceptually related identity PINs.

1.3 Behavioural differences in the perception of familiar and unfamiliar faces

There is a widely held belief that we are experts in recognising faces, particularly unfamiliar individuals. For instance, a study reported that 75% of police officers believed that eyewitnesses were never or rarely incorrect (Kebbell & Milne, 1998). However, experimental findings challenge this assumption. In a line up task using unfamiliar faces, recognition accuracy rates were only 70% when a target was present (Bruce et al., 1999). Similar limitations are evident in real-world settings, such as matching a live unfamiliar person to an image of a face (Kemp et al., 1997). In contrast, familiar faces are recognised with high accuracy across substantial visual changes including those presented in degraded conditions like low-quality CCTV images (Burton, Wilson, et al., 1999), where unfamiliar face performance remains poor. These disparities underscore the fundamental differences between familiar and unfamiliar face recognition.

The critical distinction lies in the disproportionate effect of image change on the processing of unfamiliar faces compared to familiar faces. Familiar faces can be recognised across substantial changes in viewing conditions (Burton, 2013), such as viewing angle and changes in expression and hairstyle, and can withstand considerable image degradation and distortion (Hole et al., 2002). In contrast, unfamiliar face recognition breaks down under small changes in lighting (Hill & Bruce, 1996), pose (Bruce, 1982; Hill et al., 1997) and expression. Such effects are still present when memory demands are removed, with difficulties in recognition of unfamiliar faces found when matching high-quality images of simultaneously presented faces (Burton et al., 2010). According to cognitive models of face processing, these difficulties stem from the absence of an invariant-representation for unfamiliar faces. In contrast, familiar faces are posited to have an image invariant-representation, enabling recognition across diverse visual changes.

The ability to recognise a face across visual changes is linked to person-specific changes in the face image or ‘within-person variability’. Analyses of statistical properties of face images reveal that within-person image differences are highly idiosyncratic and distinguishable from between-person image differences (Burton et al., 2016). This within-person variability has a significant effect on the recognition of unfamiliar faces. Jenkins, White, Van Montfort and Burton (2011) demonstrated this using a card sorting task. Participants were asked to sort 40 face images by identity. Participants who were unfamiliar with the faces believed there were an average of 7 (range: 3-16) identities, despite only 2 different identities being present. In contrast, participants who were familiar with the faces had little trouble sorting the photos into 2 correct piles Familiar face recognition therefore appears to require a representation which integrates the idiosyncratic ways that a face can vary, fitting with cognitive models which propose an underlying image-invariant visual representation.

A key question in face recognition is how does an image invariant representation of a familiar face develop? The generation of an image-invariant representation is thought to rely on perceptual experience with a face, whereby variable encounters of a face are integrated (Burton et al., 2011; Kramer et al., 2018). Increased visual exposure has been shown to enhance face recognition accuracy (Memon et al., 2003; Roark et al., 2006). Critically, exposure to greater within-person variability yields better face recognition than equivalent exposure with low within-person variability (Juncu et al., 2020; Ritchie & Burton, 2017). Furthermore, averaged faces made from many different exemplars are recognised more accurately than faces made of fewer exemplars (Burton et al., 2005). These findings highlight the importance of visual experience, particularly exposure to within-person variability, in the formation of robust image-invariant face representations.

While real-world familiarity with a person is often accompanied by increased perceptual experience, it is also enriched by the accumulation of non-visual, conceptual information. Knowledge about a person, such as their identity, where we usually encounter them, and how we feel about them form an integral component of familiarity. However, this information is often overlooked in discussions of face recognition. Despite its critical role in person familiarity, the integration of conceptual information with visual processing remains underexplored in current models of face recognition. Understanding how these elements interact may provide deeper insights into the mechanisms underlying familiar face processing.

1.4 Neural basis of face processing

Neuropsychological studies have provided compelling evidence for specialized regions dedicated to face processing in the human brain. Prosopagnosia is a condition characterised by severe deficits in face recognition, and can occur after damage to the occipito-temporal cortex (Barton, 2008; Damasio et al., 1982; De Renzi et al., 1994). The fact that prosopagnosia can occur with intact non-face object recognition supports the idea that specialized neural mechanisms underlie face processing (McNeil & Warrington, 1993). Conversely, cases of object agnosia have been reported in the absence of any facial recognition deficits (Moscovitch et al., 1997). This double dissociation between face and object recognition highlights a specialised role of face processing in humans. Prosopagnosia can result from brain injury (acquired prosopagnosia), which has supported the idea that face recognition is carried out by domain-specific mechanisms. More recently, it has been reported that prosopagnosia can arise in the absence of manifest brain injury (developmental prosopagnosia) (Duchaine & Nakayama, 2006).

Electroencephalography (EEG) and magnetoencephalography (MEG) have provided insights into the temporal dynamics of face processing. When comparing face stimuli with other visual stimuli, selective responses to faces have been identified at different stages of processing: 100 ms (Liu et al., 2013), 170ms (Bentin et al., 1996; Xu et al., 2005) and ~200-300ms (Simpson et al., 2015). The M100/N100 is an early face-selective response that is sensitive to the visual properties of the stimulus (Susac et al., 2009). These early responses are likely involved in the detection and categorisation of a stimulus as a face, rather than with recognition of identity (Liu et al., 2013). In comparison, the M170/N170 amplitude has been shown to correlate with perceptual awareness of the face (Rossion, 2014). Other evidence shows selectivity from 200ms onwards, with a maximum around 400-600ms, for familiar compared to unfamiliar faces (Wiese et al., 2019). Overall, these findings highlight the temporal dynamics of processing of faces, across a series of neural processing stages.

Functional magnetic resonance imaging (fMRI), with its high spatial resolution, has been important in localizing face-selective regions in the brain. By contrasting neural responses to faces with other visual stimuli, fMRI studies have revealed a number of face-selective regions in the occipito-temporal cortex. These include the fusiform face area (FFA) (Kanwisher et al., 2002; McCarthy et al., 1997), occipital face area (OFA) (Pitcher et al., 2009; Puce et al., 1996) and superior temporal sulcus (STS). These responses have been shown to be highly face selective and cannot be explained by confounding differences between faces and objects (Kanwisher et al., 2002). For instance, faces consistently evoke greater responses in the FFA compared to different images of the same object (within-category homogeneity control), images of hands (animacy control) and scrambled images of faces (low-level property control). Locations of the core face-selective regions are shown in Figure 1.3. These findings have led to the development of neural models of face processing, which attempt to attribute different stages of processing to different areas of the brain.

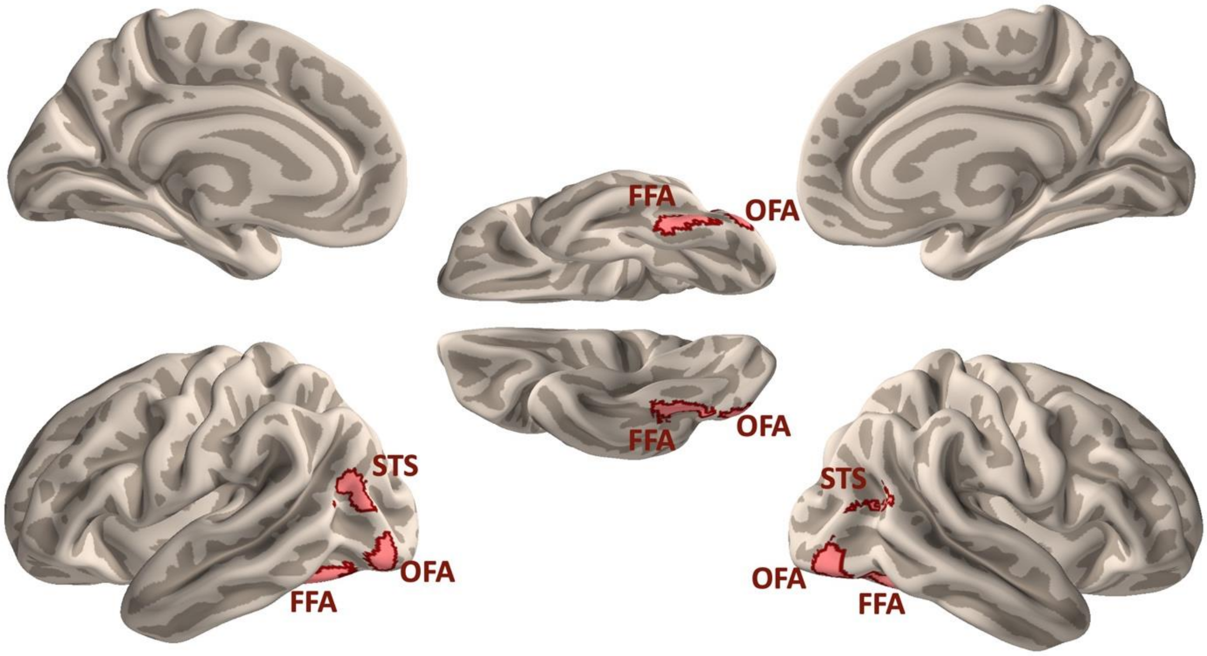
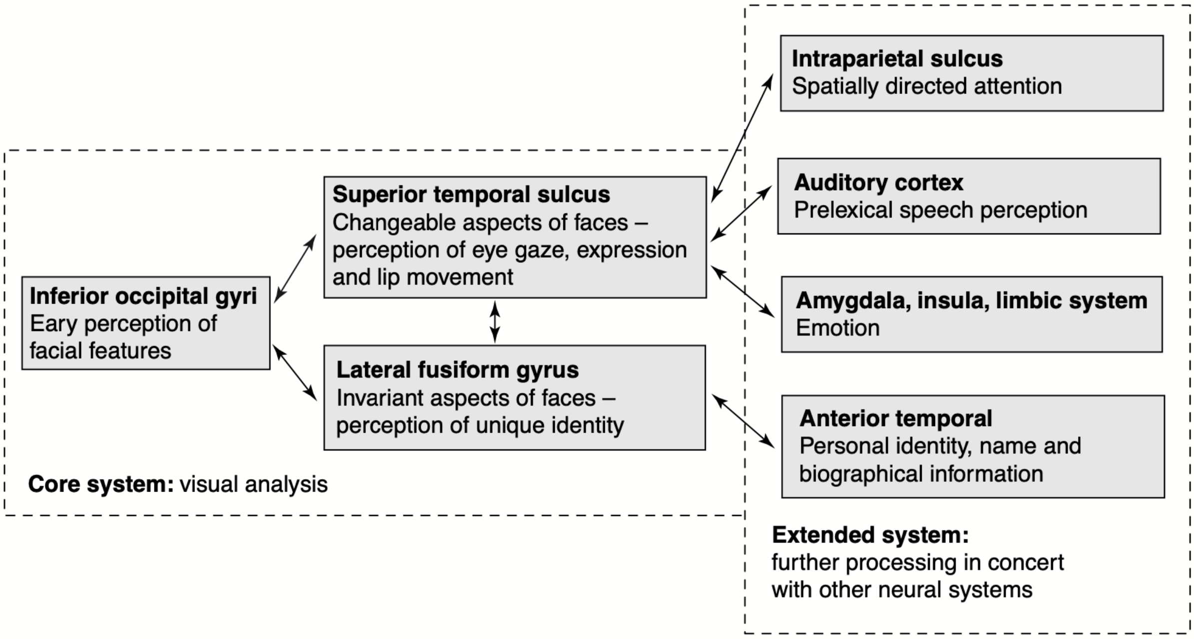


Figure 1.3. Locations of the core face-selective regions projected onto the surface of the brain. The data presented comes from a contrast of faces > scenes + scrambled faces (adapted from, Noad, Watson & Andrews, 2024).

1.5 Neural model of face processing

Haxby, Hoffman and Gobbini (2000) proposed an influential model of face processing that distinguishes between a core system for the visual analysis of a face and an extended system of regions beyond the visual brain involved in further processing, such as representing conceptual/person knowledge (Figure 1.4). Different regions within the model are independently responsible for processing different aspects of a face. In this hierarchical model, the OFA is thought to be involved in early stages of face processing, forming an image-based representation of the face (Pitcher et al., 2007; Rotshtein et al., 2005), similar to the structural representations in cognitive models of face processing. This image-based representation can be accessed for further processing by the STS and FFA. The STS is thought to process changeable aspects of a face such as expressions (Harris et al., 2012b) and eye gaze (Hoffman & Haxby, 2000; Puce et al., 1998). In contrast, the FFA is thought to be involved in processing invariant characteristics of a face, namely the identity of an individual (Hoffman & Haxby, 2000; Rotshtein et al., 2005), analogous to the image-invariant FRUs in cognitive models. In a more recent model, Duchaine and Yovel (2015) have proposed a revised framework in which the OFA projects to the FFA, but not to the STS.

The extended system incorporates regions that process additional information about the face. These regions, while not specialized for face processing, are recruited when interactions with the core system necessitate their involvement. The extended system thus facilitates complex social and cognitive processes associated with face recognition, operating in conjunction with the core system as illustrated in Fig 1.4.



trends in Cognitive Sciences

Figure 1.4. Distributed neural model for face processing taken from Haxby et al., (2000). The core system consists of face-selective regions in the visual brain which process visual properties of a face. The extended network involves regions beyond the visual brain, and processes other aspects associated with a face, such as emotion and person knowledge.

1.6 The neural response to identity

Cognitive and neural models of face processing emphasize the importance of image-invariant, visual representations for identifying individuals across varying visual conditions (Bruce & Young, 1986; Burton et al., 1990; Haxby et al., 2000). The image-invariant representations proposed in these models are thought to underlie the distinction between familiar and unfamiliar faces. Accordingly, considerable research has sought to identify brain regions which have image-invariant representations.

Early neuroimaging studies provided foundational insights into face-selective responses (Kanwisher et al., 2002; McCarthy et al., 1997), but they offered limited information about their role in face identity. FMR-adaptation paradigms (repetition suppression) have been used to explore neural selectivity for face identity. This approach assumes that repeated presentation of a stimulus leads to a reduced response in neurons which selectively respond to that stimulus (Grill-Spector & Malach, 2001). The

FFA also has shown reduced neural response (fMR-adaptation) to repeated images of the same face image (Andrews & Ewbank, 2004), suggesting that it could be linked to identity. Other studies have demonstrated that the adaptation to face identity in the FFA is invariant to some low-level stimulus changes to the face image, such as stimulus size (Andrews & Ewbank, 2004), position (Kovács et al., 2008), morphing (Rotshtein et al., 2005) and emotional expression (Winston et al., 2004), suggesting an image-invariant representation of identity, akin to the FRUs. However, a number of other studies have failed to find adaptation to the identity of familiar faces, when there are larger changes in visual appearance (Andrews & Ewbank, 2004; Davies-Thompson et al., 2009; Davies-Thompson et al., 2013; Pourtois et al., 2005; Weibert et al., 2016). Moreover, the magnitude of the adaptation to familiar faces is not different to the adaptation found for unfamiliar faces (Davies-Thompson et al., 2013; Weibert et al., 2016). The lack of neural differences in response to unfamiliar and familiar faces suggests that the response in the FFA may not be directly linked to familiar face recognition.

Multi-voxel pattern analysis (MVPA) has provided further insights into the neural basis of face identity representations. Unlike univariate methods, MVPA detects patterns of neural activity across voxels. For example, although the overall response across all the voxels in a region may not be different between conditions, there could be a difference in the pattern of response across voxels. MVPA measures these voxel-wise differences and is thus sensitive to the pattern of activation within a region. This is therefore a useful technique for investigating identity representations as it has the sensitivity to differentiate between patterns of response to one stimulus (for example one face identity) from patterns to another stimulus (for example a different face identity). Regions showing different patterns of response to one identity compared to another could therefore be involved in identity representations. Studies using MVPA have found identity representations in the FFA (Anzellotti et al., 2014; Axelrod & Yovel, 2015; Natu et al., 2010; Nestor et al., 2011; Tsantani et al., 2019). However, these effects are often small, and are not consistently replicated (Jeong & Xu, 2016; Kriegeskorte et al., 2007; Weibert et al., 2018).

This raises the question of where does the neural correlate of face recognition occur, if not in visual regions? There is a growing body of research which reveals identity-specific patterns of response in regions outside of the core-face selective regions. For instance, identity representations have been found in the anterior temporal lobes (ATL) (Anzellotti et al., 2014; Collins et al., 2016; Kriegeskorte et al., 2007; Yang et al., 2016) and frontal regions (Guntupalli et al., 2017; Visconti di Oleggio Castello et al., 2017). These findings suggest the involvement of the extended face network in processing the identity of familiar faces.

Studies using EEG have provided complementary insights into response to face identity. Face-selective neural responses emerge as early as 170 ms post-stimulus onset, reflecting initial processing stages in the visual cortex (Eimer, 2011). However, neural selectivity for face identity develops at later time points. From approximately 200 ms onwards, event-related potentials (ERPs) reveal the *N250 familiarity effect*, characterized by more negative amplitudes at occipitotemporal electrodes for familiar faces compared to unfamiliar ones (Wiese et al., 2019). This effect has been observed not only for well-known faces but also for faces that have recently been encountered during real-life interactions (Popova & Wiese, 2022, 2023). Recent studies have identified an additional ERP component associated with face familiarity: the *Sustained Familiarity Effect (SFE)*, observed approximately 400–600 ms post-stimulus onset (Wiese et al., 2022; Wiese et al., 2019). This later effect has been linked to the integration of conceptual information about the individual, with stronger responses for highly familiar faces compared to those that have been recently learned (Popova & Wiese, 2023; Schweinberger & Neumann, 2016).

While the search for invariant representations of identity have provided interesting insights, it may overlook critical aspects of familiar face processing. Research investigating the neural basis of identity representations for familiar faces has focussed on uncovering invariant representations of face identity in visual regions of the brain. However, familiar faces are associated with rich conceptual information that is absent in unfamiliar faces. Current models assume that an invariant representation of identity is achieved primarily through visual processing. However, recent evidence suggests that conceptual information also contributes to the recognition of familiar faces (Dunn et al., 2021; Schwartz & Yovel, 2016, 2019b). Therefore, to understand the neural basis of familiar face recognition it may be necessary to explore neural responses beyond the core face-selective regions.

1.7 Neural response to familiarity

The perceptual advantage for recognising familiar compared to unfamiliar faces suggests that the neural response will also differ in the brain. While some studies do show a greater response to familiar faces in core face-selective regions, such as the FFA (Gobbini et al., 2004; Sergent et al., 1992), other studies find no significant differences in these regions (Bobes et al., 2013; Gorno-Tempini & Price, 2001; Leveroni et al., 2000). In contrast to the comparable response to familiar and unfamiliar faces in the core face-selective regions, a higher response to familiar faces is evident in an extended network of regions beyond the visual brain (Bobes et al., 2013; Gimbel et al., 2017; Gobbini et al., 2004; Góngora et al., 2019; Leveroni et al., 2000; Platek et al., 2006; Ubaldi & Fairhall, 2021).

The involvement of extended brain regions in processing familiar faces has been demonstrated in a number of neuroimaging studies. For instance, Ramon et al., (2015) employed a novel paradigm in which faces were gradually presented with incrementally increasing visual information to reveal either unfamiliar or personally familiar individuals. Activation in core face-selective regions increased as visual information increased, but was independent of familiarity. In contrast, medial temporal lobe (MTL) structures, including the perirhinal cortex, amygdala and hippocampus, showed a sudden increase in signal change when visual information was sufficient for recognition of a personally familiar face. Similarly, another study showed that although the core face-selective areas show no difference in fMR-adaptation for familiar compared to unfamiliar faces, the MTL shows adaptation specifically for familiar faces (Weibert et al., 2016). These findings emphasize the critical role of regions outside of the core face system for processing familiar faces.

MVPA has also been used to investigate differences in processing between unfamiliar and familiar faces. Some studies report that patterns of activity in the core face areas, such as the FFA and OFA, can classify familiar faces from unfamiliar faces (Natu & O'Toole, 2015). However, other findings suggest that patterns of response outside the core face-selective areas, such as the precuneus and prefrontal cortex, are more sensitive in discriminating familiar from unfamiliar faces (Natu & O'Toole, 2015; Rissman et al., 2010; Thornton & Mitchell, 2017). Studies dissociating familiarity from identity have identified familiarity-related responses in the precuneus, temporoparietal junction (TPJ) and medial prefrontal cortex (MPFC) (Visconti di Oleggio Castello et al., 2017). Crucially, while responses in the core face system can classify personally familiar and visually familiar faces, only regions outside of visual areas, such as the MPFC, insula and precuneus can accurately decode the identity of personally familiar faces (Visconti di Oleggio Castello et al., 2021).

Overall, the evidence for the neural basis of familiar face processing is mixed. While some studies implicate the core face regions, a growing body of research emphasizes the involvement of regions outside of the visual brain. Early neural models of face processing, such as Haxby et al., (2000), suggest that neural areas beyond the core face regions access relevant person knowledge, but are not central for recognising a face as being familiar. However, neural evidence demonstrates that the key difference in response to familiar and unfamiliar faces lies in these extended regions. The question remains; what is the role of these extended regions, and are they critical for familiar face recognition?

1.8 Disorders of familiar face processing

Investigating disorders of familiar face processing provides a valuable alternative approach to understanding the neural basis of familiar face processing. Examining neural responses in these conditions can reveal critical insights into the brain regions necessary for familiar face recognition. A key question is whether neural differences occur in face-selective regions in the visual brain. A neural difference within the core face-selective regions would support the argument that visual areas are key in familiar face processing. Alternatively, neural differences occurring outside of core face-selective regions would demonstrate the importance of extended regions in familiar face processing.

1.8.1 Acquired prosopagnosia

Acquired prosopagnosia (AP) is the impaired ability to recognise familiar faces or learn new faces (Barton, 2003; Davies-Thompson et al., 2014). The deficit in AP is selective, meaning that the impaired ability to recognise faces cannot be explained by more general deficits, and occurs following lesions to the occipital and temporal lobes (Damasio et al., 1990). AP is more common following right hemisphere lesions (De Renzi, 1986; Landis et al., 1986) than left hemisphere, but is most associated with bilateral lesions (Damasio et al., 1982; Ettlin et al., 1992; Meadows, 1974).

Acquired prosopagnosia can be split into two functional subtypes: apperceptive and associative (Barton, 2008; De Renzi et al., 1991). Apperceptive prosopagnosia is a deficit in the ability to form an accurate visual representation of a face specific to an identity. This can occur following lesions to occipitotemporal regions, such as the OFA or FFA (Barton, 2008; Barton et al., 2002; Rossion et al., 2003). In contrast, in associative prosopagnosia the visual representation of a face is preserved, but there is a failure in using this perceptual information to access memory. This variant is most associated with anterior temporal lesions (Barton & Cherkasova, 2003; Barton et al., 2003). These variants of AP demonstrate the importance of both visual and non-visual regions of the brain in recognition of faces. Together, they demonstrate that core face-selective regions, which process visual aspects of a face, are certainly necessary for familiar face recognition. However, they may not be sufficient, and processing in non-visual brain regions is required to allow for recognition.

1.8.2 Developmental prosopagnosia

Developmental prosopagnosia (DP) is associated with deficits in recognizing familiar faces despite otherwise normal vision (Duchaine & Nakayama, 2006). Developmental prosopagnosia differs from acquired prosopagnosia in that it occurs without evident brain injury (Duchaine & Nakayama, 2006). A key question is where in the brain do differences occur? Differences in neural response in the core face-selective network would provide support for the importance of these regions in recognising familiar faces. Alternatively, disruptions in extended regions might indicate their critical role in this process.

Studies on the neural response in the core face regions of DPs have found mixed results. Some studies show reduced activity in the core face regions of DPs compared to neurotypical controls (Furl et al., 2011; Hadjikhani & de Gelder, 2002; Jiahui et al., 2018; Lohse et al., 2016), whereas other studies find no significant differences in activation within these regions (Avidan et al., 2005; Avidan et al., 2014; Hasson et al., 2003). These inconsistencies suggest that the neural basis of DP may extend beyond the core face regions.

Differences in the neural response to faces in DPs have been identified in regions beyond the visual brain. For instance, DPs fail to show activity in a number of regions in the extended face processing network compared to neurotypical controls, such as the precuneus, posterior cingulate and anterior paracingulate (Avidan & Behrmann, 2009), and show reduced sensitivity to faces in the anterior temporal lobes (Rivolta et al., 2014; Zhao et al., 2022). Both structural and functional connectivity to these extended regions from visual areas has also been demonstrated to be compromised in DPs (Avidan et al., 2014; Epihova et al., 2024; Rosenthal et al., 2017; Thomas et al., 2009; Zhao et al., 2018). These findings suggest that the impairments in DP involve a broader network of regions beyond the core face-selective regions. However, the specific contributions of core and extended regions to the deficits in DP remain uncertain.

1.8.3 Disorders of familiarity

A number of neuropsychological disorders disrupt the sense of familiarity associated with a face. For instance, Fregoli's syndrome is characterised by the mistaken belief that an unfamiliar stranger is a familiar person in disguise (Devinsky, 2009). On the other hand, Capgras syndrome is characterised by the belief that familiar individuals have been replaced by unfamiliar imposters (Devinsky, 2009). While individuals with such disorders are able to visually recognise an individual, there are abnormal sensations of familiarity or unfamiliarity, leading to delusional misidentifications.

Hyperfamiliarity for faces (HFF) is a rare condition in which a person has a feeling of familiarity for unfamiliar faces (Amlerova et al., 2012; Devinsky et al., 2010; Michelucci et al., 2010; Negro et al., 2015; Vuilleumier et al., 2003). HFF does not affect the ability to recognise familiar faces, it is just that unfamiliar faces are often perceived as being familiar. HFF could therefore provide valuable insights into the mechanisms underpinning the sensation that a face is familiar. Unlike Fregoli's and Capgras syndromes, HFF does not involve delusions but rather an abnormal attribution of familiarity to unfamiliar faces. This provides evidence for distinct neural systems responsible for recognition of faces and the sense of familiarity.

Previous research investigating the neural basis of HFF has shown changes in the temporal lobes. For instance, structural abnormalities have been found in the left temporal lobe of individuals with HFF (Devinsky et al., 2010; Negro et al., 2015; Vuilleumier et al., 2003). HFF also has been reported in individuals with temporal lobe epilepsy (Amlerova et al., 2012; Bujarski & Sperling, 2008). Functional imaging has revealed hyper-activity in medial and lateral temporal cortex, including the fusiform gyrus and parahippocampal gyrus, when viewing faces (Negro et al., 2015). These findings have led to the suggestion that there is an interhemispheric processing imbalance between the temporal lobes in HFF. Nevertheless, other studies report the involvement of brain regions in the anterior cingulate cortex (Nente et al., 2007), temporo-parietal cortex (Van den Stock et al., 2013) and hippocampus (Bujarski & Sperling, 2008; Michelucci et al., 2010). These findings suggest that neural mechanisms underlying HFF extend beyond the core face-selective regions.

Disorders of face processing provide complementary insights into the neural mechanisms of familiar face processing. The involvement of extended regions in these disorders suggest that familiar face recognition relies on a distributed network of regions rather than solely on the core face regions.

1.9 Neural models of familiar face processing

Traditional cognitive and neural models have provided robust frameworks for understanding the visual processing of faces. However, growing evidence suggests the primary involvement of a more extensive network of brain regions in familiar face recognition. This extended system incorporates brain regions that are not solely dedicated to face perception, but are integral to processing conceptual information about faces.

Building on Haxby et al.'s 2000 influential model of face processing, Gobbini and Haxby (2007) developed a model of familiar face recognition incorporating an updated extended system. The model includes the core system which processes the visual appearance of a familiar face, consisting of the posterior STS (pSTS), the inferior occipital gyri (OFA) and fusiform gyri (FFA). The extended system includes regions which are associated with conceptual information, such as personality traits, mental states, biographical information and emotional significance (Fig. 1.5). This extended system is proposed to have top-down modulatory feedback to the core system.

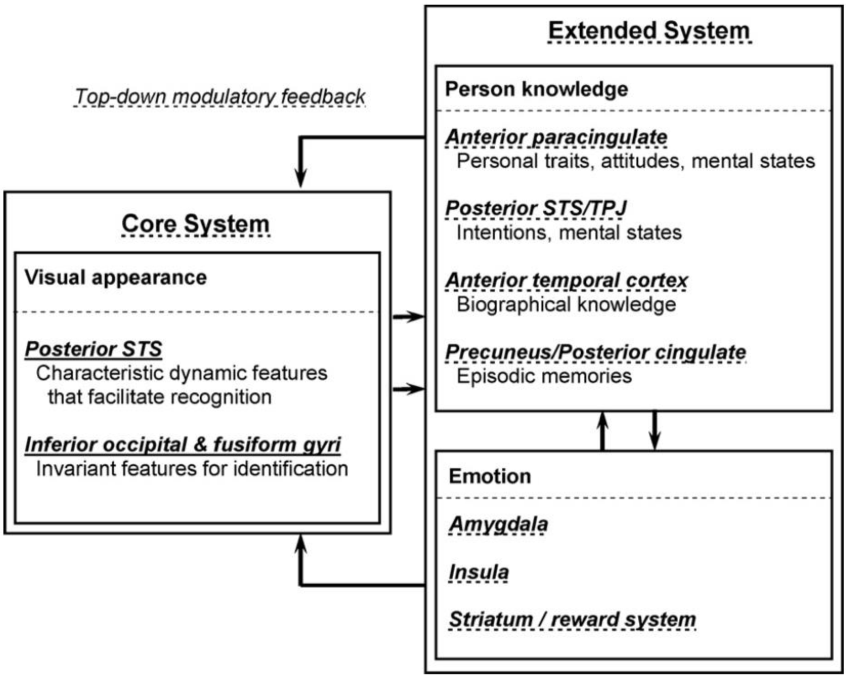
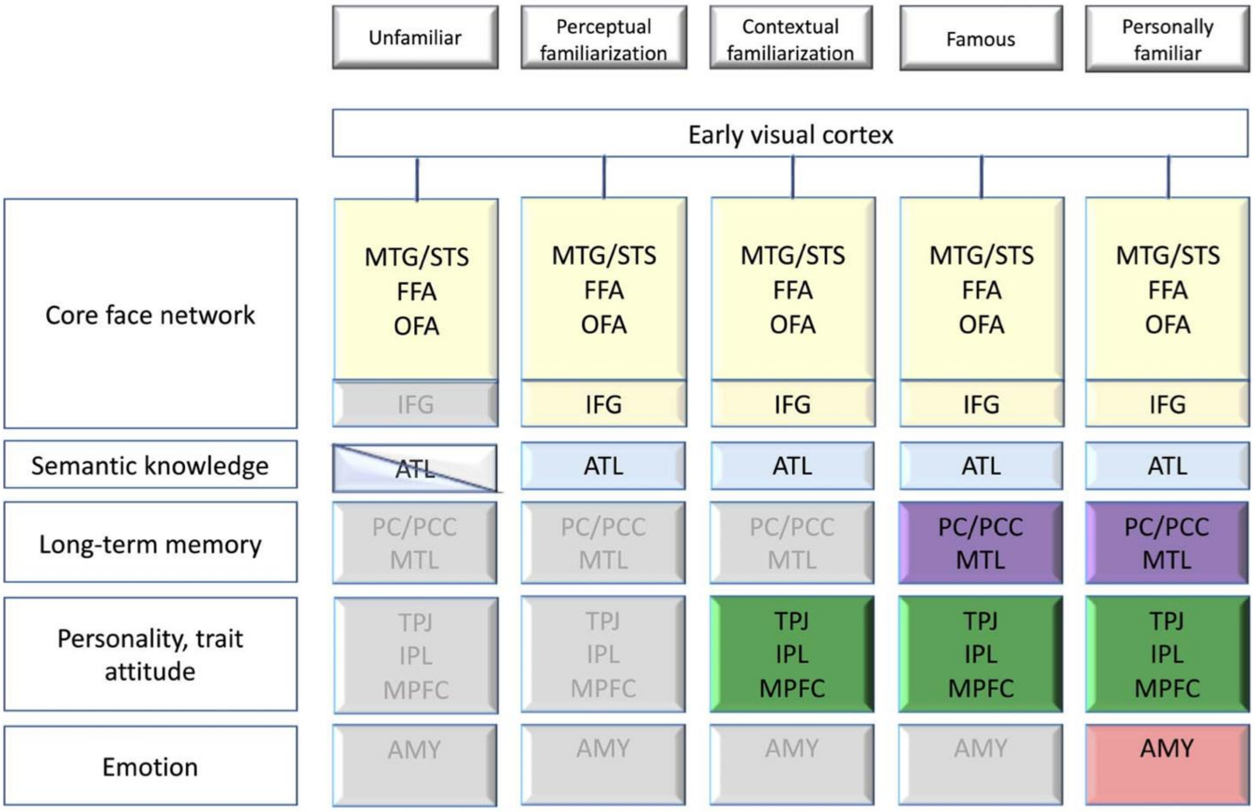


Figure 1.5. Distributed model of face recognition from Gobbini and Haxby (2007). The core system processes visual properties of a face. The extended system represents other information associated with a face, such as conceptual information and emotion.

Kovács (2020) proposed a model of familiar face processing which also focuses on the role of the extended face network. In this model, the different levels of familiarity modulate the response of different brain regions (Fig. 1.6). This model suggests that the difference in neural response for familiar compared to unfamiliar faces occurs in the extended face system. Much like Gobbini and Haxby's model, the regions in the extended face system are thought to process conceptual information, such as semantic knowledge, long-term memories, personality information and emotional response.

Both Gobbini and Haxby's and Kovács's models suggest that regions associated with semantic knowledge, or person information, are important in familiar face processing. The anterior temporal lobes (ATL) have been shown to represent person information associated with a face, such as name and occupation (Liu et al., 2017; Tsukiura et al., 2010; Wang et al., 2017). Further work suggests there is a distinct network of regions in the ATL, functionally connected to the hippocampus, that represent knowledge about familiar faces (Morton et al., 2021). Evidence suggests the ATL may be important in familiar face processing. For instance, lesions to the ATL lead to deficits in face memory (Collins &



Olson, 2014), and responses in the ATL have been shown to be selective to familiar faces (Ramon et al., 2015; Ubaldi & Fairhall, 2021; Visconti di Oleggio Castello et al., 2021; Yang et al., 2016).

Figure 1.6. Neural model of familiar face recognition from Kovacs (2020). The core system responds to all faces irrelevant of familiarity. In contrast, there is a graded response in the extended regions depending on the level of familiarity with a face. Coloured shading represents identity-specific representations within an area.

Another aspect of the extended system in these models is processing of person-specific long-term episodic memories. The precuneus, posterior cingulate cortex and medial temporal lobes (MTL) are known to be involved in long-term memory retrieval processes (Burgess et al., 2001; Gilmore et al., 2015; Squire & Zola-Morgan, 1991). The posterior cingulate cortex has been found to represent knowledge about familiar faces (Afzalian & Rajimehr, 2021). Furthermore, findings from single unit recordings show neurons in the MTL which are abstractly responsive to specific identities, for instance responding to an image of a familiar face, but also the person's name and related conceptual information (Quiroga et al., 2005). Responses in the precuneus, posterior cingulate cortex and MTL are consistently found in response to familiar compared to unfamiliar faces (Gobbini et al., 2004; Leveroni et al., 2000; Visconti di Oleggio Castello et al., 2017; Weibert et al., 2016).

The extended network also includes regions such as the medial prefrontal cortex (mPFC), temporoparietal junction (TPJ) and inferior parietal lobule (IPL). These regions are thought to be involved in encoding personality traits, attitudes and mental states of others (Frith & Frith, 1999). The mPFC is involved in making social judgements about familiar faces (Cloutier et al., 2011; Krienen et al., 2010) and distinct patterns of response in the mPFC have been found to represent identity-specific information about personally familiar faces (Visconti di Oleggio Castello et al., 2021). Responses in the mPFC, TPJ and IPL have been found for familiar compared to unfamiliar face processing (Gobbini et al., 2004; Leveroni et al., 2000; Platek et al., 2006; Sugiura et al., 2011).

The emotional response to familiar faces is also highlighted in these neural models. Neural responses to familiar compared to unfamiliar faces are consistently found in regions typically associated with processing emotion, such as the amygdala and insula (Góngora et al., 2019; Leibenluft et al., 2004; Platek et al., 2006; Ubaldi & Fairhall, 2021; Visconti di Oleggio Castello et al., 2017). White-matter pathways connect visual face-selective regions to the insula and amygdala (Góngora et al., 2019; Gschwind et al., 2012), and a rapid coupling between the amygdala and cortical face areas has been identified during processing of familiar compared to unfamiliar faces (Fan et al., 2023). Familiar faces evoke greater autonomic arousal compared to unfamiliar faces (Ellis et al., 1999), and emotional expression and context can slightly interfere with familiar, but not unfamiliar, face processing (Ganel & Goshen-Gottstein, 2004; Kaufmann & Schweinberger, 2004; Van den Stock & de Gelder, 2012), suggesting that affective responses may be important in familiar face processing.

Overall, these models are particularly notable as they provide a new framework for understanding how familiar faces are represented. There is a greater focus on the conceptual information associated with a face which may be crucial in the processing of familiar compared to unfamiliar faces. The extension of familiarity beyond purely visual processing may be key in highlighting the cognitive and neural mechanisms underlying familiar face recognition.

1.10 The role of conceptual knowledge in face recognition

There is growing evidence that conceptual information about a person is also important in becoming familiar with a face. For instance, priming studies have found participants to be faster at recognising a face when it has been preceded by faces that are associated with similar conceptual knowledge (Bruce, 1983; Bruce & Valentine, 1986). Consistent with this finding, faces paired with conceptual information, such as a name or occupation, are better recognised compared to faces that vary in visual properties (Bonner et al., 2003; Schwartz & Yovel, 2016). Moreover, faces that are learned while participants make conceptual rather than visual judgements are better recognised (Bower & Karlin, 1974; Patterson & Baddeley, 1977; Schwartz & Yovel, 2019b). Similarly, mismatched conceptual information, such as incorrect labelling of faces, can hinder the development of robust face representations (Dunn et al., 2021). A number of studies have also shown that faces are difficult to recognize in atypical contexts (Thomson, 1986; Young et al., 1985). Indeed, providing the context with which a face was learnt has been shown to improve face recognition (Hanczakowski et al., 2015; Reder et al., 2013), and faces that are accompanied by contexts are often recognised better than faces that are learnt without contexts (Mattarozzi et al., 2015; McCrackin et al., 2021). This suggests that conceptual information contributes not only to the recognition of familiar faces but also to the process of becoming familiar with them.

The level of processing (LoP) framework provides a theoretical basis for understanding the mechanism by which conceptual information could influence face recognition. The LoP framework proposes that memory retention is not solely determined by perceptual exposure with a stimulus, but rather depends on the depth of processing during encoding (Bower & Karlin, 1974; Craik, 2002; Craik & Lockhart, 1972). According to the LoP framework, faces associated with conceptual information undergo a deeper level of processing. However, it is not clear where this deeper processing occurs. One possibility is that conceptual information enhances perceptual processing of a face, leading to more robust representations of learned faces within the core face-selective regions of the visual cortex (Oh et al., 2021; Winograd, 1981). This would suggest that familiarisation with a face tunes bottom-up, visual processing areas which improves visual recognition of a familiar face. Support for this comes from findings which show that the representations of individual faces become more perceptually similar when two individuals are deemed to be more similar in their personalities (conceptual information) (Oh et al., 2021). An alternative explanation is that activity in brain regions directly involved in conceptual knowledge is instead modulated (Gobbini & Haxby, 2007; Haxby et al., 2000; Ishai, 2008; Kovács, 2020). This would suggest that regions beyond the visual brain involved in representing person knowledge are important in familiar face recognition, and may have a top-down modulation effect on face representations. Support for this hypothesis comes from neuroimaging studies showing that making social evaluations of faces during learning leads to better recognition, and engages brain regions in the extended system in the non-visual brain, compared to when participants perform a purely perceptual task (Shoham et al., 2022).

The extended system proposed by Gobbini and Haxby (2007) and Kovacs (2020) provide a framework for exploring the neural processes underlying familiar face recognition. Conceptual knowledge may play a pivotal role, not only in the recognition process, but also in becoming familiar with a face. However, further research is needed to elucidate the precise mechanisms in which conceptual information modulates the neural response in the extended network. Understanding these processes may offer valuable insights into the way we recognise faces.

1.11 Naturalistic viewing of faces

In real-world contexts, we encounter faces in a rich and dynamic context, which may be important in learning and recognition. For example, motion has been shown to facilitate face recognition (Butcher et al., 2011; Hill & Johnston, 2001; Knight & Johnston, 1997; Lander & Pitcher, 2017), while contextual information significantly influences the recognition of familiar individuals (Hanczakowski et al., 2015; Laurence et al., 2021). Conceptual information, which is inherently tied to familiar faces, may be a critical component in learning and recognising processes (Schwartz & Yovel, 2016, 2019b). Although a number of studies have shown that the recognition of faces can be influenced by conceptual knowledge, prior studies have predominantly used highly controlled experimental designs, often using static faces. While these approaches have provided some insights into the underlying processes, they fail to capture the dynamic and context-rich nature of real-world face perception.

To advance our understanding of familiar face processing, future research should prioritize naturalistic paradigms. There are obvious constraints to studying the neural basis of face recognition in the real-world with techniques such as MRI. However, movie-watching provides a unique opportunity to study face processing under naturalistic conditions. Movies capture the richness and complexity of real-world interactions, while also being more engaging for the participant (Vanderwal et al., 2017). Film also preserves the within-person variations of a face, which more closely replicates the perception of faces in real life. They also reflect the dynamic nature of real life, where faces appear within complex environments in which people interact within an ongoing narrative. Although the complex, unconstrained nature of movies provides some challenges for experimental design, a number of analysis approaches have been developed to study cognitive processes in these naturalistic paradigms.

1.11.1 Behavioural measures

Naturalistic stimuli can be a useful tool for understanding aspects of social cognition in the real world (Baldassano, 2023; Chen & Whitney, 2019; Dima et al., 2023; Wagner et al., 2016). These stimuli provide ecologically-valid insights into real world processes, including the recognition of familiar faces. Measuring recognition of faces seen from movies is a good reflection of how faces are learned during real-life. For example, one study measured face recognition of actors from the TV series Game of Thrones, finding that the faces of the lead actors were recognised best, and recognition was better for faces viewed more recently (Devue et al., 2019). Thus, movie-watching serves as a robust paradigm for understanding real-world face recognition. Naturalistic paradigms can be manipulated to explore the types information critical for social cognition. By varying contextual information prior to viewing a movie, it is possible to alter participants' interpretation of events (Bacha-Trams et al., 2017; Kauttonen et al., 2018; Tylén et al., 2015; Van Kesteren et al., 2010; Yeshurun et al., 2017). This approach could be adapted to study face recognition by comparing the recognition of faces with different levels of conceptual information.

1.11.2 Intersubject correlation

Intersubject correlation (ISC) is a powerful analytical method for assessing the similarity of neural response across viewers. ISC measures the degree to which brain activity in one individual correlates with activity in corresponding regions of another individual (Fig. 1.6; Hasson et al., 2004). Similarity between viewers in a given region suggests that that brain region is selectively involved in processing some aspect of the shared experience. The model free properties of ISC make it ideally suited to naturalistic viewing. ISC has demonstrated high similarities in neural response between viewers during free viewing of a film (Hasson et al., 2004). This shows that despite viewing complex and dynamic scenes, individual brain activity can synchronise across viewers. The highest intersubject correlations are typically evident in posterior regions of the brain which are associated with sensory processing of the stimulus, such as visual regions. Later studies have shown that the degree of ISC varies across different types of movies, with higher ISC found in more anterior regions when movies contain a coherent narrative (Hasson et al., 2010; Hasson, Yang, et al., 2008; Nguyen et al., 2019).

ISC measures can also be used to investigate differences between groups. For example, Andrews et al., (2019) examined neural responses in rival football fans watching the same football games between the two teams. While the ISCs in visual areas of the brain were similar regardless of which team the participants supported, group differences were found in higher-order, non-sensory regions of the brain. Critically, both groups viewed the same stimulus, but the brain response differed based on group affiliation and the interpretation of the stimulus. Similar findings have been reported in studies of political ideology (van Baar et al., 2021), spoken languages (Honey et al., 2012), understanding of narrative (Jääskeläinen et al., 2020; Yeshurun et al., 2017) and even psychiatric disorders (Gruskin et al., 2020; Yang et al., 2020). ISC, therefore, offers a promising avenue for investigating group differences, for instance comparing groups who are familiar or unfamiliar with faces in a movie.

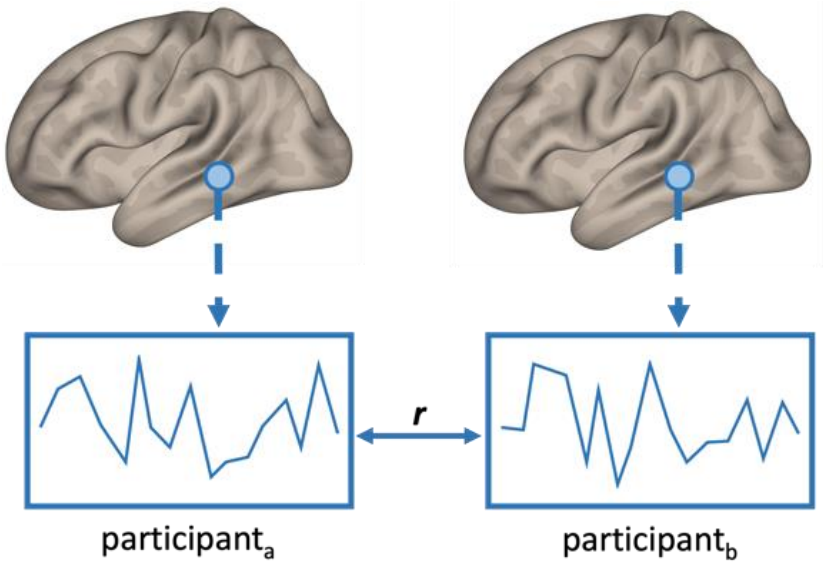


Figure 1.6. Intersubject correlation. The time-course of neural response from one individual is correlated with the corresponding time-course from a different individual. This correlation can be performed across all regions in the brain, and thus can highlight regions with high intersubject correlations. To address group differences in ISC, the time-course of neural response of one individual is correlated with the corresponding time-course of response from a different individual from the same group (within-group) or from a different group (between-group). These within-group and between-group correlations are calculated for each combination of individuals across the whole brain.

1.11.3 Functional Connectivity

Functional connectivity (FC) is another model free method that can be used effectively to study neural responses during naturalistic viewing. FC measures changes in neural activity between regions of the brain. The time-course of neural response in one brain region can be correlated with the time-course of neural response of another brain region within a participant to examine functional connectivity (Fig. 1.7). A correlation between the time-course of response of two brain regions is interpreted as a functional coupling between the regions, or rather, that they are jointly involved in processing the stimuli.

Unlike resting-state FC, FC during movie-watching can reveal reliable task-relevant neural coupling (Finn & Bandettini, 2021; Finn et al., 2017; Vanderwal et al., 2017). Group differences in FC during movie watching can reveal differences in the network dynamics associated with group-specific experiences or interpretations (Richardson et al., 2018; Van Kesteren et al., 2010). As such, functional connectivity during movie-watching could be a valuable technique for understanding how different regions of the brain work together to recognise familiar faces. Indeed, similarities between indivdiuals in functional connectivity during movie watching has been found to relate to face recognition abilities (Levakov et al., 2023).

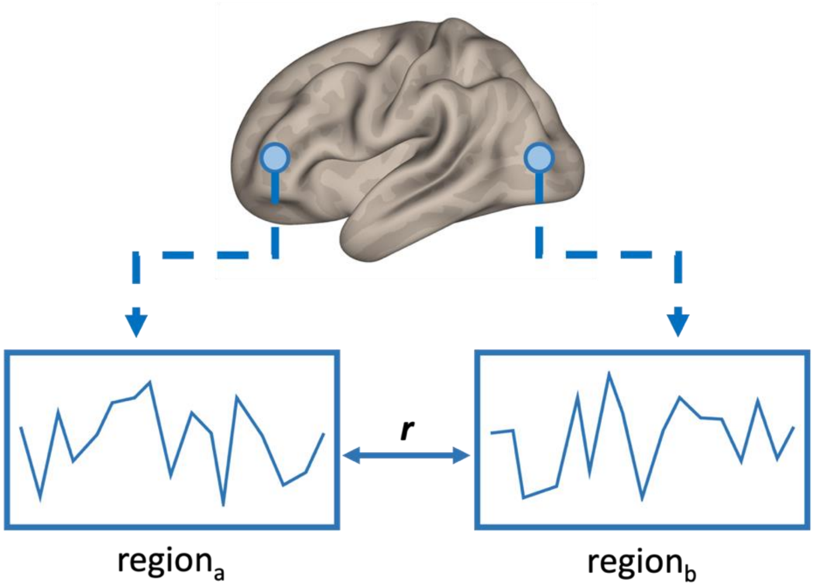


Figure 1.7. Intra-subject functional connectivity. The neural time-course of response from one region in one participant is correlated with the neural time-course of response from another region in the same participant.

1.11.4 Multivoxel Pattern Analysis

Multivoxel pattern analysis (MVPA) provides a fine-grained approach to studying neural activity measuring spatial patterns of neural response during movie-watching. A particular advantage of MVPA is that it can reveal distinct patterns of neural response which may not be revealed through differences in the magnitude of the response that are revealed by univariate contrasts (Haxby et al., 2001). MVPA can be applied to naturalistic stimuli by tagging events, such as the appearance of a face or location. The pattern of response to a specific event can be determined by investigating whether within-stimuli patterns of response are greater than between-stimuli patterns of response. Previous research has found identity-specific patterns of response across the brain during movie-watching (Lally et al., 2023; Milivojevic et al., 2016). This approach offers a useful tool to probe the pattern of response to familiar compared to unfamiliar faces.

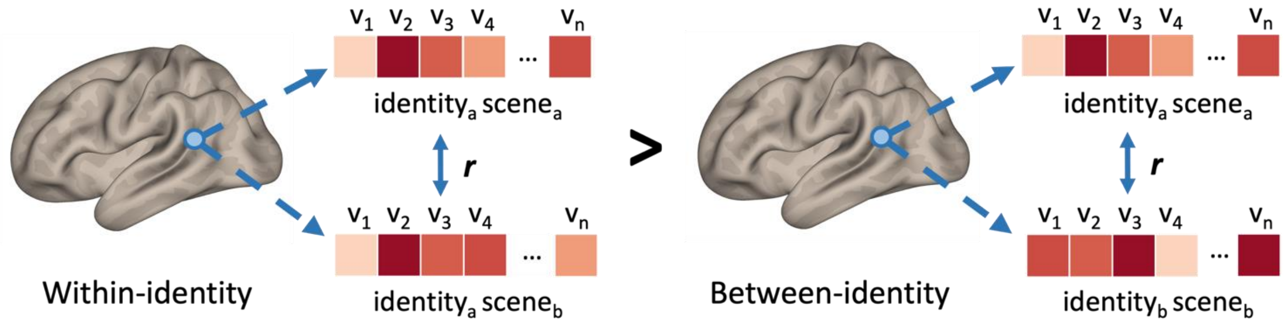


Figure 1.8. Multivoxel pattern analysis. The voxelwise pattern of response to the same identity (within-identity) or to different identities (between-identity) is correlated across different scenes. Greater within-identity correlations compared to between-identity correlations suggest an identity-specific representation within that brain region.

1.12 Thesis Aims

While familiar face recognition is rapid and effortless for most, the neural mechanisms underlying this process remain unclear. Moreover, the process by which a face becomes familiar in the real world is not fully understood. While previous work has focussed on the importance of perceptual information in the recognition of familiar faces, conceptual information may also play a critical role. This thesis will explore the neural correlates of familiar face perception in naturalistic conditions, and elucidate the role of naturally occurring conceptual information in this process.

1.12.1 Aim 1: Neural basis of familiar face perception during naturalistic viewing

The first objective of this thesis is to investigate the neural basis of familiar face perception during naturalistic viewing. A key question is whether neural differences occur in core face-selective regions within the visual brain, or in extended regions beyond the visual brain. Previous research has largely utilized controlled, laboratory-based paradigms that may not capture the full complexity of brain activity involved in recognizing faces in dynamic and contextually rich environments.

Chapter 2 investigates the neural basis of familiar face processing using a naturalistic viewing paradigm where participants view clips from the TV series Game of Thrones, while neural activity is recorded using fMRI. The neural response was compared between participants who are either familiar or unfamiliar with the TV series. To directly address how patterns of neural response were relevant to face recognition, neurotypical participants were compared to participants with developmental prosopagnosia (DP), in which face recognition is impaired.

Building on this paradigm, Chapter 3 investigates a unique case of an individual with hyperfamiliarity for faces (HFF), characterized by the perception of unfamiliar faces as familiar. HFF provides a unique opportunity to investigate the neural basis of familiar face perception. To investigate the neural correlates of HFF, neural response was compared to familiar and unfamiliar participants. Together, these findings address the question of whether familiar face processing relies primarily on visual brain or involves non-visual areas.

1.12.2 Aim 2: Role of conceptual information in familiar face processing

The second objective is to explore the role of conceptual information in familiar face processing using natural viewing paradigms. Previous research has focussed on the importance of perceptual experience in becoming familiar with a face. However, in natural viewing, perceptual experience with a face is accompanied by increased conceptual knowledge about the person. It is currently unclear whether this conceptual information is important for becoming familiar with a face. It is also unclear whether conceptual information modulates brain responses to faces in visual or non-visual areas of the brain. Chapter 4 addresses whether the understanding of events during natural viewing paradigm (conceptual knowledge) can influence the recognition of faces. Building on this, Chapter 5 extends the natural viewing paradigm in fMRI to investigate whether conceptual knowledge modulates neural responses to faces, focusing on whether these effects are localised to visual or non-visual regions of the brain.

1.12.3 Aim 3: The acquisition of conceptual knowledge in developmental prosopagnosia

The final aim of the thesis is to investigate the relationship between conceptual information and face processing in individuals with a deficit in recognition (developmental prosopagnosia). While much research has investigated the perceptual difficulties in DP, less attention has been given to the broader implications of these impairments. Having established the importance of conceptual information in face processing, the aim asks the question in reverse; is face recognition important for gathering conceptual information about other peoples? Chapter 6 employs a naturalistic viewing paradigm to investigate whether individuals with DP experience difficulties in acquiring conceptual information and how these could have broader social-cognitive consequences.

Overall, the experiments presented in this thesis aim to provide an account of the cognitive and neural mechanisms underpinning familiar face processing during naturalistic viewing. Particular emphasis is placed on the importance of conceptual information in becoming familiar with a face. This thesis investigates these processes in neurotypical participants and those with disorders of face perception. Collectively, these findings contribute to theoretical models of face recognition and provide a deeper understanding of the interplay between perceptual and conceptual processes in social cognition.

Chapter 2

Familiarity enhances functional connectivity between visual and non-visual regions of the brain during natural viewing

This chapter is adapted from: Noad, K. N., Watson, D. M., & Andrews, T. J. (2024). Familiarity enhances functional connectivity between visual and nonvisual regions of the brain during natural viewing. *Cerebral Cortex*, *34*(7), bhae285.

2.1 Abstract

We explored the neural correlates of familiarity with people and places using a naturalistic viewing paradigm. Neural responses were measured using fMRI while participants viewed a movie taken from Game of Thrones. We compared inter-subject correlations (ISC) and functional connectivity in participants who were either familiar or unfamiliar with the TV series. Higher ISC were found between familiar participants in regions, beyond the visual brain, that are typically associated with the processing of semantic, episodic and affective information. However, familiarity also increased functional connectivity between face and scene regions in the visual brain and the non-visual regions of the familiarity network. To determine whether these regions play an important role in face recognition, we measured responses in participants with developmental prosopagnosia (DP). Consistent with a deficit in face recognition, the effect of familiarity was significantly attenuated across the familiarity network. There was also a reduced effect of familiarity on functional connectivity between face regions and the familiarity network. These results show that the neural response to familiarity involves an extended network of brain regions, and that functional connectivity between visual and non-visual regions of the brain plays an important role in the recognition of people and places during natural viewing.

2.2 Introduction

The ability to recognise familiar people and places is important for our ability to navigate and interact in the real world. A key challenge is that, during natural viewing, substantial changes can occur to the image of a person's face or a scene. Nevertheless, it is possible to recognise familiar people and places across these dynamic changes. Cognitive models propose that faces are initially encoded in an image-dependent code, which is then transformed into a structural or image-invariant representation that can be used to support recognition of familiar faces (Bruce & Young, 1986; Burton, Bruce, et al., 1999; Hancock et al., 2000; Young & Burton, 2017). Activation of these image-invariant representations are thought to lead to the sensation that a face is familiar. This is then followed by access to relevant semantic, episodic and affective information about a person (Bruce & Young, 1986; Burton, 1994).

Neural models propose an analogous pathway in the brain for processing familiar faces (Duchaine & Yovel, 2015; Haxby et al., 2000; Ishai, 2008). A core network in the visual brain represents the visual properties of faces. Within this core network, an initial view-dependent representation of faces emerges in the occipital face area (OFA), which then projects to a view-invariant representation in the fusiform face area (FFA) for the recognition of identity. The ability to access appropriate person knowledge following the recognition of a face is thought to occur through the activation of the extended face network. The extended network contains regions that do not exclusively process faces, but are important for processing non-visual information associated with the face. This links the visual representation of the face with semantic, episodic and affective knowledge about the person (Gobbini & Haxby, 2007; Haxby et al., 2000; Ishai, 2008; Kovács, 2020).

Despite the efforts of many studies, evidence for an effect of familiarity in core face regions, such as the FFA, has been mixed. Some studies report stronger FFA activity for familiar compared to unfamiliar faces (Sergent et al., 1992; Weibert & Andrews, 2015), while others find no difference in response (Gobbini et al., 2004; Gorno-Tempini & Price, 2001; Leveroni et al., 2000). Other studies, using adaptation or multivoxel pattern analysis to probe image-invariant responses to familiar faces also show inconsistent effects within the core face regions, with some studies showing an effect of familiarity (Andrews et al., 2010; Axelrod & Yovel, 2015; Ewbank & Andrews, 2008; Rotshtein et al., 2005), whereas other studies show no difference between familiar and unfamiliar faces (Davies-Thompson et al., 2009; Davies-Thompson et al., 2013; Pourtois et al., 2005; Weibert et al., 2016). In contrast, regions of the extended face network are typically defined by their response to familiar faces. For example, a higher response to familiar compared to unfamiliar faces is evident across a range of regions involved in semantic and episodic memory, personality traits and affective responses (Gobbini et al., 2004; Gorno-Tempini & Price, 2001; Leveroni et al., 2000; Visconti di Oleggio Castello et al., 2017; Visconti di Oleggio Castello et al., 2021).

An alternative approach to understanding familiar face processing is to measure neural responses in people with a deficit in recognition, such as developmental prosopagnosia (DP) (Duchaine & Nakayama, 2006). Again, there is conflicting evidence for the role of the core face regions in recognition (Manippa et al., 2023). Some reports find neural responses to faces in DP are similar to neurotypical controls (Avidan et al., 2005; Hasson et al., 2003; Rivolta et al., 2014), whereas other studies report reduced activity in the core face-selective areas of DPs (Furl et al., 2011; Hadjikhani & de Gelder, 2002; Jiahui et al., 2018). In contrast, other studies have shown attenuated responses in the extended face network of DPs (Avidan & Behrmann, 2009), which could result from a disruption in the connectivity with the core face regions (Avidan et al., 2014; Rosenthal et al., 2017; Thomas et al., 2009).

The neural basis of familiar places, relative to faces, is less well understood. Neuroimaging studies have shown a number of regions in the visual brain that show selective responses to scenes compared to faces and other objects (Aguirre et al., 1998; Epstein & Kanwisher, 1998; Epstein & Baker, 2019). These regions can be divided into a posterior network that connects more strongly with early visual regions and is involved in processing visual properties and a more anterior network that is involved in higher-level aspects of scene processing such as navigation, recognition, and memory recall (Baldassano et al., 2016; Watson & Andrews, 2023). Some studies have found an effect of familiarity in posterior scene regions (Epstein, Higgins, et al., 2007), whereas other studies do not (Epstein et al., 1999; Epstein, Parker, et al., 2007). The effect of familiarity is more consistent in anterior scene regions (Epstein et al., 1999; Epstein, Parker, et al., 2007) and in regions of the medial and lateral parietal lobe that are beyond the core scene network (Epstein, Parker, et al., 2007; Silson et al., 2019; Steel et al., 2021; Sugiura et al., 2005).

A potential limitation of previous neuroimaging studies is that faces and places are often presented separately and in controlled experimental settings, which do not reflect our experience in real life (Hasson et al., 2010; Redcay & Moraczewski, 2020). Recent studies of social cognition have attempted to overcome this limitation by using natural viewing approaches to capture the complexity and context in which we typically view faces (Hasson et al., 2004; Jääskeläinen et al., 2021). Key to the success of this approach is the development of model-free methods such as inter-subject correlation (ISC) and functional connectivity. These approaches differ from standard univariate analyses in which the experimenter provides a model of the expected neural activity with which to compare the observed neural activity. In contrast, model free methods make no assumption about the expected response. This is necessary as it allows the analysis of complex natural stimuli for which it would be difficult to provide an adequate *a priori* model. Model free methods simply compare the time courses of response in the same brain region between participants (ISC) or the time courses in different regions within the same participant (functional connectivity) (Hasson et al., 2004) Recent studies have used ISC to explore the neural basis of group differences during natural viewing, by revealing regions that are more similar in individuals from the same group, compared to individuals from a different group (Andrews et al., 2019; Leong et al., 2020; van Baar et al., 2021).

Here, we develop these natural viewing paradigms to explore the neural basis of familiarity (Fig. 2.1). Natural viewing conditions were simulated by showing a movie of excerpts from the TV series Game of Thrones (GoT). Our first objective was to determine which brain regions showed an effect of familiarity. We compared neural responses between groups of participants who were either familiar or unfamiliar with GoT. We predicted that regions involved in familiarity should show a higher ISC between familiar participants when compared to unfamiliar participants. Our second objective was to explore how regions in the visual brain interact with non-visual regions involved in familiarity. We predicted that functional connectivity with regions involved in familiarity should be higher in familiar compared to unfamiliar participants. Our third objective was to determine the extent to which regions involved in familiarity are specific to faces. To address this, we measured the responses in participants with a deficit in face recognition (DP). Our prediction is that activity and connectivity in regions of the brain that are directly linked to familiar face recognition will be attenuated in DP.

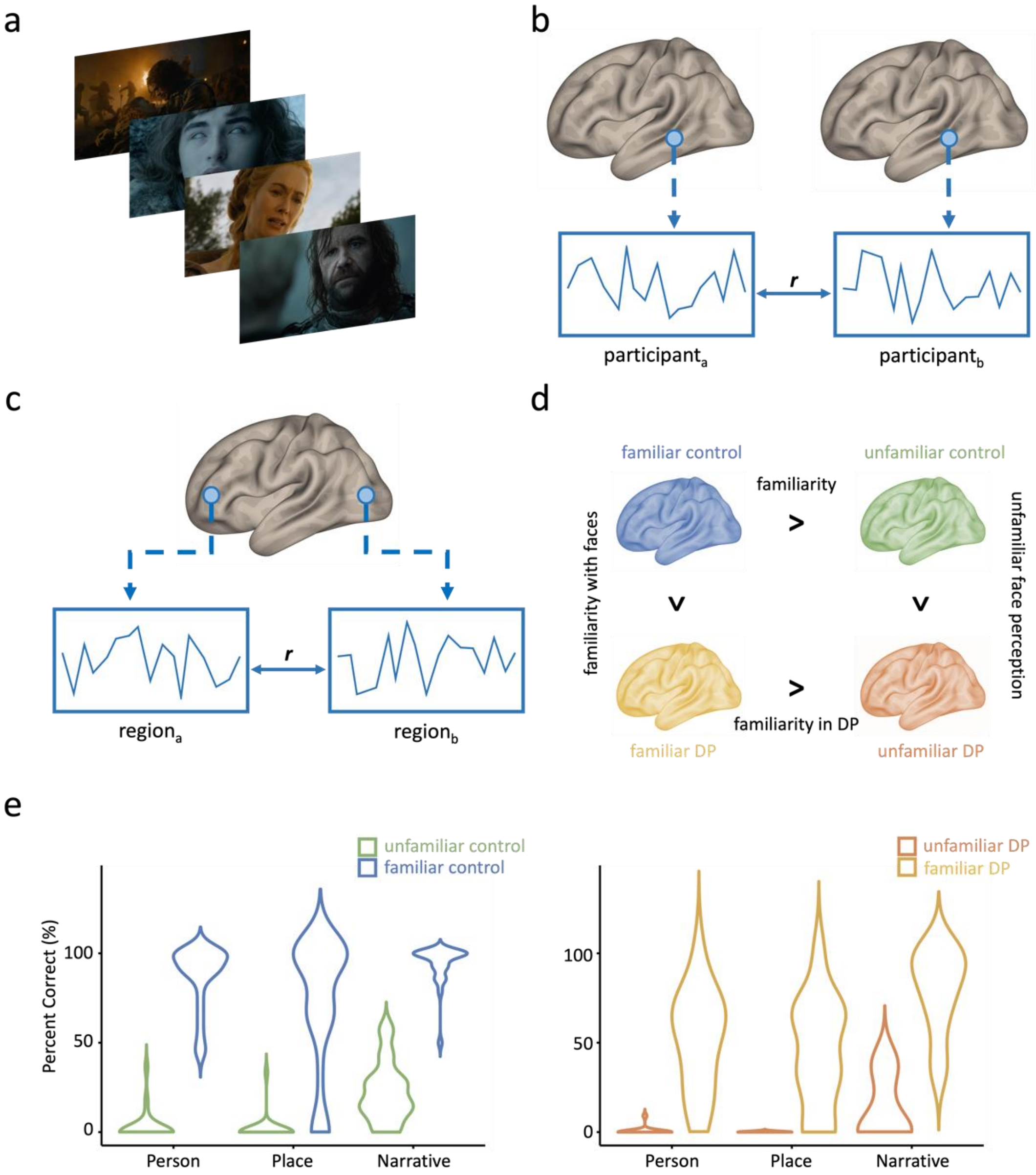


Figure 2.1. Natural viewing paradigm and experimental design. **a**) Participants watched a movie that was taken from Game of Thrones while brain activity was measured using fMRI. **b**) Neural responses were compared across individuals using inter-subject correlation (ISC, top) in which the time-course of response in corresponding voxels was correlated (r) between participants or **c**) using functional connectivity (bottom) in which the time-course of response between two different regions was correlated (r) within a participant. **d**) Neural responses were measured in control participants and participants with developmental prosopagnosia (DP), who were either familiar or unfamiliar with Game of Thrones. Differences in ISC or functional connectivity were compared across different groups to determine neural correlates of (i) familiarity (familiar control > unfamiliar control), (ii) familiarity with faces (familiar control > familiar DP), (iii) familiarity in DP (familiar DP > unfamiliar DP) and (iv) unfamiliar face perception (unfamiliar control > unfamiliar DP). **e**) Participants completed a behavioural test to determine their familiarity with Game of Thrones. Plots show percent correct on tests of narrative understanding and person and place recognition for familiar and unfamiliar controls and for familiar and unfamiliar DPs. Familiar controls and familiar DPs performed significantly better on face, place and narrative understanding compared to their unfamiliar counterparts.

2.3 Methods

2.3.1 Participants

We recruited participants from 4 groups: (1) control participants who were familiar with the TV series Game of Thrones, (2) control participants who were not familiar with Game of Thrones, (3) DP participants who were familiar with Game of Thrones, (4) DP participants who were not familiar with Game of Thrones.

45 control participants (median age: 19 years, age range: 18-32, 15 male) took part in this study. All control participants were neurologically healthy, right-handed and had normal or corrected-to-normal vision. 22 of the control participants had watched Game of Thrones. The remaining 23 control participants had not watched Game of Thrones. 28 participants with developmental prosopagnosia also took part in the study (median age: 47 years, age range: 23-69, 12 male). The sample size was determined *a priori* based on prior fMRI studies using naturalistic stimuli and employing analysis techniques similar to those in the current study (Andrews et al., 2019; Chen et al., 2017; Hasson et al., 2009; Hasson, Yang, et al., 2008). All developmental prosopagnosic participants were neurologically healthy, had normal or corrected-to-normal vision and 2 were left-handed. 15 developmental prosopagnosic participants were unfamiliar with Game of Thrones and 13 were familiar. DP participants were recruited through www.troublewithfaces.org and other online sources. To determine diagnostic evidence for the presence of DP, all DP participants completed the PI20 (20-item prosopagnosia index to measure self-reported face recognition abilities; Shah et al., 2015) and the Cambridge Face Memory Test (Duchaine & Nakayama, 2006; CFMT). To be classified with DP, a participant had to score above 65 on the PI20 (M= 80, SE= 1.51) and below 65% on the CFMT (M= 52.5%, SE= 1.54%) (Supplementary Table 1). Written informed consent was obtained for all participants and the study was approved by the York Neuroimaging Centre Ethics Committee.

2.3.2 fMRI Data Acquisition

All scanning was completed at the York Neuroimaging Centre using a 3T Siemens Magnetom Prisma MRI scanner and a 64-channel phased array head coil. A gradient-echo echo-planner imaging (EPI) sequence was used to collect data from 60 axial slices, EPI (TR = 2s, TE = 30ms, FOV = 240 x 240 mm, matrix size = 80 x 80, voxel dimensions = 3 x 3 x 3mm, slice thickness = 3mm, flip angle = 80°, phase encoding direction = anterior to posterior, multiband acceleration factor = 2). T1-weighted structural images were acquired from 176 sagittal slices (TR = 2300ms, TE = 2.26ms, matrix size = 256 x 256, voxel dimensions = 1 x 1 x 1mm, slice thickness = 1mm, flip angle = 8°). Field maps were collected from 60 slices (TR = 554ms, short TE = 4.90ms, long TE = 7.38ms, matrix size = 80 x 80, voxel dimensions = 3 x 3 x 3mm, slice thickness = 3mm, flip angle = 60°).

The fMRI data were analysed using FSL's FEAT v6.0 (http://www.fmrib.ox.ac.uk/fsl; Jenkinson et al., 2012). Motion correction (MCFLIRT; Jenkinson et al., 2002), temporal high-pass filtering (Gaussian-weighted least squares straight line fittings, sigma = 50 s) and slice timing correction were applied. Spatial smoothing (Gaussian) was applied at 6mm FWHM. Removal of non-brain material was performed with BET (Smith, 2002). Functional data were first registered to a high-resolution T1-anatomical image via boundary-based registration (Greve & Fischl, 2009), and then onto the standard MRI brain (MNI152) via a non-linear registration computed via FNIRT. Field maps were used to apply correction to distortion of functional images as part of the registration step.

2.3.3 Game of Thrones Scan

Participants viewed and listened to a movie that was constructed with audio-visual segments from Seasons 3 and 4 of Game of Thrones. The movie was projected onto an in-bore screen at a distance of 57 cm from the participant with the image subtending approximately 38.7 × 22.3 degrees of visual angle. Accompanying audio (that included some speech) was also played to participants in the scanner. There were a total of 10 distinct scenes that ranged in length from 50-117 seconds, for a total movie length of 12 minutes 58 seconds (778s). The movie was presented using PsychoPy (Peirce et al., 2019).

First, we measured inter-subject correlations (ISC) within participants from the different groups during the Game of Thrones scan. To do this, the time series from each voxel in each participant was converted to % signal change, and 6 head motion parameters were regressed out of the data. These time series were then correlated (Pearson's r) with corresponding voxels from participants from the same group. This was done for all combinations of participants within each group. To compare ISC across groups, a Fisher's z transform was applied to the correlations. Then, for each voxel, a one-tailed Welch's independent-samples t-test was performed to determine differences in ISC between groups. When applied to all voxels, this produced whole-brain p-statistic maps for each contrast, which we represented in negative log units. A cluster correction for multiple comparisons was then applied to these maps using an initial cluster forming threshold of $-\log_{10}(p) > 4$ ($p < .0001$) and a cluster significance threshold of $p < .05$.

To determine whether ISC could be influenced by the age of participants, we ran an additional regression analysis. For each voxel in the brain, the ages of each pair of participants plus the interaction of those ages were use as predictors for the ISC. Significance was determined by a permutation test (5000 permutations) based on randomising the order of participants' ages. Across the whole brain, only a few voxels had ISCs that were significantly predicted by participant age (Supplementary Fig. 2.1), and these did not survive cluster correction for multiple comparisons (using an initial cluster forming threshold of $-\log_{10}(p) > 3$ ($p < .001$) and a cluster significance threshold of $p < .05$).

Next, we measured functional connectivity within participants between the face and scene regions defined in the localiser scan and the familiarity network defined using ISC. The time course of response of all voxels within a region was averaged in each participant to create an average time course of response. To measure connectivity, pairwise correlations (Pearson's r) of timeseries were computed between regions for each participant. The correlations between each face or scene region and every other region (i.e., averaging within rows of the connectivity matrix) was calculated for each participant. A Fisher's z transform was applied to all correlations prior to any statistics.

To determine if there were differences between groups, the resulting average correlation values from each face or scene region were compared across groups using Welch's independent-samples t-test. A Bonferroni-Holm correction (Holm, 1979) was applied to correct for familywise errors over regions. To determine whether functional connectivity could be influenced by the age of participants, we correlated age of participant with each functional connection for the main regions of interest. Significance was determined by a permutation test (10000 permutations) based on randomising the order of participants' ages. No functional connections were significantly correlated with age after correction for multiple comparisons (all $p > .05$ after Bonferroni-Holm correction).

In a further analysis, we explored the effect of age on variance in the signal to determine whether this could influence the ISC or functional connectivity. We calculated the average temporal standard deviation across all voxels. We then correlated this value with the mean age of the participants. However, we did not find a significant correlation between the mean temporal standard deviation and age ($r(71)=-.18$, $p=.122$).

All participants performed a behavioural test after the scan to determine their familiarity with Game of Thrones. First, we measured understanding of the narrative using a set of 14, 4-alternative, multiple-choice questions. Next, we tested the ability to recognize the faces of key people in the video. Participants viewed faces and were asked to name the person or provide information about them that was relevant to Game of Thrones. Finally, we tested the ability to recognize key places or landmarks.

Participants viewed scenes and were asked to provide the name or key information about the scene that was relevant to Game of Thrones. When participants provided key information rather than the name of the face or scene, two independent observers who were familiar with Game of Thrones had to both agree that the information provided was sufficient to show familiarity. All tests were self-paced.

2.3.4 Localizer Scan

A localizer scan was used to define face-selective and scene-selective regions. There were 3 stimulus conditions: faces, scenes, and phase scrambled faces. Face stimuli had three viewpoints (-45°,0°,45°) and were taken from the Radbound database of face stimuli (Langner et al., 2010). Faces were presented on a greyscale 1/f amplitude-mask background. Scrambled faces were created by randomising the phase spectra while maintaining the amplitude spectra of the face images including the amplitude mask background. Scenes were indoor, outdoor man-made and outdoor natural stimuli from the SUN database (Xiao et al., 2010). Images subtended 8.4 x 8.4 degrees of visual angle. 4 images from each condition were presented in each block for 600ms with a 200ms ISI for a total of 9 seconds per block. 9 blocks were presented for each condition in a pseudorandomized order, for a total scan time of 244s. To maintain attention, participants performed an orthogonal task detecting periodic colour changes in the fixation cross, responding via a button press.

Data from the localiser scan were used to both define face- and scene-selective regions of interest (ROIs) from control participants. Boxcar models of each stimulus block were convolved with a single-gamma haemodynamic response function to generate regressors for each condition. These were then entered into a first-level GLM analysis (Woolrich et al., 2001) alongside their temporal derivatives plus confound regressors for 6 head motion parameters. Individual participant data from the controls were entered into a higher-level group analysis using a mixed-effects GLM using FLAME (Woolrich et al., 2004). Face-selective and scene-selective regions were then defined using the contrast of the response to either faces or scenes compared to both other conditions (faces > scenes + scrambled face; scene > faces + scrambled faces). To define ROIs, we used a clustering algorithm that iteratively adjusted the statistical threshold to grow clusters of 250 spatially contiguous voxels (2000 mm^3) around seed voxels within each region. Figure 2.2 shows face-selective ROIs in the Fusiform Face Area (FFA), Occipital Face Area (OFA), Superior Temporal Sulcus (STS), Amygdala (AMG) and Inferior Frontal Gyrus (IFG), and scene-selective ROIs in the Occipital Place Area (OPA), Parahippocampal Place Area (PPA) and Retrosplenial cortex (RSC). A summary of the locations of these ROIs is provided in Supplementary Table 2. Finally, we did a whole-brain group contrasts between the control and DP groups. Individual participant data were entered into a higher-level group analysis using a mixed-effects GLM using

FLAME (Woolrich et al., 2004). We defined group-level contrasts of controls > DPs to compare univariate category selectivity between the groups for the first-level face- and scene-selective contrasts.

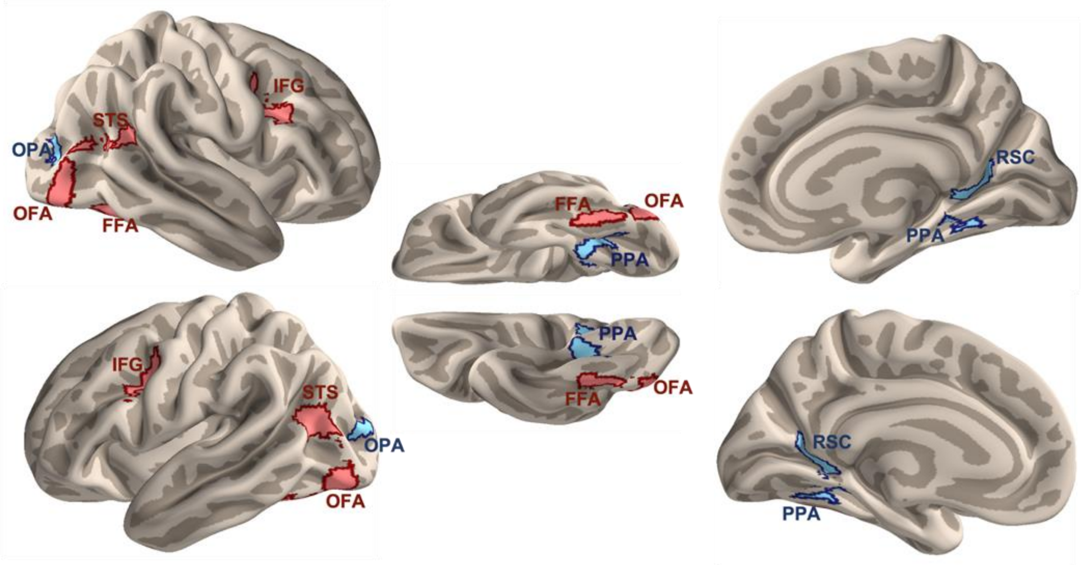


Figure 2.2. Face- and scene-selective ROIs defined from the localizer scan in the control participants. Red regions are face-selective and blue regions are scene-selective. (OFA: occipital face area, FFA: fusiform face area, STS: superior temporal sulcus, IFG: inferior frontal gyrus, OPA: occipital place area, PPA: parahippocampal place area, RSC: retrosplenial cortex).

2.4 Results

2.4.1 Behavioural effects of familiarity

First, we measured person, place and narrative knowledge in participants who were familiar and unfamiliar with the TV series Game of Thrones. Figure 2.1e shows the scores of the behavioural test in the Control and DP groups. As expected, there was significantly higher recollection in the familiar controls compared to unfamiliar controls on the narrative test ($t(37.1) = 16.8$, $p < .001$, $d = 5.04$), the person recognition test ($t(31.9) = 20.2$, $p < .001$, $d = 5.93$) and the place recognition test ($t(23.6) = 8.61$, $p < .001$, $d = 2.51$). We compared performance between the familiar control and familiar DP group. No significant differences were found for the narrative test ($t(15.3) = 2.1$, $p = .052$, $d = 0.87$). There was a small but significant difference between familiar controls and familiar DPs for the place recognition test ($t(29.1) = 2.3$, $p = .027$, $d = 0.76$). However, a larger difference between familiar controls and familiar DPs was evident in the person recognition test ($t(17.5) = 4.1$, $p < .001$, $d = 1.62$). In the comparison between familiar DPs and unfamiliar DPs, there was a significant difference on the narrative test ($t(22.1) = 8.1$, $p < .001$, $d = 3.14$), the person recognition test ($t(12.1) = 6.4$, $p < .001$, $d = 2.60$) and the place recognition test ($t(12) = 5.0$, $p < .001$, $d = 2.03$). Finally, there was no difference in the behavioural scores between the unfamiliar controls and unfamiliar DPs on the narrative test (t(28.9) = 1.35, p = .188 , d = 0.46), the person recognition test (t(25.4) = 1.18, p = .247 , d = 0.34) or the scene recognition test (t(21) = 1.00, p = .329 , d = 0.28).

2.4.2 Network of regions involved in familiarity

Next, we compared differences in the neural response of control participants who were familiar or unfamiliar with Game of Thrones. We measured ISC across all voxels in the brain for all combinations of control participants in either the familiar or unfamiliar groups. We then directly compared the correlations between the familiar and unfamiliar groups at each voxel to create a whole brain statistical map with a cluster correction for multiple comparisons. Figure 2.3a shows regions with higher ISCs in the familiar than unfamiliar group (red/yellow) voxels and vice versa (blue). A clear distinction is evident between regions in the temporal, parietal and frontal lobes that show higher ISC values in the familiar group and regions in the occipital and posterior temporal lobes that show higher ISC values in the unfamiliar group.

A cluster analysis was used to reveal different regions that showed higher ISCs between familiar participants. This revealed 23 regions, many of which appeared bilaterally. The statistical values and coordinates of the peak voxel in each cluster are shown in Table 2.1 and Supplementary Table 2.3. Next, we asked if the regions in the familiarity network overlapped with the face and scene regions found in the localizer scan, we determined the overlap with the familiarity network revealed by the cluster analysis. There was limited overlap with the core face and scene regions (Table 2.2) and the effect of familiarity was generally lower or even reversed compared to the familiarity network (see Table 2.1 for comparison). Finally, we analysed the location of the clusters that showed higher ISC for the unfamiliar group compared to the familiar group. These regions overlapped with early visual areas (V1-V3; Supplementary Table 2.4). In summary, the ISC analysis revealed a network of regions beyond the core face and scene areas that show significantly higher ISCs in the familiar group. In contrast, posterior regions in the occipital lobe show higher ISCs in the unfamiliar group.

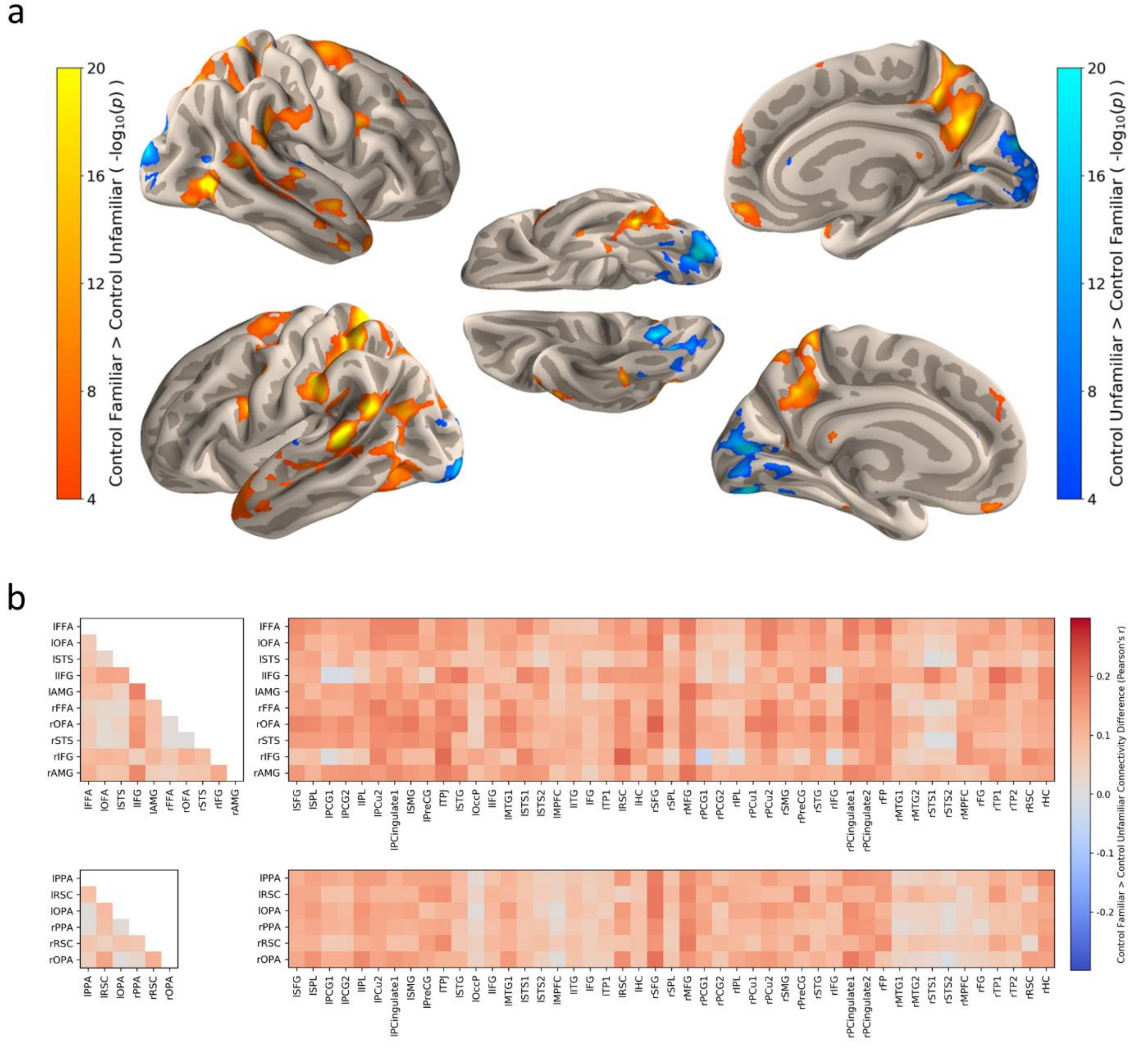


Figure 2.3. A network of regions across the brain involved in familiarity. **a**) ISC differences between familiar controls and unfamiliar controls. Voxels across temporal, parietal and frontal cortex showed higher ISC between familiar controls compared to the unfamiliar controls (red-yellow). In contrast, regions in occipital and posterior temporal cortex showed higher ISC in the unfamiliar controls compared to the familiar controls (blue-light blue). P-values are represented in negative log units (-$\log_{10}(p)$). **b**) Functional connectivity differences between familiar controls and unfamiliar controls. There was enhanced connectivity between regions within the face and scene network in the familiar

control group compared to the unfamiliar control group. There was also enhanced connectivity between the face and scene regions and the familiarity network in the familiar controls compared to the unfamiliar controls.

Table 2.1. Regions showing higher ISC in familiar controls compared to unfamiliar controls during movie watching. Maximum t-value and percentage overlap with the familiarity network for each ISC contrast. The familiar control > familiar DP contrast shows large overlap with the familiarity network defined by the familiar control > unfamiliar control contrast. The familiar DP > unfamiliar DP contrast does not demonstrate an overlap with the familiarity network.

		Familiar Control > Unfamiliar Control		**Familiar Control > Familiar DP**		**Familiar DP > Unfamiliar DP**	
Region	**Hemisphere**	***t***	***% overlap***	***t***	***% overlap***	***t***	***% overlap***
Superior Frontal Gyrus	R	7.67	100	7.66	87	-7.00	0
	L	7.97	100	9.39	99	-3.84	0
Superior Parietal Lobule	R	10.02	100	10.54	93	-6.41	0
	L	10.87	100	9.60	100	1.87	0
Medial Frontal Gyrus	R	5.34	100	6.13	40.3	2.67	0
Postcentral Gyrus 1	R	6.27	100	5.77	17	-1.89	0
	L	10.55	100	8.97	85	-3.97	0
Precuneus 1	R	9.74	100	10.45	97	-7.11	0
Intraparietal Lobule	R	9.31	100	9.51	100	-5.80	0
	L	7.39	100	10.10	100	3.28	0
Postcentral Gyrus 2	R	8.91	100	8.96	96	-4.34	0
	L	10.89	100	10.56	100	-6.01	0
Precuneus 2	R	10.70	100	8.63	72	-2.66	0
	L	10.13	100	7.73	47	-2.40	0
Posterior Cingulate 1	R	6.24	100	4.68	6.4	2.21	0
	L	8.68	100	7.29	57	3.63	0
Supramarginal Gyrus	R	7.76	100	8.83	83	-5.35	0
	L	9.37	100	11.76	100	-6.72	0
Precentral Gyrus	R	5.55	100	6.75	73	-3.73	0
	L	8.68	100	9.88	97.8	-3.11	0
Temporoparietal junction	L	11.01	100	13.15	100	-7.34	0
Superior Temporal Gyrus	R	10.25	100	8.71	84	-7.11	0
	L	7.21	100	7.99	90	-4.58	0
Occipital Pole	L	9.36	100	8.51	21.6	-4.51	0
Inferior Frontal Gyrus	R	8.85	100	6.46	54	-4.23	0
	L	9.70	100	8.58	93	-2.97	0
Posterior Cingulate 2	R	6.39	100	5.49	82.9	-4.35	0
Frontal Pole	R	6.93	100	6.35	56	2.17	0
Retrosplenial Cortex	R	6.87	100	5.48	0	3.63	0
	L	6.81	100	7.27	33.8	3.74	0
Middle Temporal Gyrus 2	R	9.12	100	13.03	96	4.80	12
Middle Temporal Gyrus 1	R	11.93	100	12.06	97	4.52	3
	L	7.25	100	8.70	59.6	-3.60	0
Superior Temporal Sulcus 1	R	8.87	100	12.71	89	-2.87	0

	L	8.43	100	8.89	99	3.58	0
Superior Temporal Sulcus 2	R	8.76	100	9.51	100	-2.33	0
	L	13.91	100	8.23	91	3.69	0
Medial Prefrontal Cortex	R	8.01	100	4.71	0	4.82	0
	L	7.13	100	4.36	0	2.01	0
Hippocampus	R	5.65	100	7.02	17.9	1.58	0
	L	5.44	100	3.83	0	3.22	0
Inferior Temporal Gyrus	L	10.04	100	12.21	100	-6.23	0
Fusiform Gyrus	R	8.38	100	4.25	1.1	1.89	0
	L	6.56	100	7.06	35	-3.18	0
Temporal Pole 1	R	8.04	100	9.65	88	3.19	0
	L	7.91	100	8.34	100	4.23	2
Temporal Pole 2	R	5.29	100	5.78	58.9	2.01	0

Table 2.2. Percentage overlap and maximum t-value of ISC group contrasts in face- and scene-selective regions. For each whole-brain ISC contrast, the overlap with core face- and scene-selective regions was calculated. The familiar control > unfamiliar control contrast and the familiar DP > unfamiliar DP contrast show limited overlap with the face- and scene-selective regions. The familiar control > familiar DP likewise show relatively limited overlap.

Region	**Hemisphere**	**Familiar Control > Unfamiliar Control**		**Familiar Control > Familiar DP**		**Familiar DP > Unfamiliar DP**	
		t	**% overlap**	***t***	**% overlap**	***t***	**% overlap**
Occipital face area	R	-4.76	2.0	5.71	8.8	5.91	10
	L	-6.32	5.2	8.37	11	-4.79	0
Fusiform face area	R	-7.73	0.4	-4.14	0.4	5.27	3.6
	L	6.86	31	9.76	65	-6.88	0.0
Superior temporal sulcus	R	6.53	14	13.64	52	-12.86	0.0
	L	8.58	52	19.68	99	-9.15	0.0
Inferior frontal gyrus	R	8.25	51	6.34	35	-3.96	0.0
	L	6.47	18	7.44	27	-2.83	0.0
Amygdala	R	3.95	0.0	3.42	0.0	-2.34	0.0
	L	4.25	2.8	5.44	0.0	-2.57	0.0
Occipital place area	R	-8.96	0.0	7.53	59	-6.18	0.0
	L	-6.80	0.0	6.89	4.8	-5.03	9.6
Parahippocampal place area	R	-4.95	0.0	9.83	70	-4.71	1.6
	L	-7.38	0.0	7.26	28	-4.73	0.0
Retrosplenial Cortex	R	6.87	18	5.59	0.4	5.28	8.4
	L	6.81	21	7.27	17	5.89	12

Table 2.3. Percentage overlap and maximum t-value of early visual regions with ISC group contrast for unfamiliar control > familiar control. In contrast to the unfamiliar control, this contrast overlaps with early visual areas.

Region	Hemisphere	*t*	% overlap
V1	R	9.45	48.9
	L	8.60	47.9
V2	R	9.27	38.5
	L	8.47	28.0
V3	R	9.02	46.7
	L	11.43	39.3

We next asked how functional connectivity across the brain was influenced by familiarity. We first measured functional connectivity between face-selective or scene-selective regions. The average correlation matrices for the participants in the familiar and unfamiliar groups are shown in Suppl. Fig. 2.2 and 2.3. A correlation between the familiar and unfamiliar matrices shows that there was a similar pattern of connectivity within the face (r(43) =.99, *p* < .001) and scene (r(13) =.97, *p* < .001) regions in the two groups. We then asked how the magnitude of connectivity differed across the familiar and unfamiliar groups (Fig. 2.3b, left). We first averaged the Fisher's z correlations over all connections and contrasted these values between conditions. There was overall higher connectivity between the face (*t*(42.2)=3.18, *p*=.003, *d*=0.96) and scene (*t*(42.7)=2.69, *p*=.010, *d*=0.82) regions in the familiar participants. We further compared the effect of familiarity for each region by comparing the average correlations for each region. In the face regions (Fig. 2.3b, top left), the effect of familiarity was due to increased connectivity with the lFFA (*t*(42.4)=3.02, *p*=.038, *d*=0.92) and lIFG (*t*(42.4)=3.22, *p*=.025, *d*=0.98). In the scene regions (Fig 2.2b, bottom left), the effect of familiarity was due to increased connectivity with the rRSC (*t*(42.7)=3.25, *p*=.011, *d*=0.99) and lRSC (*t*(42.9)=3.48, *p*=.007, *d*=1.06). No other face or scene regions showed a significant difference after correction (all *p* > .05).

Next, we measured functional connectivity between the core face and place regions in the visual brain and familiarity network defined from the ISC analysis. The average correlation matrices for the participants in the familiar and unfamiliar groups are shown in Suppl. Fig. 2.2 and 2.3. A correlation between the familiar and unfamiliar matrices shows that there was a similar pattern of connectivity between the familiarity network and the face *(*r(468) =.92, *p* < .001) and scene (r(280) =.95, *p* < .001) regions in the two groups. However, a comparison of the magnitude of the connectivity showed enhanced connectivity between the familiarity network and both the face (*t*(42.8)=4.30, *p*<.001, *d*=1.31) and scene (*t*(41.5)=3.38, *p*=.002, *d*=1.02) regions (see Fig. 2.3b, right). The effect of increased connectivity with familiarity was evident in all the face regions (rFFA: *t*(42.9)=3.95, *p*=.002, *d*=1.20;

lFFA: *t*(42.9)=4.27, *p*<.001, *d*=1.30; rOFA: *t*(42.7)=4.62, *p*<.001, *d*=1.41; lOFA: *t*(41.7)=4.13, *p*=.001, *d*=1.25; rSTS: *t*(41.9)=4.57, *p*<.001, *d*=1.39; lSTS: *t*(42.9)=3.62, *p*=.003, *d*=1.10; rIFG: *t*(41.9)=3.15, *p*=.008, *d*=0.96; lIFG: *t*(42.7)=3.04, *p*=.008, *d*=0.93; rAMG: *t*(34.9)=3.86, *p*=.002, *d*=1.16; lAMG: *t*(37.6)=3.24, *p*=.008, *d*=0.98). Similarly, the effect of increased connectivity with familiarity was evident in all the scene regions (rPPA: *t*(36.0)=3.14, *p*=.011, *d*=0.95; lPPA: *t*(40.2)=3.28, *p*=.011, *d*=0.99; rRSC: *t*(41.4)=2.96, *p*=.011, *d*=0.90; lRSC: *t*(42.3)=3.22, *p*=.011, *d*=0.98; rOPA: *t*(42.8)=3.64, *p*=.004, *d*=1.11; lOPA: *t*(43.0)=3.19, *p*=.011, *d*=0.97).

To determine if the core face and scene regions interacted with the familiarity network in a similar way, we averaged the correlation values within each row of the functional connectivity matrices (see Fig. 2.3b, right). This gave an average correlation (over face or scene regions) for each region in the familiarity network. There was a significant correlation between the two vectors (*r*(45)=.62, *p*<.001). This shows that the effect of familiarity on functional connectivity with the familiarity network is similar for face and scene regions. We also found a significantly higher effect of familiarity on the connectivity between the face regions with the familiarity network compared to the scene regions with the familiarity network (*t*(46)=4.55, *p*<.001, *d*=0.60).

2.4.3 Network of regions involved in familiarity for faces

Next, we asked which brain regions were specifically involved in processing familiar faces. To do this, we compared familiar controls and familiar DPs. Both groups of participants were familiar with the stimuli, but participants with developmental prosopagnosia have a lifelong deficit in face recognition and showed lower face recognition in the GoT behavioural test. Our hypothesis was that voxels that are important for processing familiar faces would show significantly higher ISC among familiar controls compared to familiar DPs.

Fig. 2.4a shows regions in which there were significantly higher ISCs comparing familiar controls to familiar DPs. There was a clear distinction between regions in the temporal, parietal and frontal lobe that show higher values in the familiar control group and regions in the occipital lobe that show higher values in the familiar DP group. The pattern was similar to the contrast of familiar control vs unfamiliar control (see Fig. 2.3a). To determine the similarity between these contrasts, we measured the statistical difference between the familiar controls and familiar DPs in each cluster from the familiarity network (Table 2.1). The similarity between the cluster analyses shows that the majority of the clusters from the familiarity network also show a greater difference between familiar controls and familiar DPs. In contrast, there was limited overlap between the face and scene regions and the cluster analysis for familiar controls > familiar DPs (Table 2.2). This again suggests that the difference between familiar controls and familiar DPs is primarily evident in regions beyond the visual brain.

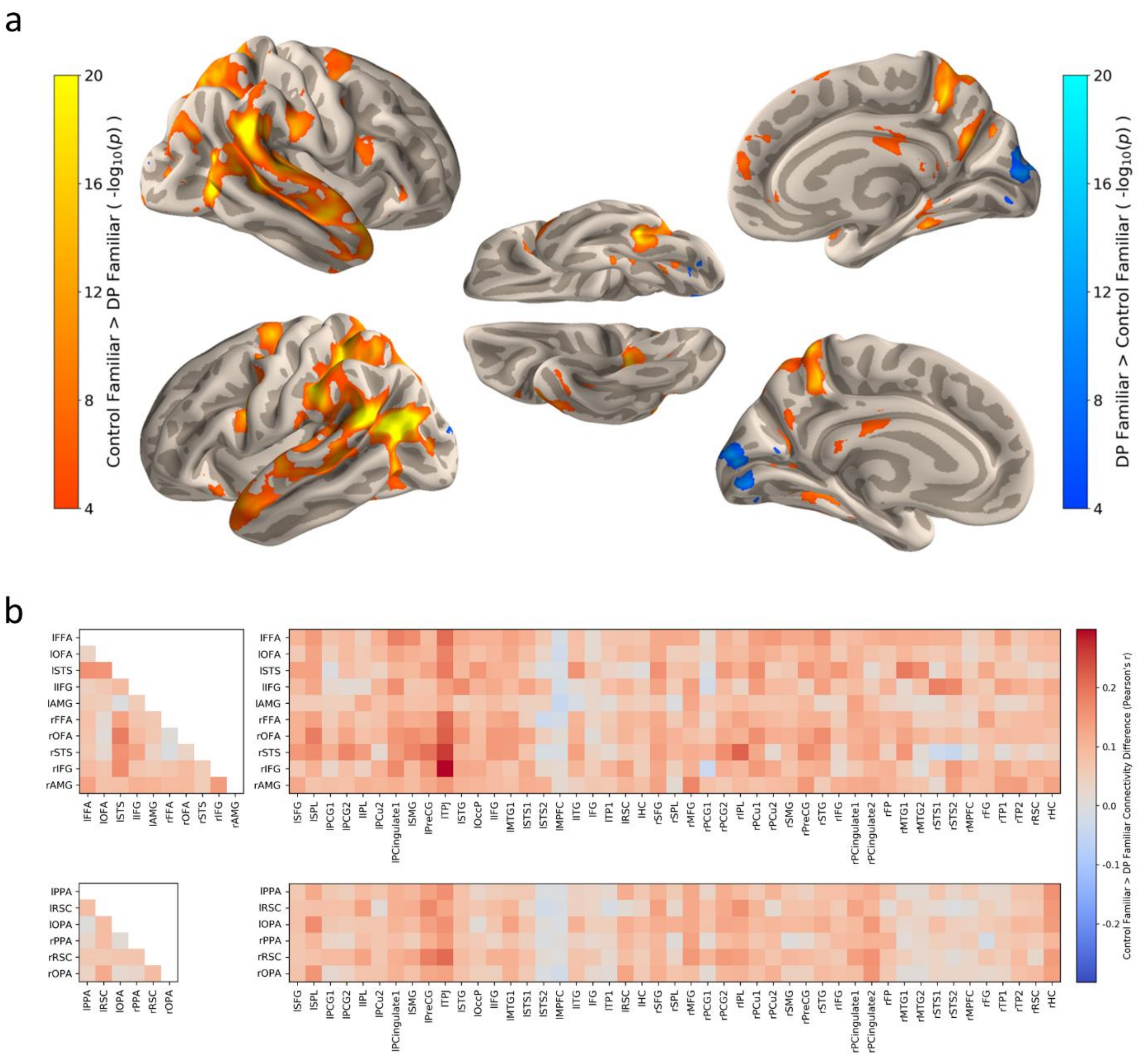


Figure 2.4. Network of regions involved in familiarity for faces. **a**) ISC differences between familiar controls and familiar DPs. Voxels in temporal, parietal and frontal cortex showed higher ISC in the familiar control compared to the familiar DPs (red-yellow). In contrast, regions in occipital and posterior temporal cortex showed higher ISC in the familiar DPs compared to the familiar controls (blue-light blue). **b**) Functional connectivity differences between familiar controls and familiar DPs. There was enhanced connectivity between regions in the core face and scene network in the familiar control group compared to the familiar DP group. There was also enhanced connectivity between the familiarity network and the face regions in the familiar controls compared to the familiar DPs.

Next, we measured the difference in functional connectivity between familiar controls and familiar DPs (Fig. 2.4b). The average correlation matrices for the participants in these groups are shown in Suppl. Fig. 2.2 and 2.3. A correlation between the familiar control and familiar DP matrices shows that there was a similar pattern of connectivity within the face (r(43) =.95, *p* < .001) and scene (r(13) =.98, *p* < .001) regions. There was, however, an overall increase in the magnitude of functional connectivity between the face regions in the familiar controls compared to the familiar DPs (*t*(23.2) = 2.59, *p* = .016, *d* = 0.95). In the face regions (Fig. 2.4b, top left), the effect of familiarity was due to increased connectivity with the rOFA (*t*(29.2) = 3.1, *p* = .045, *d* = 1.04) and lSTS (*t*(19.0) = 3.2, *p* = .045, *d* = 1.26). There was also an overall increase in connectivity between the scene-selective regions (*t*(23.3) = 2.1, *p* = .046, *d* = 0.77), although no single ROI was significant after corrections.

We next measured the functional connectivity between the face and scene regions and the familiarity network. A correlation between the familiar control and familiar DP matrices shows that there was a similar pattern of connectivity between the familiarity network and the face regions (r(468) =.90, *p* < .001) and between the familiarity network and the scene (r(280) =.94, *p* < .001) regions. However, the magnitude of connectivity between the face regions and the familiarity network was greater for familiar controls compared to familiar DPs (*t*(22.4) = 2.32, *p* = .030, *d* = 0.86). The effect of increased connectivity with familiarity was evident in the rOFA (*t*(26.9) = 3.2, *p* = .034, *d* = 1.12). Interestingly, no significant differences were found in the overall connectivity in scene-selective regions and the familiarity network for familiar controls compared to familiar DPs (*t*(21.8) = 1.71, *p* = .102, *d* = 0.64). Moreover, a direct comparison of the connectivity in the face and scene regions with the familiarity network showed a significant difference (*t*(46)=4.09, p<.001). This shows that the enhanced connectivity in familiar controls compared to familiar DPs was face specific.

2.4.4 A reduced response to familiarity in DP

To explore the neural basis of familiarity in DP, we compared familiar DPs with unfamiliar DPs. Both groups of participants had a deficit in face recognition, but only one group was familiar with GoT. Given the deficit in face recognition, we did not predict that this would reveal the network of regions involved in familiarity. Indeed, a cluster analysis of the ISC found very limited overlap with the network of regions involved in familiarity (Fig. 2.5a; Table 2.1). The pattern was also different in the face and scene regions compared to the previous contrasts (See Table 2.2).

Next, we compared the difference in connectivity between familiar and unfamiliar DPs (Fig. 2.5b). The average correlation matrices for the participants in these groups are shown in Suppl. Fig. 2.2 and 2.3. A correlation between the familiar DP and unfamiliar DP matrices shows that there was a similar pattern of connectivity within the face (r(43) =.94, *p* < .001) and scene (r(13) =.97, *p* < .001) regions. There was also no significant difference in connectivity in either the face-selective (*t*(25.1) = 1.22, *p* =

.234, *d* = 0.48) or scene-selective (*t*(24.9) =-0.69, *p* = .496, *d* = 0.27) regions, or in any individual ROI (all *p* > .05).

We compared the functional connectivity between the face and scene regions and the familiarity network. A correlation between the familiar DP and unfamiliar DP matrices shows that there was a similar pattern of connectivity between the familiarity network and the face regions (r(468) =.81, *p* < .001) and between the familiarity network and the scene regions (r(280) =.92, *p* < .001). There was no significant difference in overall functional connectivity between the face-selective regions and familiarity network for familiar DPs compared to unfamiliar DPs (*t*(23.5) = 1.51, *p* = .145, *d* = 0.60). Finally, no significant differences were found in the overall connectivity in scene-selective regions for familiar DPs compared to unfamiliar DPs (*t*(22.8) = 1.47, *p* = .154, *d* = 0.59).

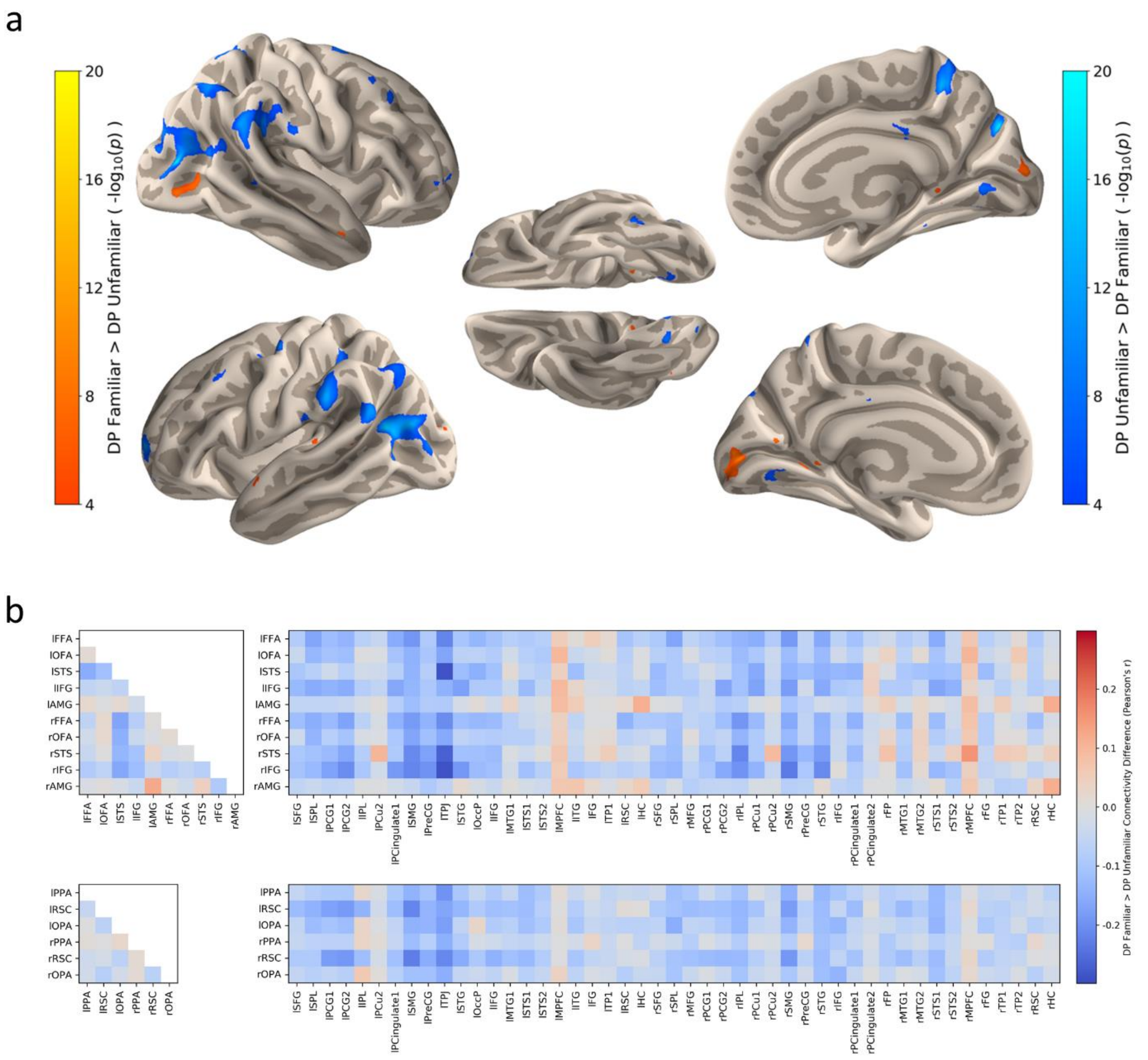


Figure 2.5. No familiarity network in DP. a) ISC differences between familiar DPs and unfamiliar DPs. The extended network for familiarity across temporal, parietal and frontal cortex was not evident for

the contrast of familiar DPs compared to unfamiliar DPs (red-yellow). **b**) Functional connectivity differences between familiar DPs and unfamiliar DPs. Familiarity did not increase functional connectivity in familiar DPs compared to unfamiliar DPs.

2.4.5 Network of regions involved in the perception of unfamiliar faces

While comparisons of familiar controls and familiar DPs highlight regions involved in processing of familiar faces, comparisons of unfamiliar controls with unfamiliar DPs should reveal regions that are important for general face perception.

First, we compared the ISC of the unfamiliar controls and the unfamiliar DPs while watching Game of Thrones. A cluster analysis showed a higher ISC in unfamiliar controls compared to unfamiliar DP participants in regions of the temporal and occipital lobe (Fig. 2.6a). Supplementary Table 2.4 shows how this pattern of difference overlapped with the core face and scene regions. This showed some overlap in the OFA, FFA and PPA. In summary, this analysis reveals a network of regions in the occipital and temporal lobe, which overlaps with the core face and scene areas, that show significantly higher ISCs in the control unfamiliar compared to the DP unfamiliar group.

Next, we analysed connectivity within the core face and scene regions (Figure 2.6b). There was no significant difference in connectivity between the unfamiliar control and DP groups within the face (*t*(25.5) = 1.28, *p* = .211, *d* = 0.46) or scene (*t*(27.1) = 0.80, *p* = .431, *d* = 0.28) regions, and no individual ROIs were significant. There was, however, reduced connectivity with the familiarity network in both face (*t*(25.5) = 2.92, *p* = .007, *d* = 1.05) and scene (*t*(26.7) = 2.86, *p* = .008, *d* = 1.02) regions for the control compared to the DP group. This connectivity was significant in the right (*t*(27.0) = 3.18, *p* = .037, *d* = 1.13) and left FFA (*t*(28.0) = 3.13, *p* = .037, *d* = 1.10) with the familiarity network, and all scene regions with the familiarity network (rPPA: *t*(21.5)=2.12, *p*=.046, *d*=0.80; lPPA: *t*(25.6)=2.83, *p*=.044, *d*=1.02; rOPA: *t*(28.2)=2.61, *p*=.044, *d*=0.91; lOPA: *t*(30.5)=2.56, *p*=.044, *d*=0.88; rRSC: *t*(28.3)=2.81, *p*=.044, *d*=0.99; lRSC: *t*(25.5)=3.26, *p*=.019, *d*=1.18).

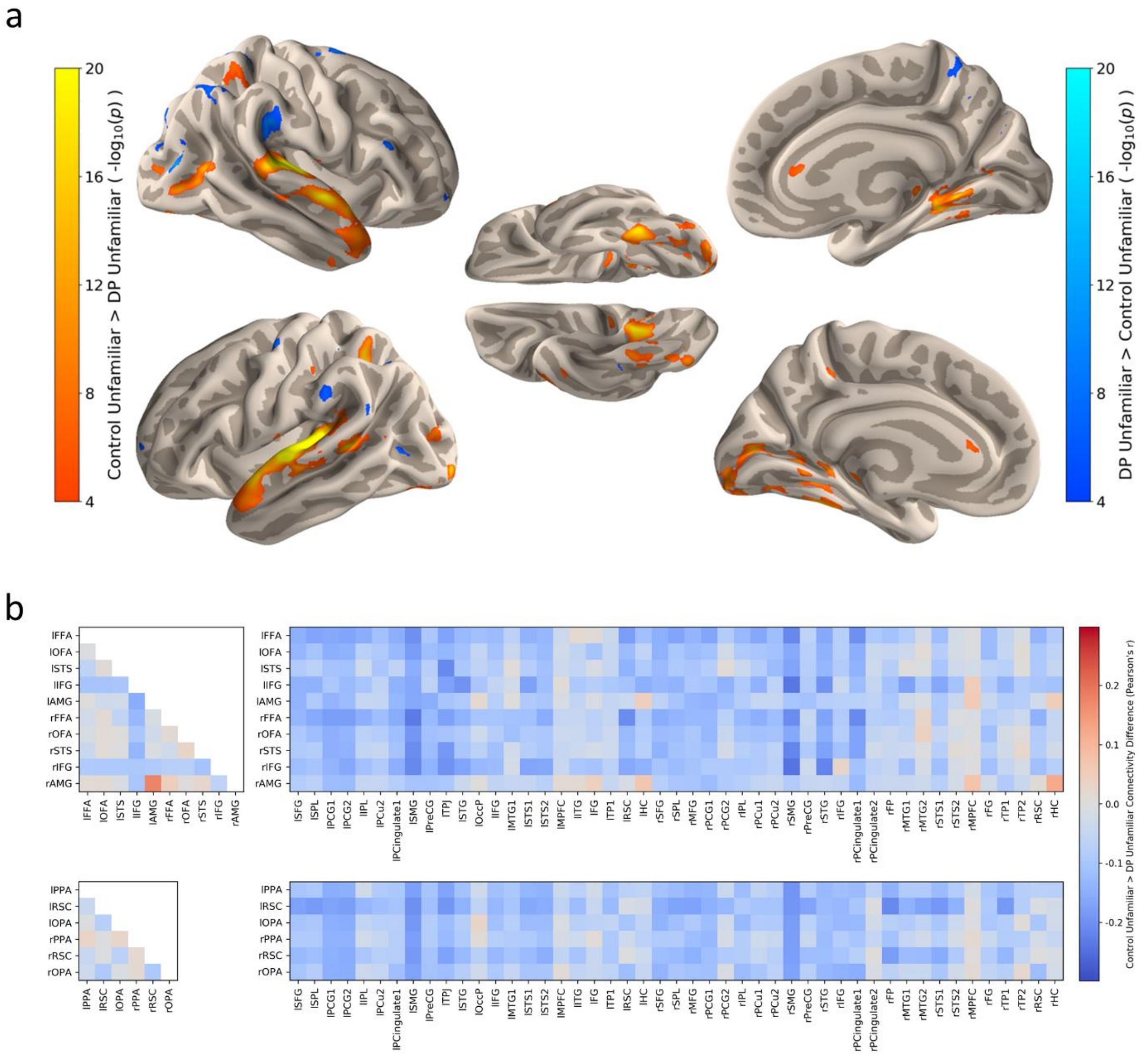


Figure 2.6. Network of regions involved in the perception of unfamiliar faces. a) ISC differences between unfamiliar controls and unfamiliar DPs. Regions across the occipital and temporal lobe showed higher ISC in the control compared to the DP group (red-yellow). Fewer clusters show significantly greater inter-subject correlations in unfamiliar DPs compared to unfamiliar controls (blue-light blue). Maps were created using one-sided Welch's t-tests and cluster corrected using an initial cluster forming threshold of $-\log_{10}(p) > 4$ ($p < .0001$) and a cluster significance of $p < .05$. **b**) Functional connectivity differences between unfamiliar controls and unfamiliar DPs. There was no increase in connectivity between regions in the unfamiliar control group compared to the unfamiliar DP group.

Finally, we compared face-selectivity and scene-selectivity in the localizer scan. Figure 2.7 shows a whole-brain group analysis of the difference in face-selectivity and scene-selectivity between controls and DPs. This shows a cluster of voxels in the left fusiform gyrus that showed greater face-selectivity in controls compared to DPs. There were also more medial clusters in the right and left parahippocampal gyrus that showed greater scene-selectivity in controls compared to DPs in response to scenes (see Supplementary Table 2.5 for peak coordinates). We also compared the difference in response between controls and DPs to faces, scrambled faces and scenes within the face-selective and scene-selective ROIs (Supplementary Figures 2.4 and 2.5 & Supplementary Table 2.6). There were significant differences in the response to faces between the control and DP groups in both the left and right OFA, the left and right FFA and the left STS. However, there were no significant differences in the response to faces between the control and DP groups for any of the scene regions. We also found significant differences in the response to scrambled faces between the control and DP group in the left OFA, the left and right FFA and the left STS. There were no significant differences in the response to scrambled images between the control and DP group in any of the scene regions. Finally, we found that there was a significant difference in the response to scenes between the control and DP group in the right PPA. No other regions showed a significant group difference in the response to scenes.

Finally, Supplementary Figures 2.6 and 2.7 show the main effects of familiarity (control familiar + DP familiar vs control unfamiliar + DP unfamiliar) and group (control familiar + control unfamiliar vs DP familiar + DP unfamiliar).

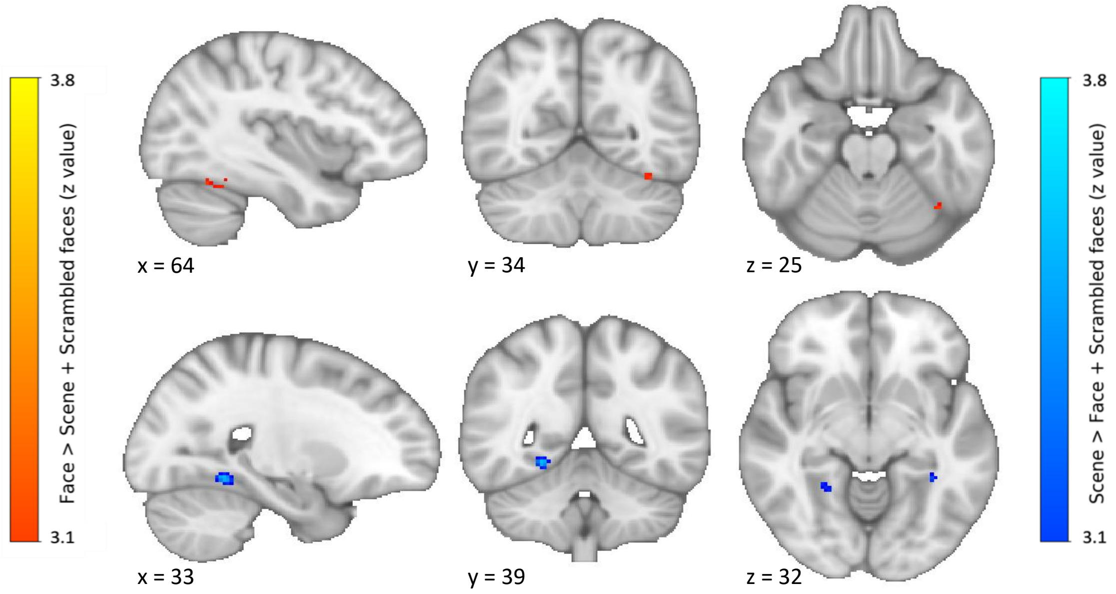


Figure 2.7. Greater face selectivity for controls compared to DPs. In the localiser scan, greater face selectivity was found in the left hemisphere (red-yellow) and greater scene selectivity was found for controls compared to DPs (blue-light blue) in the localiser scan. Statistical maps are thresholded at Z > 3.1 (one-tailed p < .001) uncorrected.

2.5 Discussion

A natural viewing paradigm was used to explore the neural correlates of familiarity. Our results show: (1) The neural response to familiarity in natural viewing is dependent on a distributed network of regions that extend beyond the visual brain; (2) Familiarity enhanced the functional connectivity between this familiarity network and face and scene regions in the visual brain; (3) The response of the familiarity network and its functional connectivity with the core face regions were significantly attenuated in participants who have a deficit in the ability to recognize faces. These findings reveal the importance of extensive interactions between visual and non-visual regions of the brain during natural viewing of familiar people and places.

The naturalistic approach (movie watching) used in this study allowed us to capture the richness and complexity associated with real-world familiarity (Hasson et al., 2010; Redcay & Moraczewski, 2020). A key feature of our paradigm was that the stimulus was the same for all participants. By comparing the neural response in participants who were either familiar or unfamiliar with the TV series Game of Thrones (GoT), it was possible to reveal regions of the brain that are involved in familiarity. We found a network of regions across the brain that showed a strong and robust effect of familiarity. The cognitive processes underlying the effect of familiarity are likely to reflect our memory of particular episodes and our understanding of the narrative and context in which they occur (Jääskeläinen et al., 2021). The ability to understand and interpret events is known to be enhanced by our prior schematic knowledge of the world (Bartlett, 1932; Baldassano et al., 2018). This schematic knowledge has been shown to influence neural processing of familiar events and stimuli in regions such as the medial prefrontal cortex - mPFC (Baldassano et al., 2018, Reagh & Ranganath, 2023; van Kesteren et al., 2013, Raykov et al., 2021; Yeshurun et al., 2017). For example, the recall of events in a movie activates a network of regions across the brain that are associated with autobiographical memory and are similar to those found in this study (Chen et al., 2017). The higher ISC in regions such as the mPFC that we find is likely to reflect a greater schematic understanding of the movie in the familiar participants. Previous studies have shown that the coherence of the narrative can have a large effect on the similarity of the neural response across participants when watching movies (Hasson, Yang, et al., 2008). For example, a movie showing an unstructured real-life event without any editing shows ISC only in sensory regions of the brain. In contrast, there is a much more widespread pattern of ISC across a larger area of the cortical surface during viewing of movies with an engaging and coherent storyline.

Our understanding of real-world social interactions relies on the ability to recognise people and to access knowledge about them. We typically recognise people through their face. The neural processing of faces involves a core network of regions that process the visual properties of the image and an extended network of regions that process non-visual image about the person (Gobbini & Haxby, 2007; Haxby et al., 2000; Ishai, 2008; Kovács, 2020). We found limited overlap between regions that have been associated with face recognition, such as the right FFA and regions that showed an effect of familiarity in the ISC analysis. In contrast, we found more overlap between regions showing an effect of familiarity and other face regions, such as the left STS and right IFG. Models of face recognition propose that the activation of an image-invariant visual representation of familiar faces occurs prior to accessing person knowledge (Bruce & Young, 1986; Burton, Bruce, et al., 1999; Haxby et al., 2000). However, neuroimaging studies have failed to find convincing empirical evidence for an image-invariant representation of familiar faces in core face regions, such as the right FFA (Davies-Thompson et al., 2009; Davies-Thompson et al., 2013; Pourtois et al., 2005; Weibert et al., 2018; Weibert et al., 2016). This suggests that the neural responses in the FFA may not be sufficient for familiar face recognition (Collins & Olson, 2014).

We found the strongest responses to familiarity in regions within the extended face network that are associated with person knowledge. For example, regions selective for familiarity were found in the temporo-parietal junction, inferior parietal lobule and medial prefrontal cortex, which have been associated with theory of mind (Frith & Frith, 1999) and the perception of personality traits (Gobbini et al., 2004; Visconti di Oleggio Castello et al., 2017). We also found familiarity effects in other regions that are associated with episodic memory, such as the hippocampus and the precuneus/posterior cingulate (Dickerson & Eichenbaum, 2010; Rugg et al., 2002; Silson et al., 2019). This fits with studies showing neural responses in the medial temporal lobe to different images of the same person, but also to related images such as the name of the person (Quiroga et al., 2009; Quiroga et al., 2005; Weibert et al., 2016). The response to familiarity in the anterior temporal lobe that we show is likely to reflect semantic information about a person (Lambon Ralph, 2014; Rice et al., 2018). Finally, the effect of familiarity in the superior temporal sulcus and amygdala may underpin the affective response to familiar faces (Harris et al., 2012a; Ramon & Gobbini, 2018). These findings showing the important role of non-sensory processing in familiarity are consistent with EEG studies showing that the difference between familiar and unfamiliar faces is most evident at later time periods (Andrews et al., 2017; Wiese et al., 2019). Together, this suggests that the representation of familiar faces is evident in a distributed neural response that extends beyond the visual brain and involves regions involved in person knowledge.

The effect of familiarity was also evident in the enhanced functional connectivity between different regions in the core face network, and also between the core face regions and the extended network in the visual brain. The increased functional connectivity in familiar participants during moving watching shows the importance of interactions with the core face network during natural viewing. Previous studies have explored the relationship between face recognition ability and functional connectivity of the core face network with resting state fMRI. These studies have shown mixed results with some studies showing that the magnitude of functional connectivity between core face regions predicts behavioural ability in face recognition (Zhu, Zhan et al., 2011; Wang, Zhen et al., 2016), whereas others show no relationship (Ramot et al., 2019). A key difference between these studies is the presence of a stimulus. It is possible that movie watching elicits more structured and reliable patterns of response that better reflect cognitive differences in face processing (Finn, 2021; van der Meer, Breakspear et al., 2024).

To explore how the familiarity network that is evident in our analysis is critical for familiar face recognition, we measured responses in participants who have developmental prosopagnosia (DP). Familiar DPs showed reduced performance on the face recognition test of actors from GoT, consistent with their performance on other tasks of face recognition. When we compared the ISC of familiar controls with familiar DPs, we again found a network of regions that was very similar to when we compared familiar controls with unfamiliar controls. This suggests that the neural response to familiar faces in DPs is less coherent across these regions and perhaps more like unfamiliar controls. Because of the selective deficit in face recognition in DP, the contrast between familiar controls and familiar DPs provides a more direct link between regions in the familiarity network and face recognition. Our findings are consistent with previous studies that have shown an attenuated response to familiar faces across some regions of the extended face network in DP (Avidan & Behrmann, 2009). Interestingly, we found a difference in functional connectivity between face regions (but not scene regions) in familiar controls compared to familiar DPs. Similarly, there was greater connectivity between the core face regions (but not scene regions) and familiarity network in familiar controls compared to familiar DPs. This again suggests a selective attenuation in connectivity between core and extended face regions in DP (see also, (Avidan et al., 2014; Rosenthal et al., 2017; Thomas et al., 2009).

We also compared familiar DPs with unfamiliar DPs. This contrast did not reveal a difference in ISC across familiarity network, nor was there any difference in functional connectivity. This was somewhat surprising given that familiar DPs were able to recognise some of the faces on the behavioural GoT task. One possible explanation could be that the familiar DPs used a range of non-face cues to help with recognition that were not consistent across the group. Consistent with this explanation, the variance across the DP group in the behavioural study was larger than for the control participants. This would be consistent with DPs being a more heterogenous group. The greater heterogeneity in the DP group could also explain the contrast between the familiar controls and familiar DPs. Nonetheless, our results show a selective attenuation of the effect of familiarity on ISC and functional connectivity in the core and extended face regions.

The deficit in face recognition in DP is typically shown by significantly below average performance on tests of unfamiliar face perception (Duchaine & Nakayama, 2006). To determine the neural correlates of the deficit in unfamiliar face perception, we compared unfamiliar controls with unfamiliar DPs during movie watching. We found higher ISC in the unfamiliar controls compared to the unfamiliar DPs across the occipital and temporal lobes. Interestingly, the regions showing differences overlapped with the core face and scene regions. These findings suggest that the deficit in DP involves the visual encoding of the face. Next, we compared the selectivity of the response to unfamiliar faces relative to unfamiliar scenes and scrambled faces from the localiser scan. Some previous studies have reported reduced activity in the core face-selective areas when viewing faces in DP (Furl et al., 2011; Hadjikhani & de Gelder, 2002; Jiahui et al., 2018), whereas other studies have reported activity that is comparable to that found in control participants (Avidan et al., 2005; Hasson et al., 2003; Rivolta et al., 2014). One possible reason for the inconsistency across previous studies has been variation in the number of participants used in each study (Jiahui et al., 2018). In this analysis, we compared the responses of 45 controls with 28 DPs, which is significantly higher than most previous studies. Our results show that there was reduced selectivity to faces in DPs in the FFA. This suggests that the deficit in DPs may involve an inability to encode information about face images. A finer grained analysis revealed that there was a reduced response in the FFA of DPs for both intact and scrambled faces compared to scenes. This fits with a recent behavioural study showing a reduced sensitivity in DPs to pareidolic objects with similar image properties to faces, but not to pareidolic objects with dissimilar properties to faces (Epihova et al., 2022) and suggests that the deficit in DP may also reflect the ability to encode image properties that are typically found in faces. We also found lower selectivity for scenes in the PPA (Jiahui et al., 2018). This fits with the lower ISC in DPs during movie watching. It is not clear why DPs show this deficit in scene processing, but it may shed light on a wider debate about the underlying mechanisms of DP (Bate, Bennetts, et al., 2019; Garrido et al., 2018; Geskin & Behrmann, 2020).

Our ability to recognise familiar places is important for understanding the context of real-world situations. Neuroimaging studies have shown that there are number of regions in the visual brain that respond selectively to scenes (Aguirre et al., 1998; Epstein & Kanwisher, 1998; Epstein & Baker, 2019). Studies using conventional neuroimaging designs have found mixed evidence for an effect of familiarity in these regions (Epstein et al., 1999; Epstein, Higgins, et al., 2007; Epstein, Parker, et al., 2007). We found limited overlap between the familiarity network in the ISC analysis and the scene regions. However, we did find that connectivity between regions in the scene network was enhanced by the familiarity of the participants. Differences between familiar and unfamiliar scenes have been more consistently reported outside the core scene network in regions of the medial and lateral parietal lobe (Epstein, Parker, et al., 2007; Silson et al., 2019; Steel et al., 2021; Sugiura et al., 2005). We also found higher ISC in familiar participants in these regions. We also show that familiarity enhanced the functional connectivity between scene regions and the familiarity network. This suggests that our ability to recognize familiar places may also depend on interactions within the visual brain and between visual and non-visual regions of the brain.

Previous neuroimaging studies have found conflicting evidence for whether knowledge about people or places involves distinct or overlapping representations in memory (Gorno-Tempini & Price, 2001; Morton et al., 2021; Simmons et al., 2010). To address this question, we compared connectivity between the familiarity network and either the face or scene regions. Despite the fact that distinct regions are involved in processing faces and scenes within the visual brain, we found a similar effect of familiarity on the pattern of connectivity between face or scene regions and the familiarity network. This suggests that there is an overlapping representation of familiar people and places in non-visual regions of the brain.

An alternative explanation of our data is that differences in attention to the stimulus could explain the effects of familiarity that we report in the neural response. However, an interesting finding from our analyses was that early visual regions showed higher ISC in unfamiliar compared to familiar control participants. This shows that the higher ISC in the familiar control group is not an inherited response from early stages of processing. One possibility for the higher ISC in the unfamiliar group is that top-down expectations may have influenced the response in early visual regions (Bar, 2003; Friston, 2005). A growing body of evidence suggests that higher order cortical regions can influence responses in early visual regions if they are predictable (Murray et al., 2002; Summerfield & De Lange, 2014). It is possible, therefore, that the knowledge and understanding of the stimulus in the familiar control group led to top-down influences on the neural processing in early visual regions.

In conclusion, natural viewing reveals a network of regions, beyond sensory cortex, that are involved in our familiarity with people and places. The role of this familiarity network in face recognition is evident by its attenuation in participants with developmental prosopagnosia. We found that familiarity enhanced the functional connectivity within core face and scene regions, but also between these core regions and non-visual regions in the brain. These findings suggest that the representation of familiar people and places arises from widespread functional connectivity between visual and non-visual regions of the brain.

Chapter 3

Hyperfamiliarity for faces enhances functional connectivity between visual and non-visual regions of the brain during natural viewing

3.1 Abstract

Hyperfamiliarity for faces is a rare condition characterised by an abnormal sense of familiarity for unknown faces. Here, we ask whether this disorder can provide insights into the brain regions involved in the neural representation of familiar faces. We describe a 49-year-old woman (JP) who began experiencing hyperfamiliarity after a severe migraine. She reports having a strong sense of familiarity for faces of people that she does not know, which was not evident before the onset of the disorder. To determine the neural correlates of hyperfamiliarity, we compared the neural responses of JP with neurotypical participants. Structural MRI scans failed to reveal any discernible abnormalities. We then measured fMRI responses in the core face-selective regions to images of unfamiliar faces. JP showed a normal pattern of face-selective responses in the core face regions of the visual brain. To explore the neural response to faces in a more naturalistic setting, we recorded fMRI responses during movie watching. JP watched a movie composed of clips from the TV series Game of Thrones (GoT), which she had not seen before. We measured the response across different regions of the brain in JP and neurotypical participants who were either familiar or unfamiliar with GoT. We found neural responses in the medial temporal lobe of JP were more like familiar participants than unfamiliar participants. We also found that functional connectivity between core face regions and the medial temporal lobe in JP was more like familiar participants than unfamiliar participants. Together, these results demonstrate that hyperfamiliarity for faces manifests in both visual and non-visual parts of the brain, and that connectivity between these regions may play a critical role in the recognition of familiar faces during natural viewing.

3.2 Introduction

Cognitive models of face processing propose that familiar faces are processed through a sequence of stages that eventually lead to a sense of familiarity and then recognition (Bruce & Young, 1986). Faces are initially encoded in an image-dependent representation, which is then transformed into a structural or image-invariant representation if the face is familiar (Burton, Bruce, et al., 1999; Hancock et al., 2000; Young & Burton, 2017). Activation of these image-invariant representations, or face recognition units (FRUs), is thought to lead to the sensation that a face is familiar. This is then followed by access to relevant semantic, episodic and affective information about a person that allows us to recognize them (Gobbini & Haxby, 2007; Kovács, 2020). Support for these models comes from observations that we can perceive a face as being familiar, but not recognize who it is, whereas recognition of a person is always accompanied by a sense of familiarity (Young et al., 1985).

Neural models of face processing suggest a core network of regions are involved in the visual processing of the face (Duchaine & Yovel, 2015; Haxby et al., 2000; Ishai, 2008). An initial image-dependent representation of faces emerges in the occipital face area (OFA), which then projects to the superior temporal sulcus (STS) and the fusiform face area (FFA). The pathway from the OFA to the STS is important for the processing of changeable aspects of faces, whereas the pathway from the OFA to the FFA is important for generating an image-invariant representation for the recognition of identity. Despite the efforts of many studies, evidence for an effect of familiarity in core face regions, such as the FFA, has been mixed. Some studies report stronger FFA activity for familiar compared to unfamiliar faces (Sergent et al., 1992; Weibert & Andrews, 2015), while others find no difference in response (Gobbini et al., 2004; Gorno-Tempini & Price, 2001; Leveroni et al., 2000). The ability to access appropriate person knowledge following the recognition of a face is thought to occur through the activation of the extended face network. The extended network contains regions that do not exclusively process faces, but are important for processing non-visual information associated with the face (Gobbini & Haxby, 2007; Haxby et al., 2000; Ishai, 2008; Kovács, 2020).

Here, we investigate the neural correlates of familiarity with faces by measuring neural responses in an individual with hyperfamiliarity with faces (HFF). HFF is rare condition in which individuals perceive unfamiliar faces as being familiar (Amlerova et al., 2012; Devinsky et al., 2010; Michelucci et al., 2010; Negro et al., 2015; Vuilleumier et al., 2003). This can lead to the mistaken belief that unfamiliar faces are known or have been previously encountered. Nevertheless, individuals with HFF are still able to recognise the faces of people they know and do not have any deficits in basic visual processing. Previous investigations of patients with HFF have found damage in left temporal lobe regions, which has been suggested to influence interhemispheric processing (Negro et al., 2015). However, a full understanding of the neural basis of HFF remains unclear. Nevertheless, HFF provides a unique opportunity to address the question of where familiarity for faces is represented in the brain.

In this study, we measured the neural processing of faces in an individual with HFF. First, we used structural MRI to determine if the disorder resulted from damage to a particular region of the brain. Next, we compared the neural response using fMRI to images of faces and scenes to explore whether the neural processing of faces in the visual brain was intact. Finally, we compared the fMRI response to faces in a naturalistic setting. Natural viewing conditions were simulated by showing clips from the TV series Game of Thrones (GoT), which JP had not previously seen**.** We compared the time course of response in JP to control participants who were either familiar or unfamiliar with GoT (Noad et al., 2024). Our aim was to determine if there were any brain regions in which JP showed more similar responses to familiar participants compared to unfamiliar participants. Our prediction was that regions that show more similar responses to familiar than unfamiliar control participants would reflect the neural correlates of HFF and familiarity for faces more generally.

3.3 Methods

3.3.1 Participants

JP is a 49-year-old woman who had a severe migraine in August 2020. Since then, she has reported that unfamiliar faces often appear familiar. Behavioural evidence supporting her self-report of hyperfamiliarity with faces has been shown across a range of behavioural tasks (Kieseler et al., 2023). For example, in an old-new recognition test, she correctly reported old faces, but miscategorized 63% of the new faces as being old. When presented with a sequence of unfamiliar faces she categorized every face as 'probably familiar' or 'definitively familiar'. Nevertheless, her ability to recognise and name familiar faces remains intact.

To determine the neural correlates of hyperfamiliarity, we compared neural responses in JP with 45 control participants (median age: 19 years, age range: 18-32, 15 male, see Noad, Watson & Andrews, 2024). All control participants were neurologically healthy, right-handed, had normal or corrected-to-normal vision and reported no issues with recognition of faces. 23 of the control participants had watched Game of Thrones. The remaining 22 control participants had not watched Game of Thrones. Written informed consent was obtained for all participants and the study was approved by the York Neuroimaging Centre Ethics Committee. All participants performed a 1) localizer scan and 2) movie watching scan to measure the neural response to faces.

3.3.2 fMRI data acquisition

All scanning was completed at the York Neuroimaging Centre using a 3T Siemens Magnetom Prisma MRI scanner and a 64-channel phased array head coil. A gradient-echo echo-planner imaging (EPI) sequence was used to collect data from 60 axial slices, EPI (TR = 2s, TE = 30ms, FOV = 240 x 240 mm, matrix size = 80 x 80, voxel dimensions = 3 x 3 x 3mm, slice thickness = 3mm, flip angle = 80°, phase encoding direction = anterior to posterior, multiband acceleration factor = 2). T1-weighted structural images were acquired from 176 sagittal slices (TR = 2300ms, TE = 2.26ms, matrix size = 256 x 256, voxel dimensions = 1 x 1 x 1mm, slice thickness = 1mm, flip angle = 8°). Field maps were collected from 60 slices (TR = 554ms, short TE = 4.90ms, long TE = 7.38ms, matrix size = 80 x 80, voxel dimensions = 3 x 3 x 3mm, slice thickness = 3mm, flip angle = 60°).

The fMRI data were analysed using FSL's FEAT v6.0 (http://www.fmrib.ox.ac.uk/fsl; Jenkinson et al., 2012). Motion correction (MCFLIRT; Jenkinson et al., 2002), temporal high-pass filtering (Gaussian-weighted least squares straight line fittings, sigma = 50 s) and slice timing correction were applied. Spatial smoothing (Gaussian) was applied at 6mm FWHM. Removal of non-brain material was performed with BET (Smith, 2002). Functional data were first registered to a high-resolution T1-anatomical image via boundary-based registration (Greve & Fischl, 2009), and then onto the standard MRI brain (MNI152) via a non-linear registration computed via FNIRT. Field maps were used to apply correction to distortion of functional images as part of the registration step.

3.3.3 Localizer scan

A localizer scan was used to define face-selective and scene-selective regions. There were 3 stimulus conditions: faces, scenes, and phase scrambled faces. Face stimuli had three viewpoints (-45°,0°,45°) and were taken from the Radbound database of face stimuli (Langner et al., 2010). Faces were presented on a greyscale 1/f amplitude-mask background. Scrambled faces were created by randomising the phase spectra while maintaining the amplitude spectra of the face images including the amplitude mask background. Scenes were indoor, outdoor man-made and outdoor natural stimuli from the SUN database (Xiao et al., 2010). Images subtended 8.4 x 8.4 degrees of visual angle. 4 images from each condition were presented in each block for 600ms with a 200ms ISI for a total of 9 seconds per block. 9 blocks were presented for each condition in a pseudorandomized order, for a total scan time of 244s. To maintain attention, participants performed an orthogonal task detecting periodic colour changes in the fixation cross, responding via a button press.

Data from the localizer scan were used to both define face- and scene-selective regions of interest (ROIs) from control participants, and to establish whether JP showed typical responses to static unfamiliar face stimuli. Boxcar models of each stimulus block were convolved with a single-gamma haemodynamic response function to generate regressors for each condition. These were then entered into a first-level GLM analysis (Woolrich et al., 2001) alongside their temporal derivatives plus confound regressors for 6 head motion parameters. Individual participant data from the controls were entered into a higher-level group analysis using a mixed-effects GLM using FLAME (Woolrich et al., 2004). Face-selective and scene-selective regions were then defined using the contrast of the response to either faces or scenes compared to both other conditions (faces > scenes + scrambled face; scene > faces + scrambled faces). To define ROIs, we used a clustering algorithm that iteratively adjusted the statistical threshold to grow clusters of 250 spatially contiguous voxels (2000 mm^3) around seed voxels within each region.

To determine whether JP demonstrated typical face-selective regions, a first-level analysis of JP's localizer scan was performed in the same way for the control participants. To make a direct comparison between JP and control participants, we compared face-selective and scene-selective responses in face and scene regions, respectively. A Crawford-Howell t-test was used to test for differences in the magnitude of response in JP compared to controls.

3.3.4 Movie watching scan

Participants viewed and listened to a movie that was constructed with audio-visual segments from Seasons 3 and 4 of Game of Thrones. The movie was projected onto an in-bore screen at a distance of 57 cm from the participant with the image subtending approximately 38.7 × 22.3 degrees of visual angle. Accompanying audio was also played to participants in the scanner. There were a total of 10 distinct scenes that ranged in length from 50-117 seconds, for a total movie length of 12 minutes 58 seconds (778s). The movie was presented using PsychoPy (Peirce et al., 2019).

First, we compared functional responses between JP and control participants who were familiar or unfamiliar with GoT. The time series from each voxel in each participant was converted to % signal change, 6 head motion parameters were regressed out of the data and data was aligned into a standard space (MNI152). To investigate where JP showed more similar neural responses to familiar participants (despite being unfamiliar with Game of Thrones), we calculated the intersubject correlations (Pearson's *r*) between JP and each participant from both groups. A Fisher's *z* transform was applied to the correlations. To determine whether the ISCs were greater between JP and the familiar group compared to JP and the unfamiliar group, a one-tailed Welch's independent-samples t-test was performed on each voxel in the brain. This produced whole-brain *p*-statistic maps for each contrast (JP correlated with familiar controls vs JP correlated with unfamiliar controls, and vice versa).

Next, we compared functional connectivity between regions in JP and the familiar or unfamiliar control participants. The time course of response of all voxels within a region was averaged in each participant. To measure connectivity, pairwise correlations (Pearson's *r*) of timeseries were computed between regions for each participant. A Fisher's *z* transform was applied to all correlations prior to any statistics. To test whether JP was significantly different from unfamiliar but not familiar participants in average connectivity between these functional regions, we performed Crawford-Howell t-tests (Crawford & Howell, 1998) on the Fisher's *z* average connectivity scores for JP vs the familiar participants and JP vs the unfamiliar participants.

We compared functional connectivity in early visual regions using visual field map masks from Wang and colleagues (Wang et al., 2015). This included left and right V1, V2 and V3. We also compared functional connectivity between face and scene regions defined in the localizer scan. Finally, we measured functional connectivity between the face and scene regions and a network of non-visual regions that we had previously shown to have an effect of familiarity (Noad, Watson & Andrews, 2024).

All participants performed a behavioural test to determine their familiarity with Game of Thrones. First, we measured understanding of the narrative using a set of 14, 4-alternative, multiple-choice questions. Next, we tested the ability to recognize the faces of key people from Game of Thrones. Participants viewed faces and were asked to name the person or provide relevant information about them. Finally, we tested the ability to recognize key places or landmarks. Participants viewed scenes and were asked to provide the name or key information about the scene that was relevant to Game of Thrones. When participants provided key information rather than the name of the face or scene, two independent observers who were familiar with Game of Thrones had to both agree that the information provided was sufficient to show familiarity. All tests were self-paced. Differences in scores between the familiar and unfamiliar control participants were tested using independent sample t-tests. Differences between JP and familiar and unfamiliar control participants were tested using Crawford-Howell tests.

3.4 Results

3.4.1 Structural MRI

We performed T1 and T2 structural scans. Neither of these scans revealed any structural abnormalities. Figure 3.1 shows images from the structural scan.

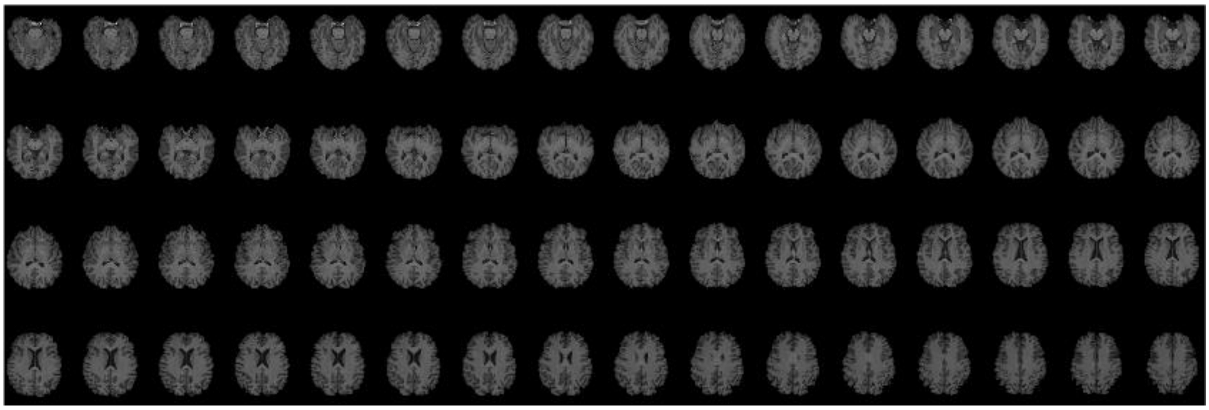


Figure 3.1. T1 structural scans for participant JP. These did not reveal any structural abnormalities that explain the hyperfamiliarity with faces.

3.4.2 Localizer scan

To investigate whether hyperfamiliarity manifests in face-selective regions of the brain, the response to static unfamiliar faces was compared to scenes and scrambled faces using a functional localizer scan. Figure 3.2 shows a group analysis of neurotypical controls and JP. JP showed a similar pattern of face-selective regions when compared to neurotypical controls. Next, we compared the neural response to scenes with faces and scrambled faces. Again, JP showed a similar pattern of scene-selective regions compared to a group analysis of neurotypical controls.

Finally, we directly compared the magnitude of the face- and scene-selective responses across different regions in JP and controls (Figure 3.2 c&d). In face-selective regions, JP showed a similar selectivity to controls for faces (lOFA: t(44) = 2.09, p = .042; rOFA: t(44) = 0.03, p = .973; lFFA: t(44) = 0.63, p = .533; rFFA: t(44) = 0.46, p = .650; lSTS: t(44) = 0.22, p = .829; rSTS: t(44) = 1.42, p = .163). Similar selectivity to controls was also found in JP’s response to scenes in scene-selective regions (lOPA: t(44) = 0.09, p = .928; rOPA: t(44) = 0.64, p = .528; lPPA: t(44) = 0.69, p = .492; rPPA: t(44) = 1.05, p = .299; lRSC: t(44) = 0.39, p = .697; rRSC: t(44) = 0.20, p = .846).

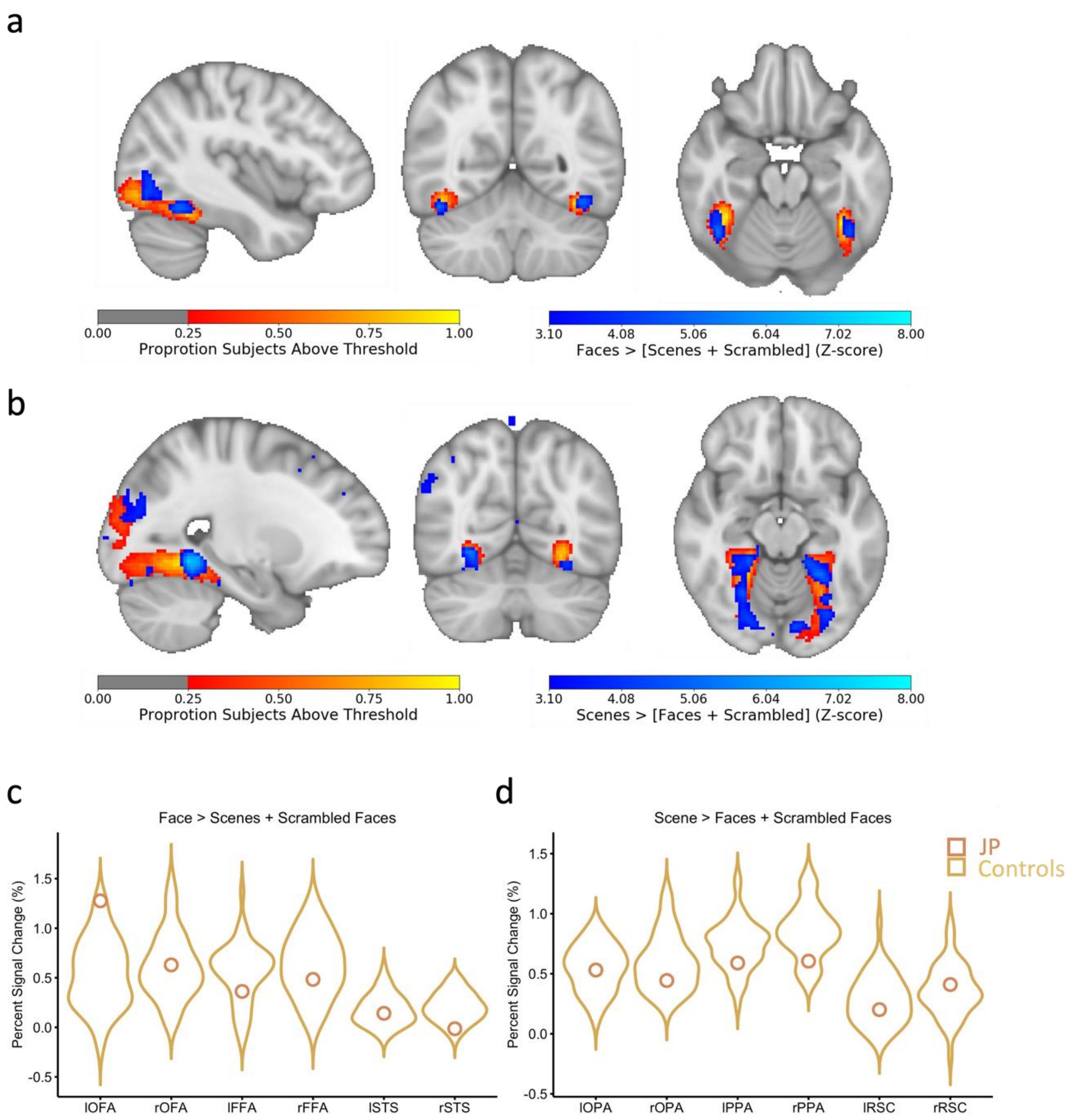


Figure 3.2. Category selective responses. **a**) Face-selective regions were found in JP (face > scene + scrambled faces). Red-orange demonstrates the proportion of control participants' showing face selective activity of Z > 3.1. Blue-light blue shows the face-selective activity in participant JP thresholded at Z > 3.1 (voxel coordinates, -40, -56, -20). **b**) Scene-selective regions were found in JP (scene > face + scrambled faces). Red-orange demonstrates the proportion of control participants' showing scene selective activity of Z > 3.1. Blue-light blue shows the scene-selective activity in participant JP thresholded at Z > 3.1 (voxel coordinates, -24, -64, -14). **c**) Response to face images compared to scene and scrambled face images in face-selective regions in JP (orange circle) and control participants (yellow). JP shows similar responses to control participants in all regions except the left OFA. **d**) Response to scene images compared to faces and scrambled face images in scene selective regions in JP (orange circle) and control participants (yellow). JP shows similar responses to control participants in all regions.

3.4.3 Movie watching scan

To determine how JP responded to faces in more natural viewing, we measured knowledge of the TV series Game of Thrones in JP, and control participants who were either familiar or unfamiliar with the show (Figure 3.3). Since JP is unfamiliar with Game of Thrones, we expected her behavioural responses to be more similar to unfamiliar participants. We found significantly higher performance in the familiar controls compared to unfamiliar controls on the narrative test ($t(37.1) = 16.8$, $p < .001$, $d = 5.04$), the person recognition test ($t(31.9) = 20.2$, $p < .001$, $d = 5.93$) and the place recognition test ($t(23.6) = 8.61$, $p < .001$, $d = 2.51$). As expected, JP had lower performance when compared to familiar controls on the narrative test ($t(22) = 7.4$, $p < .001$), person recognition test ($t(22) = 4.75$, $p < .001$) and place recognition test ($t(22) = 1.83$, $p = .081$). However, there was no difference between JP and the unfamiliar controls (narrative: $t(21) = 0.88$, $p = .390$, person: $t(21) = 0.31$, $p = .745$, place: $t(21) = 0.21$, $p = .837$). On the person recognition questions, JP made incorrect familiarity responses that are characteristic of hyperfamiliarity for faces. For example, one character was thought to be a friend of the family, or her yoga teacher.

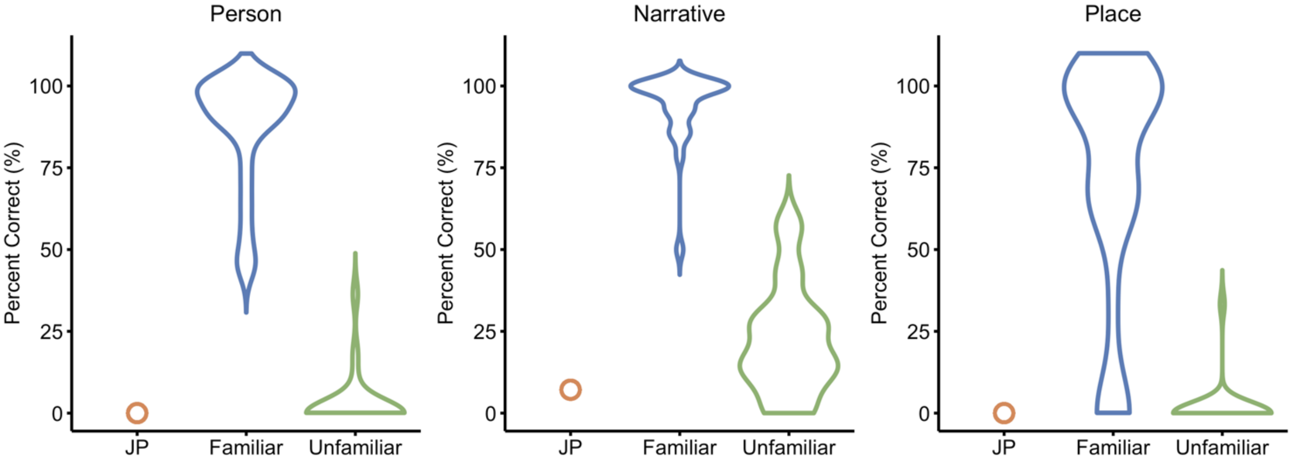


Figure 3.3. JP is unfamiliar with the TV series Game of Thrones, and shows a similar behavioural performance to unfamiliar control participants on a test about the show.

We compared the neural response of JP with control participants who were familiar, or JP with control participants who were unfamiliar, with Game of Thrones. We measured ISCs across all voxels in the brain for JP with each of the familiar and unfamiliar participants. We then compared the correlations of JP with familiar participants to JP with unfamiliar participants to create a whole brain statistical map. Figure 3.4 shows voxels where ISCs were significantly greater between JP and familiar participants than JP and unfamiliar participants (red-yellow) and vice versa (blue).

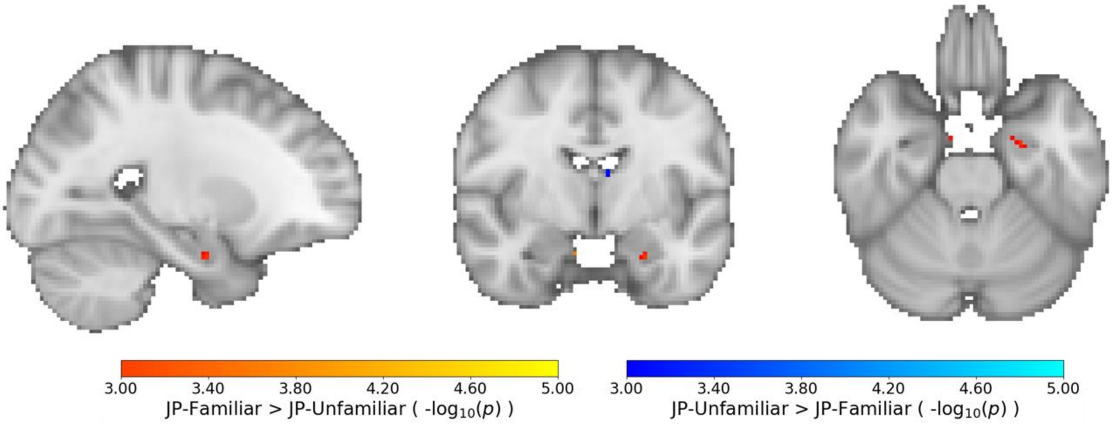


Figure 3.4. JP shows greater intersubject correlations with familiar controls (red-yellow) compared to unfamiliar controls (blue-light blue) bilaterally in medial temporal regions of the brain (thresholded at p < .001, uncorrected for multiple comparisons) (MNI coordinates -24, -6, -26).

Next, we investigated whether functional connectivity in JP would be more similar to familiar or unfamiliar participants when watching Game of Thrones. To do this, we measured functional connectivity between regions in JP and then compared that to functional connectivity in familiar and unfamiliar controls. First, we compared connectivity between early and high-level visual cortex (Figure 3.5a). The magnitude of connectivity between early visual regions was similar between JP and both familiar and unfamiliar controls (JP vs familiar: *t*(22) = 0.45, *p* = .659; JP vs unfamiliar: *t*(21) = 1.34, *p* = .195). There was also no significant difference in magnitude of connectivity between JP and unfamiliar controls compared to JP and familiar controls in the either the face (JP vs familiar: *t*(22) = 0.48, *p* = .639; JP vs unfamiliar: *t*(21) = 1.59, *p* = .127) or scene regions (JP vs familiar: *t*(22) = 0.45, *p* = .659; JP vs unfamiliar: *t*(21) = 1.33, *p* = .195). However, unlike the early visual regions, JP's connectivity magnitude does trend more towards familiar controls than unfamiliar controls in these face- and scene-selective regions (Figure 3.5 b&c).

Next, we asked if there were differences in the patterns of connectivity for JP compared to familiar and unfamiliar controls. Here, we compared the difference matrices from Figure 3.5 by correlating JP's connectivity to familiar controls and to unfamiliar controls for the EVC, face and scene regions separately. To test whether the pattern of connectivity was more similar between JP and familiar compared to JP and unfamiliar participants, we compared the correlations of JP to the familiar with JP to the unfamiliar controls to see if they were significantly different using a two-tailed back transformed average Fisher's Z procedure (Diedenhofen & Musch, 2015; Hittner et al., 2003). Only face regions showed significantly different patterns of connectivity between JP and familiar compared to JP and unfamiliar participants (*z* = 2.3, *p* = .021), suggesting that altered patterns of connectivity face regions may be involved in hyperfamiliarity for faces. EVC (*z* = 0.4, *p* = .707) and scene regions (*z* = 0.4, *p* = .726) did not show such differences.

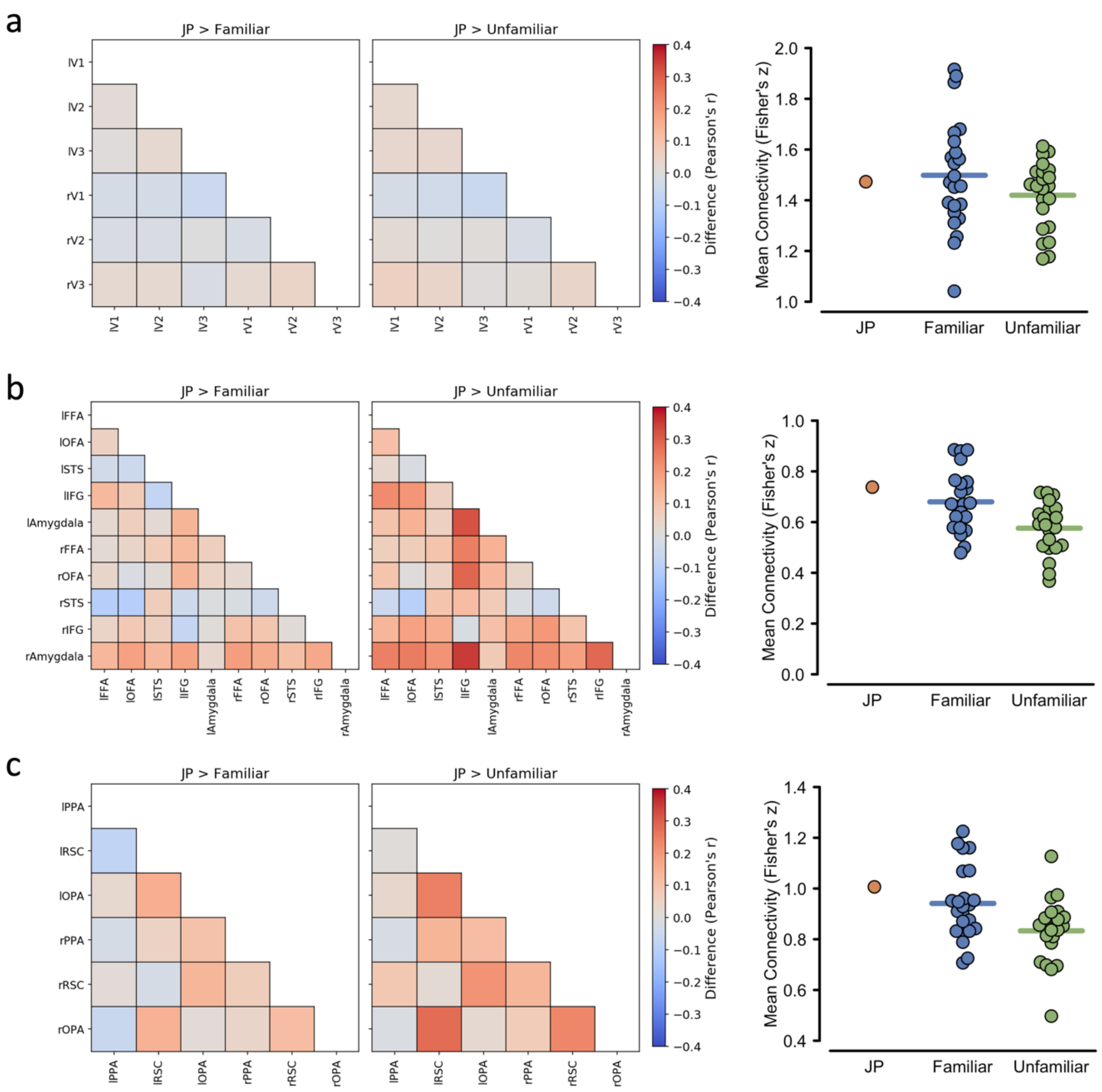


Figure 3.5. Functional connectivity during Game of Thrones movie. JP's intrasubject functional connectivity is more dissimilar to unfamiliar than familiar participants in face- and scene-selective regions. a) Connectivity between EVC is similar in JP, familiar and unfamiliar participants. b) Connectivity is more dissimilar to unfamiliar than familiar participants in face and c) scene regions (individual performance is not statistically significant with Crawford-Howell t-tests)

In a previous study, we found connectivity between core face-selective regions and an extended network of regions beyond the visual brain was greater in familiar compared to unfamiliar participants (Noad, Watson & Andrews, 2024). Here, we tested whether JP would also show greater connectivity between these regions (Figure 3.6). JP showed significantly different connectivity to unfamiliar but not familiar controls in both face- (JP vs familiar: $t(22) = 1.09$, $p = .236$; JP vs unfamiliar: $t(21) = 2.92$, $p = .008$) and scene-selective region (JP vs familiar: $t(22) = 1.65$, $p = .114$; JP vs unfamiliar: $t(21) = 3.22$, $p = .004$) connectivity to this extended network. To test whether the pattern of connectivity was more similar between JP and familiar compared to JP and unfamiliar participants, we compared the correlations of JP with the familiar to JP with the unfamiliar controls to see if they were significantly different using a two-tailed back transformed average Fisher's Z procedure (Diedenhofen & Musch, 2015; Hittner et al., 2003). Both face ($z = 2.3$, $p = .021$) and scene ($z = 5.3$, $p < .001$) region connectivity to the extended network showed significantly different patterns of connectivity between JP and familiar compared to JP and unfamiliar participants, suggesting that altered patterns of connectivity from visual regions to an extended network for familiarity may be involved in hyperfamiliarity for faces.

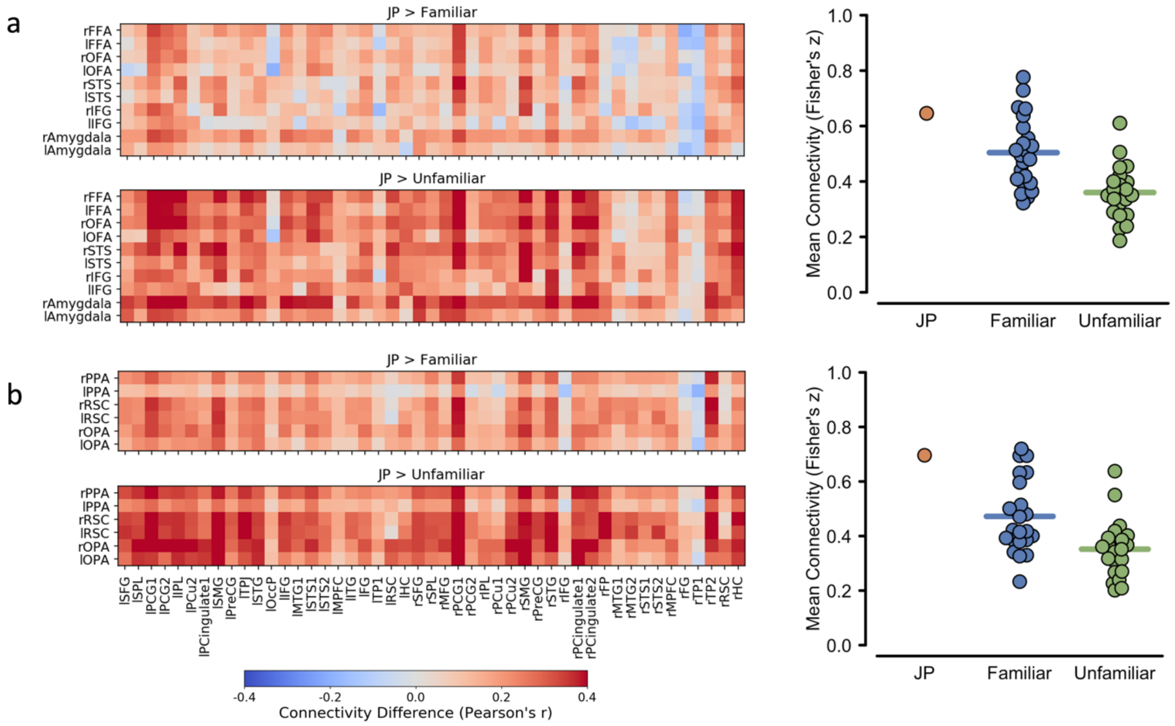


Figure 3.6. JP's intrasubject functional connectivity is more dissimilar to unfamiliar than familiar participants in a) face- and b) scene-selective regions to a network of regions associated with familiarity processing.

Finally, since JP showed greater neural similarity in medial temporal lobes with familiar compared to unfamiliar participants, we looked at connectivity specifically between the hippocampus and face-selective regions (Figure 3.7). Here, JP showed significantly greater connectivity to unfamiliar but not familiar controls in both the left (JP vs familiar: *t*(22) = 0.95, *p* = .354; JP vs unfamiliar: *t*(21) = 2.10, *p* = .048) and right hippocampus (JP vs familiar: *t*(22) = 1.47, *p* = .155; JP vs unfamiliar: *t*(21) = 3.02, *p* = .007).

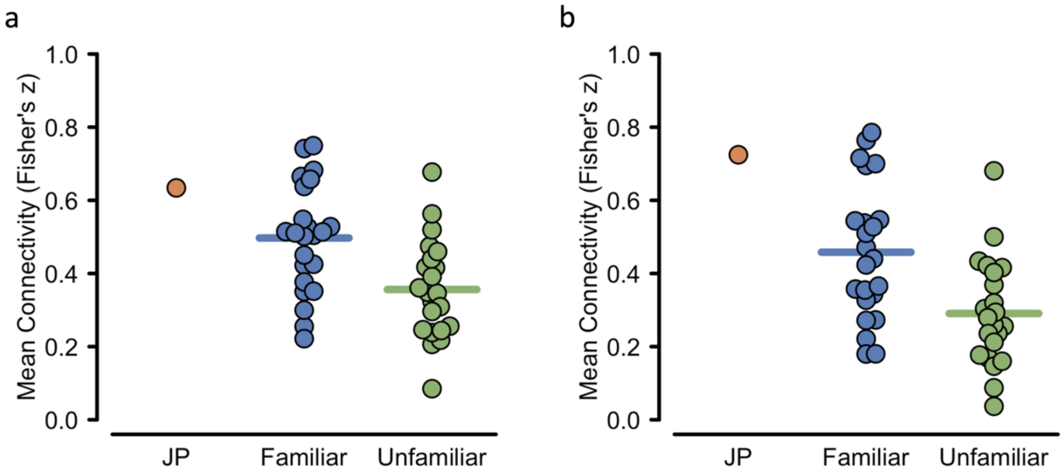


Figure 3.7. JP's intrasubject functional connectivity is significantly different to unfamiliar but not familiar participants between face regions and the a) left and b) right hippocampus.

3.5 Discussion

In this study, we describe the neural response to unfamiliar faces in a woman (JP) who developed a condition known as hyperfamiliarity for faces (HFF) following a migraine. After the onset of the condition, she began to perceive unfamiliar faces as being familiar. We measured neural responses in the brain using fMRI. Neurotypical responses to faces were found in the core face regions of the visual brain. However, the neural correlates of HFF were evident in the connectivity between the core face regions and non-visual regions of the extended face network, particularly in the medial temporal lobe.

HFF provides an opportunity to explore the cognitive processes that underlie the recognition of familiar faces. To explore if there was any structural damage in JP that might underlie the hyperfamiliarity, we scanned her using structural MRI. We did not find any obvious abnormalities in the structural MRI scans. This contrasts with previous studies which have found that HFF can occur following structural damage to the left lateral temporal lobe (Negro et al., 2015; Vuilleumier et al., 2003). Other studies have reported left temporal epileptiform abnormalities and amygdalo-hippocampal lesions are associated with hyperfamiliarity (Amlerova et al., 2012; Bujarski & Sperling, 2008; Michelucci et al., 2010). The onset of the HFF in JP coincided with a migraine. Migraines can affect the brain through a variety of complex mechanisms involving neurological, vascular and neurochemical changes that may not always be detected by structural changes in MRI (Goadsby et al., 2017). Therefore, the inability to detect any structural change with MRI does not mean that changes have not occurred in the brain.

We next asked whether the neural correlates of HFF were evident in the functional response to faces. Functional imaging studies have consistently found regions in the occipital and temporal lobes that respond selectively to faces (Kanwisher et al., 1997). Models of face processing suggest that one region within this core network—the fusiform face area (FFA)—is important for the representation of facial properties that are necessary for familiar face recognition (Haxby et al., 2000). Consistent with these predictions, neuropsychological studies show that lesions in the approximate location of the FFA can lead to selective impairments in face recognition (Barton et al., 2002; Damasio et al., 1982). Previous fMRI studies have also found that there are higher neural responses to familiar compared to unfamiliar faces in the FFA (Weibert et al., 2016) and that responses in the FFA can predict the behavioural advantage for recognition of familiar faces (Weibert & Andrews, 2015). To determine the neural correlates of HFF, we compared the response to static unfamiliar faces with scenes and scrambled faces in a localizer scan. We found that JP had face-selective activation in regions typically found in control participants. If the neural basis of HFF was evident in the response of face-selective regions, such as the FFA, we would expect higher selectivity to unfamiliar faces in JP compared to control participants. However, we found that JP's response in these regions was similar to neurotypical participants. Taken together, these results suggest that the response in the core face regions was not contributing to the hyperfamiliarity.

To further explore the neural basis of HFF, we measured the neural response to faces in a more naturalistic situation (movie watching). The neural response to a movie showing clips from the TV series Game of Thrones (GoT) was recorded in JP and control participants. The control participants were either familiar or unfamiliar with GoT. JP had not watched GoT, and in a separate behavioural study we found her ability to recognise characters from the TV series was similar to unfamiliar controls and significantly lower than to familiar controls. To determine the neural correlates of HFF, we compared the neural response in JP with unfamiliar and familiar control participants using intersubject correlation (ISC). ISC measures the similarity in neural response of the same brain region in two participants by correlating the time series of response (Hasson et al., 2004). Our hypothesis was that regions of the brain involved in HFF should show higher ISC between JP and familiar participants compared to JP and unfamiliar control participants. We found regions in the medial temporal lobe (MTL) showed higher ISC between JP and familiar participants compared to between JP and unfamiliar participants. This region overlapped with the hippocampus and was most evident in the left hemisphere.

The importance of the MTL in the recognition of familiar identity has been shown in a number of studies that have recorded neural responses in the MTL (Nielson et al., 2010; Quiroga et al., 2009; Weibert et al., 2016). Electrophysiological studies have revealed that neurons in the MTL respond selectively to familiar identities across different stimuli, such as different face images, or even across modalities, such as face images and corresponding names (Quiroga et al., 2005). For example, Quiroga et al. (2005) found subsets of neurons within the MTL seemed to respond selectively to a familiar identity across different stimuli, e.g., the actress Halle Berry. These neurons increased their firing rate for different photos of Halle Berry, her name, line drawings of her and even images depicting her masked as cat woman, a character she played. These findings are consistent with models of face processing which propose that the core face regions access appropriate person knowledge through the activation of the extended face network. The extended network contains regions (such as the MTL) that do not exclusively process faces, but are important for processing non-visual information associated with the face. This links the visual representation of the face with semantic, episodic and affective knowledge about the person (Gobbini & Haxby, 2007; Haxby et al., 2000; Ishai, 2008; Kovács, 2020). Interestingly, disruption of processing in the MTL has also been associated with HFF (Amlerova et al., 2012; Bujarski & Sperling, 2008; Michelucci et al., 2010). In neurotypical participants, semantic knowledge for familiar people and places has been shown to be represented in the hippocampus, with accompanying activation in distinct cortical networks for people compared to places (Morton et al., 2021). This demonstrates how neural differences in domain-general areas such as the MTL may lead to the domain-specific impairment seen in HFF.

To determine the face-selective nature of the difference in response, we measured functional connectivity between the core face regions. Previously, we had shown higher functional connectivity between face regions in familiar participants compared to unfamiliar participants in this paradigm (Noad et al., 2024). Our hypothesis was that JP would have higher functional connectivity compared to unfamiliar control participants. Although JP showed higher functional connectivity between the face regions compared to unfamiliar participants, this was not significantly different. JP did not show greater connectivity in early visual areas compared to unfamiliar controls, showing that higher connectivity in other regions was not due to a general increase in connectivity in JP. Next, we compared functional connectivity between the core face regions and an extended network of brain regions associated with familiarity with faces (Noad et al., 2024). Previously, we reported that there was increased functional connectivity between the core face regions and this extended network in familiar participants. Our hypothesis was that regions involved in HFF should show higher functional connectivity in JP compared to unfamiliar control participants. We found that functional connectivity between the core face regions and this extended network was significantly higher in JP compared to controls. This was particularly evident in the connectivity between the face regions and hippocampus. There was no difference between the functional connectivity in JP and familiar control participants. These findings are consistent with models of face processing which suggest visual recognition of a face in core face regions is accompanied by accessing person-specific knowledge in non-visual regions (Gobbini & Haxby, 2007). Previous work has shown that connectivity between face-selective regions and non-visual regions, including the hippocampus, relates to face memory performance (Ramot et al., 2019). Enhanced connectivity between domain-specific face regions and non-visual domain-general regions therefore may be important for signalling familiarity with a face.

The findings of these studies are consistent with other disorders of face perception that show that a sense of familiarity can occur independently of explicit recognition. For example, acquired prosopagnosia occurs following damage to the temporal lobe and is characterised by a deficit in the ability to recognise familiar people from their face. In apperceptive prosopagnosia, individuals have difficulty with the perceptual processing of faces making it difficult to discriminate between different face images (Barton, 2008; Damasio et al., 1982), whereas in associative prosopagnosia, individuals can perceive faces, but cannot link the perceptual information with stored knowledge about the identity of the person (De Renzi, 1986; Gainotti & Marra, 2011). Despite the inability to recognise faces in prosopagnosia, there is evidence for the implicit processing of familiarity. This is shown by differences in the physiological (Bobes et al., 2004; Tranel & Damasio, 1988) and behavioural (Haan et al., 1987) response to familiar compared to unfamiliar faces. Capgras and Fregoli syndromes provide further evidence for a dissociation between the processes of familiarity and recognition in face recognition. Capgras syndrome is a psychiatric disorder in which an individual believes that a person they know has been replace by an identical imposter (Ellis & Lewis, 2001; Hirstein & Ramachandran, 1997). In Fregoli syndrome, they believe they are interacting with a person they know, but the face has been disguised (De Pauw and Szulecka, 1988). These conditions also demonstrate that it is possible to dissociate the sense of familiarity from recognition.

In conclusion, these findings show that the neural correlates of hyperfamiliarity for faces are evident in the response of non-visual parts of the brain, and in the connectivity between visual and non-visual regions. Together, this suggests that the interplay between core face regions in the visual brain and an extended system of non-visual regions may play a critical role in the recognition of familiar faces during natural viewing.

Chapter 4

The importance of conceptual knowledge when becoming familiar with faces during naturalistic viewing

This chapter is adapted from: Noad, K. N., & Andrews, T. J. (2024). The importance of conceptual knowledge when becoming familiar with faces during naturalistic viewing. *Cortex*.

4.1 Abstract

Although the ability to recognise familiar faces is a critical part of everyday life, the process by which a face becomes familiar in the real world is not fully understood. Previous research has focussed on the importance of perceptual experience. However, in natural viewing, perceptual experience with faces is accompanied by increased knowledge about the person and the context in which they are encountered. Although conceptual information is known to be crucial for the formation of new episodic memories, it requires a period of consolidation. It is unclear, however, whether a similar process occurs when we learn new faces. Using a natural viewing paradigm, we investigated how the context in which events are presented influences our understanding of those events and whether, after a period of consolidation, this has a subsequent effect on face recognition. The context was manipulated by presenting events in 1) the original sequence, or 2) a scrambled sequence. Although this manipulation was predicted to have a significant effect on conceptual understanding of events, it had no effect on overall visual experience with the faces. Our prediction was that this contextual manipulation would affect face recognition after the information has been consolidated into memory. We found that understanding of the narrative was greater for participants who viewed the movie in the original sequence compared to those that viewed the movie in a scrambled order. To determine if the context in which the movie was viewed had an effect on face recognition, we compared recognition in the original and scrambled condition. We found an overall effect of conceptual knowledge on face recognition. That is, participants who viewed the original sequence had higher face recognition compared to participants who viewed the scrambled sequence. However, our planned comparisons did not reveal a greater effect of conceptual knowledge on face recognition after consolidation. In an exploratory analysis, we found that overlap in conceptual knowledge between

participants was significantly correlated with the overlap in face recognition. We also found that this relationship was greater after a period of consolidation. Together, these findings provide new insights into the role of non-visual, conceptual knowledge for face recognition during natural viewing.

4.2 Introduction

Recognising the identity of a familiar face is a straightforward process for most human observers if we are familiar with the person. However, the computational challenge of face recognition becomes apparent when we attempt to recognize people who are less familiar. While familiar face recognition is highly accurate across substantial changes in the image (Bruce, 1982; Burton, 2013; Burton, Wilson, et al., 1999), unfamiliar face recognition breaks down under small changes in viewing conditions (Bruce & Young, 1986; Burton et al., 2011; Kramer et al., 2018; Young & Burton, 2017). Cognitive models of face perception suggest that we become familiar with a face by generating image-invariant representations (Bruce & Young, 1986; Young & Burton, 2017). During familiarisation, the representation of a face must transition from an image-based representation based on specific encounters into an invariant representation that can be used to recognize the face across different visual environments.

The successful generation of image-invariant representations is thought to depend on perceptual experience whereby different encounters with a face are integrated to create an invariant representation of a facial identity (Burton et al., 2011; Kramer et al., 2018). Support for this idea comes from studies that show more visual exposure leads to better recognition of faces (Memon et al., 2003; Roark et al., 2006). A key feature of the familiarisation process appears to be the exposure to the variety of encounters with a person (Juncu et al., 2020; Ritchie & Burton, 2017). For example, averaged faces made from many different exemplars from the same person are recognised more accurately than faces made from fewer exemplars (Burton et al., 2005). These findings provide clear evidence for the importance of visual experience, particularly within-person variability, in becoming familiar with a face.

However, increased perceptual experience is also accompanied by an increase in information about a person (i.e. who they are, what they do, what they are like, where we usually see them) that is distinct from the visual properties of the face. A range of evidence suggests that this conceptual information may also play an important role in the generation of invariant representations necessary for familiar face recognition. For example, it has been shown that faces are difficult to recognize in contexts that are different to those in which they are typically encountered (Thomson, 1986; Young et al., 1985), whereas providing the context in which a face was learnt has been shown to improve face recognition (Hanczakowski et al., 2015; McCrackin et al., 2021; Reder et al., 2013; Schwartz & Yovel, 2016). Despite these advances in understanding familiar face recognition, typical paradigms involve viewing a limited number of static images that are associated with arbitrary conceptual knowledge about the person, such as a name or occupation. So, it remains unclear how the recognition of faces unfolds in more naturalistic viewing conditions and over longer time periods. A recent study addressed this issue by measuring face recognition of actors in the TV series Game of Thrones (Devue et al., 2019). They found that the faces of the lead actors were recognized better than other actors and that recognition performance was generally better for faces viewed more recently. Although better recognition could reflect increased perceptual experience, it could also reflect increased knowledge about the person.

In natural viewing, we make new memories by integrating information in events or episodes that include what happened, who was present and where and when it happened (Tulving, 2002). A process of consolidation is then necessary if these episodes are to be integrated into longer term memory, which involves the binding, reactivating, and strengthening connections between the hippocampus and distributed neocortical representations (Nadel & Moscovitch, 1997; Squire & Zola-Morgan, 1991; Yonelinas et al., 2019). Interestingly, this process of acquiring new memories is enhanced when new information is acquired in a coherent context (Lewis & Durrant, 2011; Van Kesteren et al., 2010). Studies of word learning, for example, show that the successful consolidation of information increases when the words are associated with meaning (Davis & Gaskell, 2009; Henderson et al., 2015; Williams & Horst, 2014). However, it is not clear whether similar processes are evident in face learning (Bird & Burgess, 2008; Mattarozzi et al., 2019; Olsen et al., 2015). If this is the case, our prediction is that learning faces in a coherent context should lead to more stable recognition over a longer time period compared to when faces are learnt in the absence of a coherent context.

We used a natural viewing paradigm to explore the effects of perceptual and conceptual information on the recognition of faces. Participants who were unfamiliar with the TV series Life on Mars, viewed excerpts from the series in one of the following conditions: 1) Original sequence or 2) Scrambled sequence. A key feature of the design is that the overall visual input is the same for all the conditions. However, scrambling the sequence will dramatically affect the ability to understand the context or narrative (Van Kesteren et al., 2010; Zacks et al., 2007). We then assessed whether conceptual knowledge has an effect on the recognition of faces. If face recognition is dependent only on visual information, we predicted that there should be no difference between any of the conditions. However, if conceptual knowledge is important, the recognition of faces will be greater in the Original condition. We tested face recognition immediately after watching the movie (short-term) and then 4 weeks later (long-term).

Our preregistered analyses assessed 4 specific hypotheses (each has been assessed in a pilot study). Hypothesis 1: Manipulating the order of the events in the movie will affect understanding of the narrative or context. Our prediction was that there will be a greater understanding of the narrative of the stimulus when it is shown in the original sequence compared to a scrambled order. Hypothesis 2: The recognition of faces after a delay will depend on the context in which they were originally presented. Our prediction was that the reduction in face recognition following a delay will be smaller in the Original condition compared to the Scrambled condition, because the greater conceptual information in the Original condition will help consolidate the faces in memory. Hypothesis 3: Recognition of faces images will be greater if they are consistent with the appearance at encoding. Our prediction was that face images that are visually similar to the faces at encoding will be recognised to a greater extent compared to images that are not consistent with the appearance at encoding. Hypothesis 4: The effect of context on the recognition of faces, after consolidation, will be greater if the images are consistent with the appearance at encoding. Our prediction was that there will be a bigger difference in recognition scores for In Show compared to Out of Show images for the Original condition compared to the Scrambled condition at the delayed time point.

4.3 Methods

The accepted Stage 1 manuscript of this Registered Report was registered on the Open Science Framework (OSF) and can be found at: https://osf.io/8wp6f.

4.3.1 Participants

200 participants (176 female, 9 non-binary, age M = 19.24 years, SD = 0.86 years) were recruited who were native English-speaking and were unfamiliar with the TV show Life on Mars. All participants had either normal or corrected-to-normal vision (by self-report) and performed the Cambridge Face Memory Test (CFMT; Duchaine & Nakayama, 2006) to determine that their face perception was within a normal range (>65%, i.e., not less than 2 SD from the mean). Participants were compensated with an Amazon voucher or course credit for their time. The study conformed with all relevant ethical regulations at the University of York and was approved by the University of York Department of Psychology Ethics Committee. Informed consent was obtained from all participants.

4.3.2 Sampling plan

We conducted a sensitivity analysis (see Figure 4.1) for a one-sided independent t-test with a power of 0.9 and alpha level of 0.02. This showed a rapid initial decrease in the minimum effect size that could be detected, with improvements being relatively marginal beyond around 100 participants per group for our smallest theoretically important effect size (Hypothesis 2: see orange dashed line in Figure 4.1). We chose this as our sample size, as it allowed us to detect effect sizes of a similar magnitude to that found in our pilot work (Supplementary Data) and also kept the experiment feasible from a practical perspective. This is a 'medium' effect size (see Cohen, 1988), and we consider that effect sizes smaller than this are unlikely to have practical relevance for everyday face recognition performance, so it also constitutes the smallest effect size of interest for this work.

4.3.3 Design

The whole experimental design was 2*2*2 with Condition (Original, Scrambled), Image type (In Show, Out of Show) and Timepoint (Immediate, Delayed) as the factors. Condition was a between-subjects factor. Image type and Timepoint were within-subjects factors.

4.3.3 Stimuli

Two 20-minute (1170s) movies constructed from audio-visual clips from the first episode of BBC TV series Life on Mars were used as stimuli. Timings are based on previous studies using experimentally familiarised faces (Hahn & O'Toole, 2017; Hahn et al., 2016) and on our pilot study. A key aspect of the design is that each movie contains the same visual input. The first movie contains the clips in the original order (Original), so that the narrative is coherent. The second movie contains the same clips in a randomised order (Scrambled). An illustration of the different movie stimuli is shown in Figure 4.2. A total of 14 clips are used in the stimuli, with a mean length of 84s (range 39s-228s). The clips are assigned a random order for the Scrambled condition, with longer clips cut into shorter segments (mean clip length 39s). 10 unique characters are present in the clips with varying screen time (34-1170s). Participants were instructed to fully watch and attend to the movie before completing any of the other tasks.

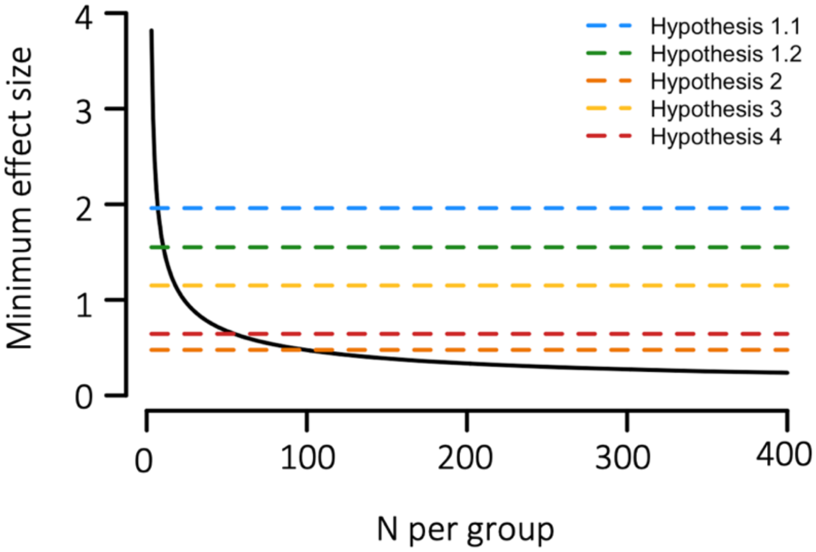


Figure 4.1. Sensitivity analysis showing the detectable effect size for a one-sided independent t-test with a power of 0.9 and alpha level of 0.02. The dashed lines represent the effect sizes found in the pilot data for each hypothesis.

For the face recognition memory task, we used images from the 10 main actors from the episode of Life on Mars. Static images were taken directly from the TV series and are referred to as "In Show" images. However, these were not images that were seen in the movie. This is critical to avoid confounding face recognition with the visual memory of a specific image (Bruce & Young, 1986; Young & Burton, 2017). Each actor also had another image from outside of the Life on Mars TV series, which are referred to as "Out of Show" images. Critically, Out of Show images contain greater within-person variability, with significant changes in physical appearance (Burton et al., 2011; Kramer et al., 2018). Previous research has shown that the amount of within-person variability affects subsequent recognition (Juncu et al., 2020; Ritchie & Burton, 2017). For each In Show or Out of Show face for each face memory test, two foils of different identities were selected that matched the targets in terms of age, expression, hairstyle, lighting, and general appearance (Colloff et al., 2021). 19 target images (Out of Show image not available for one actor) and 40 foils were used in each face recognition memory test. Images were cropped to include the head. Example target and foil images are shown in Figure 4.3. Different target and foil images were used at each test phase to avoid practice effects. So, a total of 30 In Show images and 29 Out of Show images were shown at the immediate timepoint, and a new set of 30 In Show images and 29 Out of Show images were shown at the delayed timepoint. The comparison between In Show and Out of Show face images is important to determine whether the effect of context on face memory is specific to the visual context in which the images were originally shown (Thomson, 1986; Young et al., 1985).

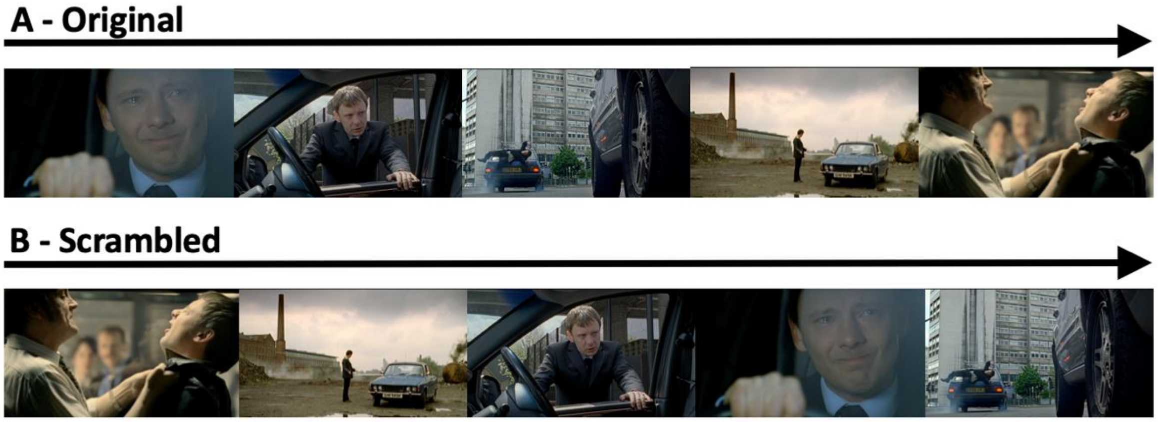


Figure 4.2. Illustration of movie conditions. a) The Original condition has the movie clips in the correct sequence, whereas **b**) the Scrambled condition had the same movie clips, but they were not presented in the correct sequence. The visual exposure is the same in both conditions, but the order of presentation is different across conditions.

4.3.5 Procedure

Participants were sent a link to a secure website hosting the online experiment. Participants were prevented from running the experiment on mobile devices. An information sheet was included with a description of the study, the data that would be collected and how it would be stored, and informed consent was given. Participants were randomly allocated to one of the 2 conditions: 1) Original condition, where movie clips are viewed in order, or 2) Scrambled condition, where movie clips are viewed in a random order.

After being allocated to a condition, participants commenced with the study. During the study phase, participants were asked to watch and fully attend to the movie stimulus. Immediately after the study phase, participants were tested on their conceptual understanding of the movie clips. They first completed a free recall test, where they were asked to provide a written description of the plot of the movie using as many details as possible. Participants then completed a face recognition memory task, with faces presented individually in a random order. In this test, participants pressed a button to indicate if the identity of the face corresponded to any of the actors in the movie. Stimuli remained on screen until the participant made a response. Finally, participants completed a second contextual understanding test (structured question test), containing a series of 8 questions about specific events in the movie accompanied by a static image of the relevant event in the movie. Task performance on the contextual understanding tasks was graded by two raters using a predefined marking scheme. Agreement between raters for the contextual understanding tests was calculated using intra-class correlation coefficient (ICC) with a two-way mixed model and Agreement definition.

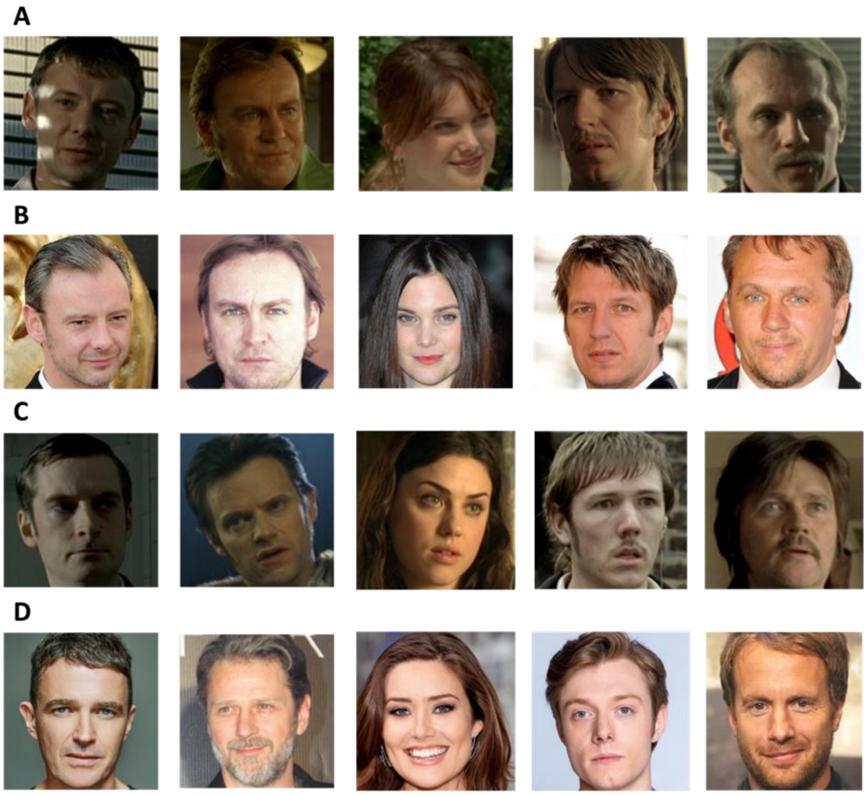


Figure 4.3. Examples of faces from the recognition test. **a**) In Show target faces were actors as they appear in the show, whereas **b**) Out of Show target faces were actors as they appear out of the show. **c**) In Show foils were other actors taken from the same show and **d**) Out of Show foils were other actors that matched the Out of Show faces.

A unique participant identifier was provided by email for participants to complete the face recognition memory task again at 4-weeks after the study phase. A link to the face recognition memory task was sent at 4-weeks for the participant to access the experiment at the final time-point. For the 4-week time-point the experiment had to be completed within 48 hours of the link being sent. Following completion of the study, a debriefing sheet detailing the aims of the experiment was provided as well as full payment or course credit.

4.3.6 Data analysis

See Supplementary Table 4.1 for our study design table with a full list of preregistered hypotheses.

Hypothesis 1: Manipulating the order of the events in the movie will affect understanding of the narrative or context

Task performance on the conceptual understanding tests was graded by two raters using a predefined marking scheme. Raters (who were blind to the condition) marked the free recall test relative to 10 key events that occurred during the movie. Raters assigned a mark of 0, 1 or 2 for each point dependent on whether the text showed no, partial or a full description of each event, for a possible total of 20 marks. The 8 questions on the structured question test were also marked by raters on a scale from 0 to 2, based on whether they show no, partial or a full understanding for a possible total of 16 marks. The analysis was based on the average scores across raters. Inter-rater reliability was assessed for both the free recall and structured question test aggregated across questions using intra-class correlation coefficients (ICC) in a two-way mixed model with agreement definition. ICC greater than 0.75 indicates good reliability between raters. While this value does not need to be achieved for the experiment to be deemed capable of testing the key hypotheses, an ICC greater than 0.75 validates the marking scheme as effective in consistently assessing the narrative score. The pilot data indicates that reliability should be higher than 0.75.

To assess whether the movie manipulation leads to differences in conceptual understanding (Hypothesis 1), the free recall scores (Hypothesis 1.1) and structured question scores (Hypothesis 1.2) for each condition were entered into a one-tailed independent groups t-test, with an alpha criterion of 0.02 for determining significance. Support for hypothesis 1.1 and 1.2 will be indicated by a significant effect, with lower scores for the Scrambled condition compared to the Original condition. Successful manipulation of movie context understanding will be shown if both hypothesis 1.1 and 1.2 are confirmed.

Hypothesis 2: The recognition of faces after a delay will depend on the context in which they were originally presented

Performance on the face recognition memory test was calculated using the mean sensitivity (*d'*) for discriminating between faces of individuals present in the movie and faces of foils who were not present in the movie. *d'* was calculated based on hit rates (i.e. correct recognition of the face as present in the movie) and false alarm rates (i.e. incorrectly responding that foil was present in the movie) for each participant. *d'* was calculated using the following equation:

$$d' = \mathrm{z(H)} - \mathrm{z(FA)}$$

where z(H) and z(FA) are the z transforms of the hit rate (number of hits / number of targets) and false alarm (number of false alarms / number of foils), respectively. Ceiling hit rates or false alarm rates (i.e. hit = 1) were replaced with 0.999 and floor hit rates or false alarm rates (i.e. false alarm = 0) were replaced with 0.001 to avoid *d′* infinity. *d′* was calculated separately for each face recognition memory test time point (0 hours, 4-weeks) and separately for In Show face images and Out of Show face images.

To determine if contextual understanding has a role in recognition of faces after a delay in stimulus encoding (Hypothesis 2), the difference between the immediate and delayed (immediate – delayed) face recognition score (*d′*) for each condition (Original and Scrambled) will be calculated separately and then compared using a one-tailed independent groups t-test for the In Show images. Support for hypothesis 2 will be shown if the difference scores are lower in the Original condition compared to the Scrambled condition at *p*<.02.

Hypothesis 3: Recognition of face images will be greater if they are consistent with the appearance at encoding

The average score (*d′*) was combined across timepoints for the In Show and Out of Show images in the Original condition. To determine whether the appearance of the images at encoding is important for subsequent recognition, a one-tailed independent groups t-test was performed on the difference between In Show and Out of Show face recognition. Support for hypothesis 3 will be indicated by a greater face recognition score for In Show images than Out of Show images at *p*<.02.

Hypothesis 4: The effect of context on the recognition of faces, after consolidation, will be greater if the images are consistent with the appearance at encoding

To investigate whether the role of contextual understanding on face recognition after consolidation is influenced by the appearance of the faces at encoding, the difference between the recognition for In Show and Out of Show images (In Show – Out of Show) was calculated for each condition (Original, Scrambled) and compared using a one-tailed independent groups t-test at the delayed time point. Support for hypothesis 4 will be indicated by a bigger difference in face recognition between In Show images compared to Out of Show images for the Original condition at *p*<.02.

4.3.7 Exclusion Criteria

Participants who did not complete the face recognition test at all time points were excluded from all analyses; participants who did complete the delayed face recognition test but not within the specified time slot were also excluded from analysis. Participants who did not complete both the free recall and structured narrative questions were excluded from analysis. Participants were asked at each time point if they have seen the TV show Life on Mars; participants who had seen the show at any point were excluded from all analyses. Participants were screened for familiarity with other popular shows characters have been in, such as Ashes to Ashes (2008) which shares characters and actors with Life on Mars. They were also excluded if they had seen the TV show Spooks (2002), as foil images were gathered from this show.

4.3.8 Reliability Analysis

Task performance was graded by two raters using a predefined marking scheme. Agreement between raters was calculated using intra-class correlation coefficient (ICC) with a two-way mixed model and Agreement definition. Excellent agreement was found between raters in the free recall test with an ICC of .90 and 95% confidence intervals of .87 to .92 ($F(201,201) = 18$, $p < .001$) and in the structured question test with an ICC of .88 and 95% confidence intervals of .84 to .90 ($F(201,201) = 15$, $p < .001$). For further analyses, the average of the free recall and structured questions from the two raters' scores was used to create a Total score.

4.3.9 Exploratory Analysis

To investigate how conceptual understanding influences face recognition, we compared individual performance on narrative and face recognition tasks. We asked whether overlap in the content of the free-recall test was correlated with overlap in the face recognition performance across all pairs of participants. Overlap in the free recall test was assessed using Latent Semantic Analysis (LSA). Latent Semantic Analysis is a technique in natural language processing and information retrieval that helps to uncover the underlying structure in a collection of text by analysing the relationships between the words (Landauer et al., 1998). LSA uncovers relationships between text datasets by mapping words and documents into a continuous semantic space. In this space, similar words and documents are positioned closer together, reflecting their underlying semantic relationships. In this study, we have compared the free-recall text summary of the narrative between different pairs of participants. The similarity between texts that is measured using LSA is taken as the overlap in semantic (or conceptual) understanding about the movie they have watched. The logic underlying this analysis is that participants may have picked up on different pieces of conceptual information from the movie and this may influence subsequent face recognition. This analysis will provide a measure of the overlap in conceptual knowledge between participants. Overlap in face recognition was calculated by taking the total number of items that were accurately reported in both participants.

Significance was assessed using a permutation test, where the rows and columns of the LSA matrix were randomly shuffled and then correlated with the face recognition overlap matrix. This shuffling was repeated 100000 times to create a null distribution for the null hypothesis that there is no relationship between narrative overlap and face recognition overlap. A Bonferroni-Holm correction (Holm, 1979) was also then applied to correct for familywise error. We were not aware of this approach at the time of pre-registration. However, it provides an alternative approach to explore how overlap in conceptual knowledge might be correlated with overlap in face recognition.

4.4 Results

4.4.1 Hypothesis 1: Manipulating the order of the events in the movie will affect understanding of the narrative or context

To determine whether manipulating the order of events in the movie had an impact on conceptual knowledge, narrative scores were compared between the Original and Scrambled conditions. Free recall scores ($t(197.6) = 17.23$, $p < .001$, $d = 2.436$) and structured question scores ($t(190.64) = 9.37$, $p < .001$, $d = 1.325$) were significantly higher for the Original condition compared to the Scrambled condition (Figure 4.4), confirming Hypotheses 1.1 and 1.2 that conceptual understanding would be greater when viewing clips in their original order. This shows that the manipulation was successful in affecting the conceptual understanding of the movie.

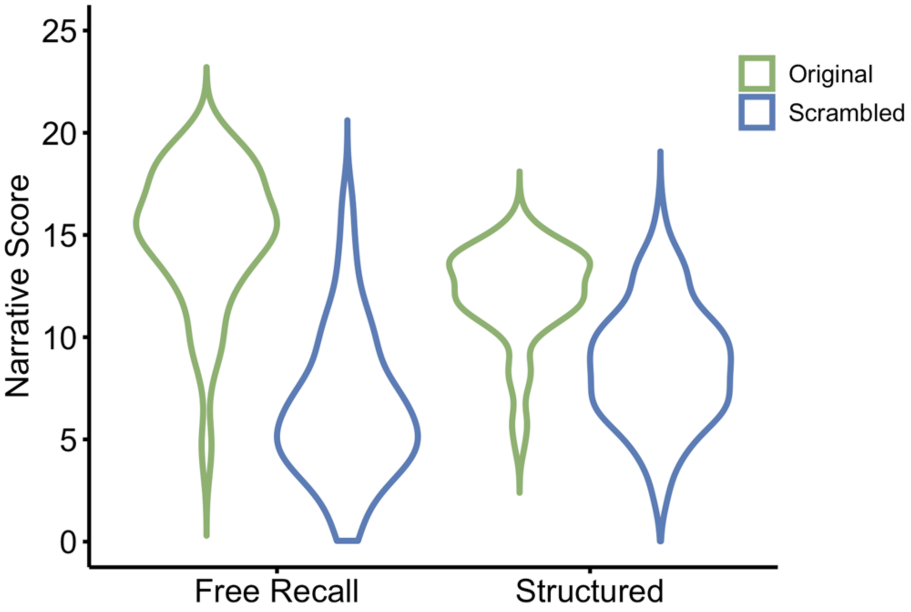


Figure 4.4. Performance on the narrative understanding tasks for the Original and Scrambled conditions. Performance on the (left) free-recall and (right) structured question narrative tests was significantly greater for the Original compared to the Scrambled group, supporting Hypothesis 1.1 and 1.2. This shows that the conceptual understanding of the narrative was better when events were presented in the original sequence.

4.4.2 Hypothesis 2: The recognition of faces after a delay will depend on the context in which they were originally presented

Next, we asked whether recognition of faces depends on the context in which they were presented by comparing performance in the Original and Scrambled conditions. We calculated the difference in face recognition scores between the immediate and delayed timepoints for the In Show faces. This difference (immediate *d'* – delayed *d'*) was then compared for participants in the Original and Scrambled groups (Fig. 4.5, left). A smaller difference between immediate and delayed recognition scores would show less forgetting of faces. However, the Original and Scrambled groups were not significantly different after a delay (*t*(196.8) = 1.18, *p* = .881, *d* = 0.168). This does not support Hypothesis 2 that conceptual knowledge has a greater effect on the recognition of faces after a delay.

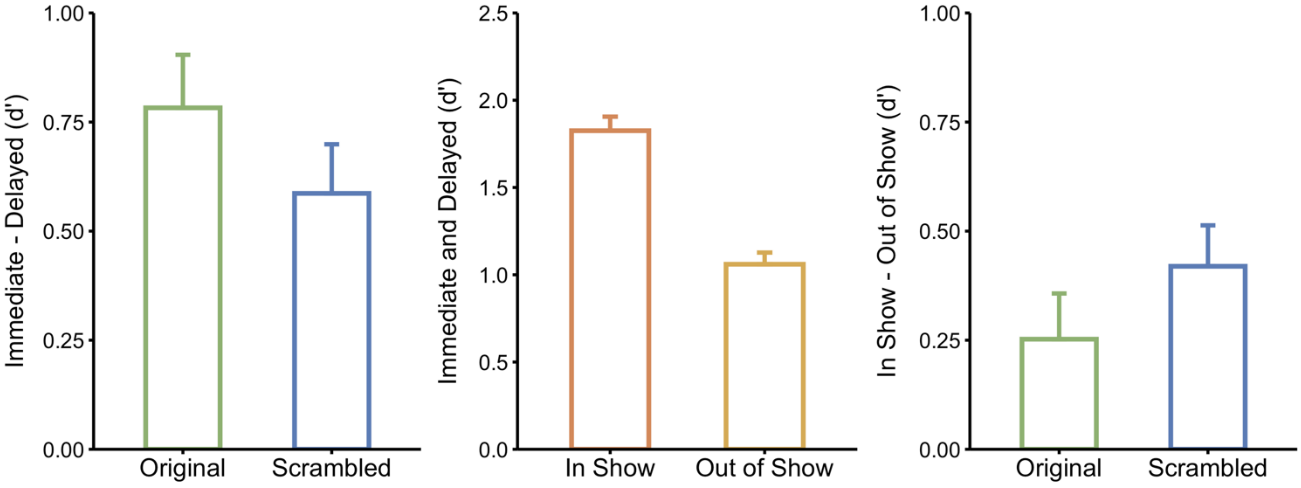


Figure 4.5. Face recognition difference scores for each pre-registered hypothesis. (left panel) The difference in recognition of In Show images at the immediate and delayed timepoints for the Original and Scrambled groups. Hypothesis 2 predicted a smaller difference in the Original compared to the Scrambled group. However, there was no significant difference. (middle panel) Recognition of In Show and Out of Show faces from the Original group, averaged across immediate and delayed time points. Higher recognition was evident for the In Show images, which supports Hypothesis 3. (right panel) The difference in recognition of In Show and Out of Show images at the delayed time point. The difference in the Original group was not significantly greater than the Scrambled condition, which does not support Hypothesis 4. Error bars represent standard error.

4.4.3 Hypothesis 3: Recognition of face images will be greater if they are consistent with the appearance at encoding

Next, we determine whether face recognition would be greater if faces were consistent with the appearance at encoding. We collapsed face recognition scores in the Original condition across the immediate and delayed timepoints for the In Show images and then for the Out of Show images (Fig. 4.5, middle). We found significantly greater recognition for In Show compared to Out of Show images (*t*(191.6) = 7.30, *p* < .001, *d* = 1.03), confirming Hypothesis 3 that face images that are taken from a similar context to those at encoding would be recognised better than face images that are taken from other contexts.

4.4.4 Hypothesis 4: The effect of context on the recognition of faces, after consolidation, will be greater if the images are consistent with the appearance at encoding

We then asked whether the role of contextual understanding on face recognition after consolidation was influenced by the appearance of the faces at encoding. The difference in recognition scores for the In Show and Out of Show images for the Original and Scrambled condition were calculated at the delayed timepoint (In Show *d'* – Out of Show *d'*). A greater difference in these scores would reflect greater recognition of faces with a similar visual appearance at encoding after consolidation. However, the difference between In Show – Out of Show scores was not significantly different between the Original and Scrambled conditions at the delayed timepoint ($t(195.7) = -1.19$, $p = .118$, $d = -0.168$). This does not support Hypothesis 4 (Fig. 4.5, right).

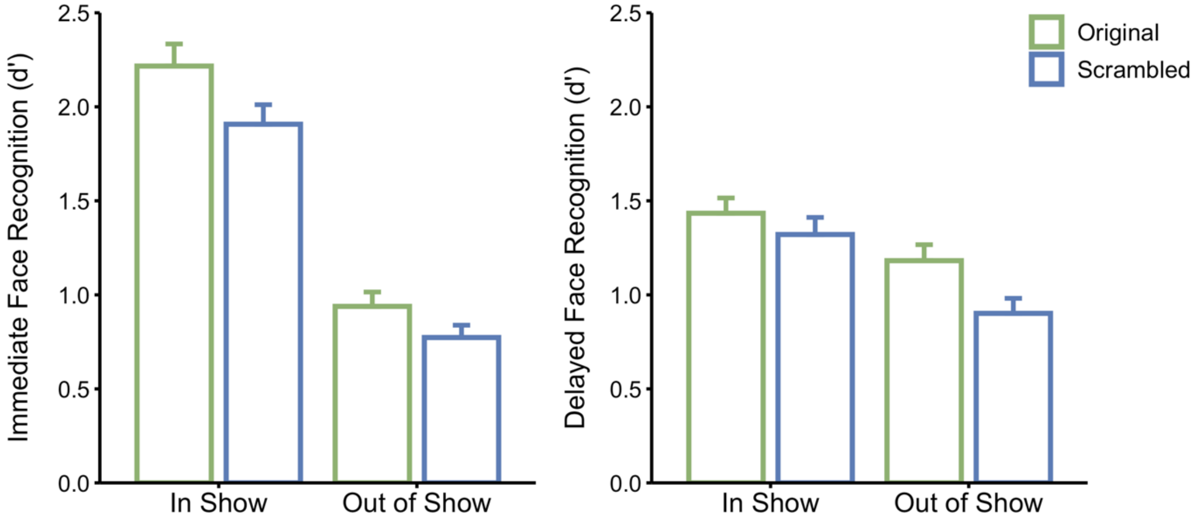


Figure 4.6. Face recognition scores for the Original and Scrambled conditions on the immediate and delayed recognition tests. There was a main effect of Image, with higher recognition of In Show compared to Out of Show images. There was also a significant main effect of condition, which reflected higher recognition in the Original compared to Scrambled conditions. Error bars represent standard error.

4.4.5 Exploratory analyses

While our pre-registered analyses focus on the importance of consolidation, they do not consider an overall role of conceptual knowledge on face recognition. To determine whether there was an overall effect of conceptual knowledge on face recognition, a mixed ANOVA was run on Condition (Original, Scrambled), Image (In Show, Out of Show) and Timepoint (immediate, delayed). There was a significant main effect of Condition on face recognition ($F(1,198) = 6.45$, $p = .015$, $\eta^2 = 0.032$), with face recognition being greater in the Original compared to the Scrambled condition (Fig. 4.6).

We report all main effects and interactions from the omnibus ANOVA. There was a significant main effect of timepoint ($F(1,198) = 23.14$, $p < .001$, $\eta^2 = 0.105$), with faces recognised better at the immediate timepoint. There was also a significant main effect of Image ($F(1,198) = 184.02$, $p < .001$, $\eta^2 = 0.482$), with In Show images being recognised greater than Out of Show images. This is consistent with our support for Hypothesis 3 (see Fig. 4.6). There was no significant interaction between Condition*Timepoint*Image ($F(1,198) = 2.35$, $p = .127$, $\eta^2 = 0.012$). This is consistent with the absence of support for Hypothesis 2. There was a significant interaction between Image and Timepoint ($F(1,198) = 73.92$, $p < .001$, $\eta^2 = 0.272$). This reflects the smaller difference in face recognition between the In Show and Out of Show images at the delayed compared to the immediate timepoint. We found no significant interactions between Condition and Image ($F(1,198) = 0.01$, $p = .918$, $\eta^2 < 0.001$) or between Condition and Timepoint ($F(1,198) = 0.16$, $p = .694$, $\eta^2 < 0.001$).

Next, we asked whether the overlap of conceptual understanding between participants could predict overlap in face recognition and whether this effect was greater at the delayed timepoint. For each pair of participants, a similarity rating of the free-recall was calculated using a semantic similarity algorithm (LSA; Landauer et al., 1998). This generated a measure of conceptual overlap across all pairwise combinations of participants. Next, we compared this with the overlap in the faces that were accurately recognised across all pairwise combinations of participants. For each pair of participants, we calculated the total number of items that were accurately reported in both participants. We then correlated the conceptual overlap with the face recognition overlap at different timepoints for the In Show and Out of Show images (Fig. 4.7).

There was a significant positive correlation between the overlap in conceptual knowledge and face recognition for In Show images at the immediate ($r = .17$, $p = .003$, lower CI = .16, upper CI = .19) and delayed ($r = .21$, $p < .001$, lower CI = .20, upper CI = .22) timepoints. For the Out of Show images, there was no significant correlation at the immediate timepoint ($r = .04$, $p = .511$, lower CI = .02, upper CI = .05), but there was a significant positive correlation at the delayed timepoint ($r = .18$, $p = .002$, lower CI = .17, upper CI = .19). Finally, we determined whether the magnitude of the correlations changed between timepoints using a one-tailed back transformed average Fisher's Z procedure (Diedenhofen & Musch, 2015; Hittner et al., 2003). We found higher correlations between the conceptual and recognition overlap at the delayed compared to the immediate timepoint for both the In Show images ($z = 5.8$, $p < .001$) and the Out of Show images ($z = 20.0$, $p < .001$). These findings are consistent with a greater effect of conceptual information after a period of consolidation.

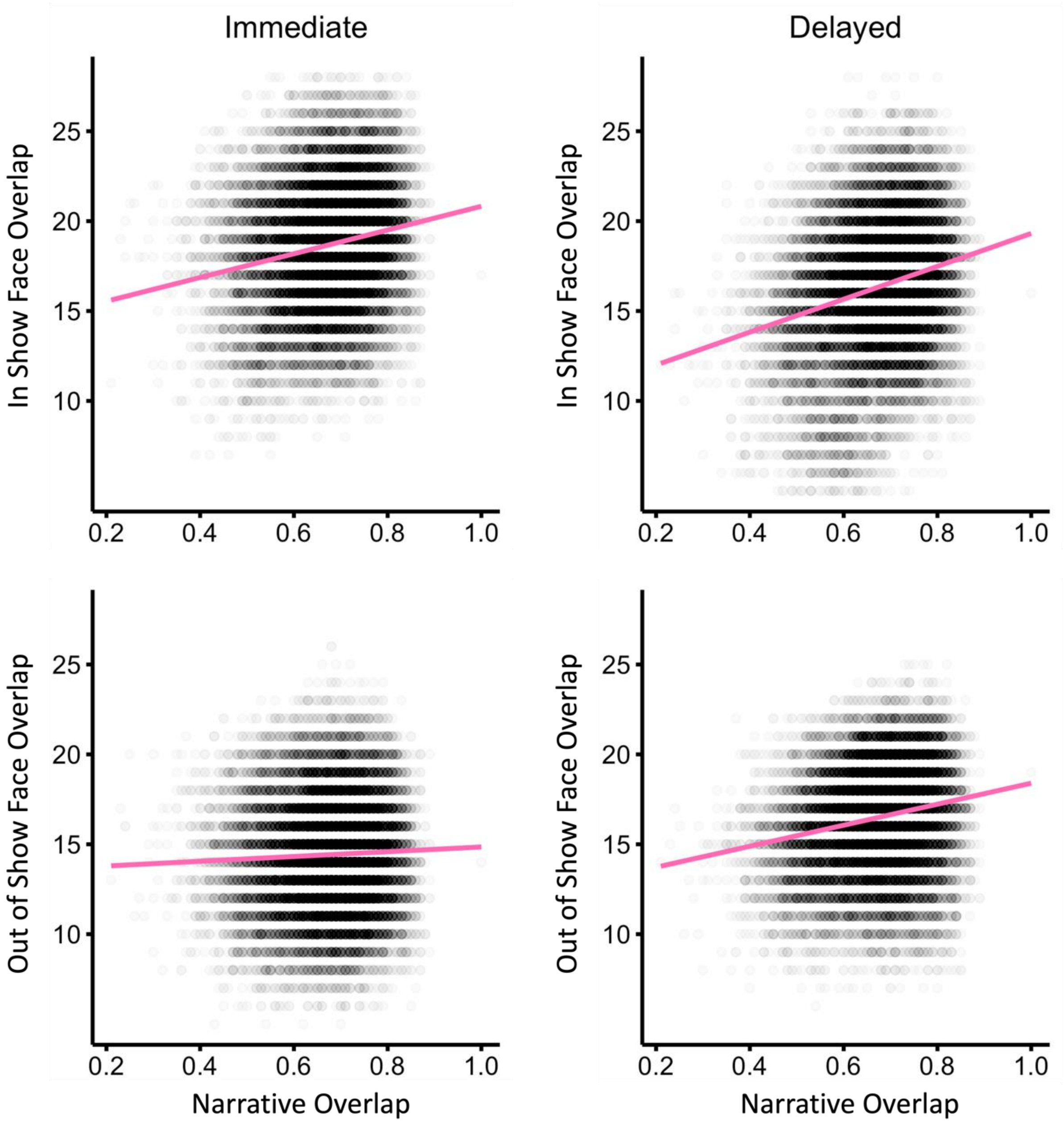


Figure 4.7. Correlations between the overlap in narrative understanding and overlap in face recognition across all combinations of participants. Overlap in narrative correlated with overlap in the recognition of In Show faces (immediate: r=.17, delayed: r=.21) and Out of Show faces (immediate: r=.04, delayed: r=.18). The correlations at the delayed timepoint were significantly greater than the immediate timepoint. Regression lines are shown in pink. Points denote an individual pairing of participants.

4.5 Discussion

The aim of this study was to investigate the importance of non-visual, conceptual knowledge in face recognition during naturalistic viewing. To address this question, we compared the face recognition of characters in a movie taken from the TV series Life on Mars (LoM) in participants who had not watched it before. The key manipulation was to present the movie in either its Original sequence or in a Scrambled sequence. Our first pre-registered hypothesis was that participants who viewed the Original sequence would have a better understanding of the narrative (conceptual knowledge) compared to participants who viewed the scrambled sequence. Our results confirmed this hypothesis showing that participants in the Original condition had more extensive and accurate recall of the events in both the free recall and structured question scores.

Next, we asked whether this difference in conceptual knowledge would have an effect on the ability to recognise the faces. There was a significant main effect of conceptual knowledge on face recognition. That is, participants who viewed the Original sequence had overall higher face recognition than participants who viewed the Scrambled sequence. However, our pre-registered hypothesis was that there would be a bigger effect of conceptual knowledge on face recognition after memory consolidation. To test this, we compared face recognition immediately after viewing the movie and then 4 weeks later. We predicted that viewing the movie in the original sequence would lead to a stronger and more robust representation of the faces. However, our results did not support our second pre-registered hypothesis of an overall effect of conceptual knowledge on face recognition following a period of consolidation.

We next performed an exploratory analysis, to determine whether overlap in conceptual knowledge between participants could explain overlap in face recognition. To do this, we compared conceptual knowledge across participants using a semantic analysis of the text from the free recall task (Landauer et al., 1998). Rather, than measure overall levels of knowledge, this method measures the overlap in semantic content between participants. This approach has previously been shown to predict similarity in neural responses between individuals (Nguyen et al., 2019). Here, we asked if the overlap in conceptual knowledge across participants predicted which faces were remembered in the recognition test. We found that the pattern of recognition of In Show faces (that were similar to those seen during encoding) was significantly correlated with the overlap in conceptual knowledge at the immediate timepoint. We then asked whether the relationship between conceptual knowledge and face recognition was greater after a delay. Interestingly, we found a greater correlation at the delayed timepoint. This suggests that consolidation may have an effect on the interaction between conceptual knowledge and face recognition. We performed the same analysis with Out of Show faces (that were visually dissimilar to those seen at encoding). We found no significant correlation at the immediate timepoint, but there was a significant correlation at the delayed timepoint. Again, this suggests that consolidation may have an effect on the interaction between conceptual knowledge and face recognition. Further research using these similarity measures may provide a useful way to probe the role of conceptual knowledge in face recognition

Cognitive models of face perception focus on visual experience and suggest that familiarisation with a face occurs through generation of an image-invariant representation (Bruce & Young, 1986; Burton et al., 2011; Young & Burton, 2017). When an invariant visual representation of the face has been established, conceptual information about the person can be accessed. However, in natural viewing when we are becoming familiar with a person, our perceptual experience with their face is typically accompanied by an increase in conceptual information, such as their name, what they are like, memories of key events and how we feel about them. Although models do not typically include conceptual knowledge as being important for the visual recognition of faces, it has been shown that better face recognition occurs when we associate a face with a name or occupation (Schwartz & Yovel, 2016) or if we make social judgements about the faces during learning (Mattarozzi et al., 2019; Schwartz & Yovel, 2019b). However, the paradigms used in these studies involve viewing a limited number of static images that are associated with arbitrary conceptual knowledge about the person. So, it remains unclear how the recognition of faces unfolds in more naturalistic viewing conditions and over longer time periods. A recent study addressed this issue by measuring face recognition of actors in the TV series Game of Thrones (Devue et al., 2019). They found that the faces of the lead actors were recognized better than other actors and that recognition performance was generally better for faces viewed more recently. Although better recognition could reflect increased conceptual knowledge, it could just reflect increased perceptual experience about the person. A key feature of our paradigm is that the visual exposure to faces is the same in both the Original and Scrambled sequences. This means that the difference in face recognition between participants in the two groups reflects differences in conceptual knowledge.

Although our results show an effect of conceptual knowledge in face recognition, visual experience with faces plays a key role in becoming familiar with faces (Devue et al., 2019; Memon et al., 2003; Roark et al., 2006), with exposure to within-person variability being particularly important for learning new faces (Andrews et al., 2015; Burton et al., 2016; Murphy et al., 2015; Ritchie & Burton, 2017). Indeed, recognition of faces in natural viewing is better when the appearance is similar to the appearance at encoding (Devue et al., 2019). Consistent with our third pre-registered hypothesis, we found that faces were better recognised when the appearance was consistent with that at encoding. For example, we found that faces taken from actors in LoM were more recognisable if they were In Show than if they were Out of Show images. This effect of appearance at encoding could reflect the relative visual similarity of the faces presented during recognition. However, it might also reflect other information in the image. For example, reinstating the context in which a face was learnt improves recognition (Hanczakowski et al., 2015; Reder et al., 2013). We were not able to find support for our final pre-registered hypothesis that the effect conceptual knowledge should be greater for images whose appearance was similar to encoding after consolidation in memory. To test this, we compared the difference in face recognition between the Original and Scrambled groups for In Show compared to Out of Show images at the delayed timepoint. We did not find that In Show images showed a greater effect of conceptual knowledge compared to Out of Show images after a delay.

A hallmark of familiar face recognition is the ability to recognise faces across substantial visual changes in the image (Hancock et al., 2000; Young & Burton, 2017). Computational models of face recognition have suggested that purely bottom-up image-based descriptions do not provide sufficient information for recognition and that top down processes are necessary to learn within-person variability (Kramer et al., 2018). However, other studies using deep convolutional neural networks show that recognition can be based purely on visual information (Blauch et al., 2021). Nevertheless, it remains unclear how familiar face recognition is achieved in humans and whether non-visual information plays an important role (Rossion, 2018; Yovel & Abudarham, 2021). Our results suggest that the increased conceptual information that accompanies our experience with faces during natural viewing is important in linking visually dissimilar faces into a robust, long-term representation that can be used for recognition. This fits with neuroimaging studies which have shown that the neural response to familiar faces engages non-visual regions of the brain (Gobbini & Haxby, 2007; Kovács, 2020; Noad et al., 2024; Visconti di Oleggio Castello et al., 2017; Visconti di Oleggio Castello et al., 2021) and behavioural studies that show the perception of identity can be influenced by non-visual conceptual information (Oh et al., 2021). Future studies using neuroimaging methods should be able to reveal whether the changes that occur as we become familiar with faces during natural viewing become more evident in visual or non-visual regions of the brain.

In conclusion, we show that conceptual knowledge was greater in participants who viewed a movie in its original sequence compared to a scrambled sequence. Despite the fact that the overall perceptual experience was the same in all participants, higher face recognition was evident in participants who viewed the original sequence. This shows an effect of conceptual knowledge on face recognition. However, planned comparisons failed to show that this effect was more sustained over time in participants who viewed the movie in the original sequence. This study provides new insights into the role of conceptual knowledge in face recognition during natural viewing.

Chapter 5

Conceptual knowledge shapes the neural representations of learned faces in non-visual regions of the brain

5.1 Abstract

Face recognition is a fundamental aspect of human social interaction, yet the mechanisms underlying how we become familiar with faces are not fully understood. While previous research has emphasized the importance of perceptual experience, everyday face recognition is accompanied by an accumulation of conceptual knowledge about individuals. This study investigated the influence of conceptual knowledge on neural responses to faces using a naturalistic viewing paradigm. Participants viewed an encoding movie from the TV series Life on Mars. Conceptual information was modulated by presenting the movie to participants in either its original sequence, or a scrambled sequence. Although participants in both groups had the same overall perceptual experience, this manipulation had a significant effect on the conceptual understanding of events. After a delay, participants viewed a new movie featuring characters from Life on Mars while neural activity was measured using functional magnetic resonance image (fMRI). Inter-subject correlation (ISC) was used to compare neural responses between participants in the Original or Scrambled groups. No significant differences were observed between the Original and Scrambled groups in core face-selective regions. This aligns with the fact that overall exposure to faces was consistent across groups, ensuring that our manipulation did not impact visual processing of faces. In contrast, higher ISCs were observed in the Original group within a network of regions that are typically associated with processing person knowledge. This network of regions was also able to discriminate the identity of the key characters based on the response to the faces. These findings suggest that conceptual information plays an important role in learning new faces, with the underlying neural processes extending beyond the core face-selective areas.

5.2 Introduction

Recognizing familiar faces is a fundamental cognitive function that plays a pivotal role in social interaction and communication. However, the process of recognising a face under natural viewing conditions poses considerable computational challenges for the brain. As observers move or as environmental conditions fluctuate, significant changes occur to the image of a face. Despite these challenges, most humans demonstrate a remarkable ability to recognise the faces of people that they are familiar with (Bruce, 1982; Mike Burton, 2013). In contrast, the task of matching unfamiliar faces is prone to errors, even when the image undergoes relatively minor changes (Hancock et al., 2000). Despite the well-established difference in the ability to recognise familiar compared to unfamiliar faces, the mechanisms underlying the process of becoming familiar with a person's face are not fully understood.

Cognitive models of face perception propose that the process of familiarization with a face involves the development of image-invariant visual representations (Bruce & Young, 1986; Young & Burton, 2017). These image-invariant representations, known as face recognition units (FRUs), are thought to underlie the sensation of familiarity (Young et al., 1985). During the familiarisation process, it is hypothesized that these image-invariant representations emerge through repeated exposure to different visual instances of a person's face (Burton et al., 2011; Kramer et al., 2018). Empirical evidence supports this theoretical framework, demonstrating that increased visual exposure enhances facial recognition accuracy (Memon et al., 2003; Roark et al., 2006). Moreover, studies suggest that exposure to a greater variety of images from the same face further improves recognition performance (Juncu et al., 2020; Murphy et al., 2015; Ritchie & Burton, 2017). This research highlights the importance of both the quality and quantity of perceptual experience in the development of face familiarity.

However, in real life, increased perceptual exposure to a face is accompanied by a corresponding increase in conceptual information about the individual. This conceptual information includes knowledge about the person and the nature of our relationship with them. Emerging evidence suggests that conceptual knowledge may play a critical role in becoming familiar with a face. Several studies have demonstrated that recognition accuracy improves when participants engage in semantic judgements while learning new faces, as opposed to purely visual tasks (Bower & Karlin, 1974; Patterson & Baddeley, 1977; Schwartz & Yovel, 2016, 2019a). Furthermore, face recognition is facilitated when a familiar face is preceded by another face associated with similar conceptual knowledge (Bruce & Valentine, 1986).

Previous studies investigating the role of conceptual knowledge in face recognition have largely focussed on the response to static faces paired with arbitrary conceptual knowledge. However, in everyday situations, faces are encountered within dynamic and context-rich scenes, where conceptual information about individuals is integrated within an evolving narrative (Jääskeläinen et al., 2021; Redcay & Moraczewski, 2020). To bridge this gap, a recent study used a naturalistic viewing paradigm in which participants viewed a movie from the TV series Life on Mars, either in its original sequence or in a scrambled sequence (Noad & Andrews, 2024). Both groups were exposed to the same overall visual content, but conceptual coherence was maintained only in the original sequence. Nevertheless, participants who viewed the original sequence developed better recognition of the faces, which was still evident after a delay of a few weeks. This suggests that conceptual knowledge may play an important role in familiar face recognition.

The aim of this study was to explore the role of conceptual knowledge in shaping neural responses to newly learned faces using a naturalistic viewing paradigm. Neural models propose that face recognition engages a core network of regions in visual cortex (Duchaine & Yovel, 2015; Haxby et al., 2000; Ishai, 2008). For example, the fusiform face area (FFA) is thought to play a critical role in the identification of individuals. However, while some studies support the involvement of the FFA in distinguishing familiar from unfamiliar faces, the evidence is inconsistent. A number of studies have reported no significant differences in FFA activation when participants view familiar compared to unfamiliar faces (Davies-Thompson et al., 2009; Davies-Thompson et al., 2013; Gobbini et al., 2004; Gorno-Tempini & Price, 2001; Leveroni et al., 2000). Moreover, even when familiarity effects are observed in the FFA, these effects tend to be modest in magnitude (Andrews et al., 2010; Axelrod & Yovel, 2015; Ewbank & Andrews, 2008; Sergent et al., 1992; Weibert & Andrews, 2015). These findings suggest that other neural mechanisms, beyond the core face-processing network, may also play a significant role in the recognition of familiar individuals.

In contrast to core face-selective regions, an extended network of regions in non-visual areas of the brain have been shown to have a higher response to familiar compared to unfamiliar faces (Gobbini et al., 2004; Gorno-Tempini & Price, 2001; Leveroni et al., 2000; Visconti di Oleggio Castello et al., 2017). Moreover, the neural activity within these regions has been shown to encode information relevant to the recognition of familiar face identities (Visconti di Oleggio Castello et al., 2021). Regions of the extended face network are thought to be essential for processing conceptual information associated with a person, including semantic, episodic and affective knowledge (Gobbini & Haxby, 2007; Haxby et al., 2000; Ishai, 2008; Kovács, 2020). A recent study employing a naturalistic viewing paradigm explored the neural correlates of familiar face recognition by presenting the TV series Game of Thrones to participants, finding that the neural responses were more synchronized in extended face regions among participants familiar with the series compared to those who were unfamiliar (Noad et al., 2024).

Here, we used a naturalistic viewing paradigm in which participants viewed an encoding movie from the TV series Life on Mars in its original sequence or in a scrambled sequence (see Noad and Andrews, 2024). After a delay of 4 weeks, we measured neural responses to a new movie featuring the main characters using functional magnetic resonance imaging (fMRI). Our goal was to determine whether conceptual knowledge affects the neural representations in the core or extended face processing networks. The data were analysed using inter-subject correlation (Hasson et al., 2004; Noad et al., 2024), which we predicted would be higher in the Original compared to the Scrambled group. Finally, we used MVPA to ask whether regions that show a group difference are able to discriminate the identity of faces.

5.3 Methods

5.3.1 Participants

We recruited participants into 2 groups: (1) participants who watched the encoding movie in the Original order, and (2) participants who watched the encoding movie in a Scrambled order.

A total of 38 participants (median age: 20 years, age range: 18-31, 13 male) took part in this study, with 19 participants assigned to the Original condition and 19 to the Scrambled condition. All participants were neurologically healthy (as indicated by self-report), right-handed and had normal or corrected-to-normal vision. None of the participants had prior familiarity with the TV show Life on Mars, which was used as the stimulus in this study. To ensure that participants had normal face recognition abilities, each individual completed the Cambridge Face Memory Test (CFMT; Duchaine & Nakayama, 2006). A minimum score of 65% was required for inclusion. The mean CFMT score for the sample was 79.9% (standard deviation: 9.3%). The sample size was determined *a priori* based on previous fMRI studies using naturalistic stimuli and similar analysis methodologies (Andrews et al., 2019; Chen et al., 2017; Hasson et al., 2009; Hasson, Yang, et al., 2008). Written informed consent was obtained from all participants and the study protocol was approved by the York Neuroimaging Centre Ethics Committee.

5.3.2 Encoding Movie

Approximately 4 weeks before the fMRI scan session, participants viewed an encoding movie outside of the scanner. The specific version of the movie they watched depended on their assigned experimental condition: (1) Original, or (2) Scrambled group (Figure 5.1a). Both versions of the movie were 20 minutes in duration (1170 seconds), constructed from audio-visual clips from the first episode of the BBC TV series Life on Mars. In the Original condition, the clips were presented in the original order, preserving the coherent narrative structure of the episode. A total of 14 clips were used, with an average duration of 84 seconds (range 39 to 228 seconds). Conversely, in the Scrambled condition, the same clips were presented in a randomized order, disrupting the narrative coherence. The clips were assigned a random order for the Scrambled condition, with longer clips subdivided into shorter segments, resulting in a mean clip length of 39 seconds. Importantly, the overall visual input remained identical between both conditions, ensuring that participants in both were exposed to the same content, but with varying narrative coherence.

5.3.3 Conceptual Knowledge

After viewing the encoding movie, participants underwent an assessment to evaluate their conceptual understanding of the presented clips. The assessment included both a free-recall task, in which participants were instructed to describe the stimulus in as much detail as possible, and a set of 8 structured questions targeting specific events in the video. Each question was accompanied by a static image representing the relevant event. Performance on these tests was independently evaluated by two raters, who were blind to the experimental condition, using a predefined scoring scheme.

The free recall test was evaluated based on 10 key events that occurred during the encoding video. Raters assigned scores of 0, 1 or 2 for each event, depending on whether the participant provided no description, a partial description, or a full description of the event, giving a maximum possible score of 20. Similarly, the 8 structured questions were scored using the same 0-2 scale, allowing for a maximum score of 16. Inter-rater reliability was evaluated using intra-class correlation coefficient (ICC) with a two-way mixed model and Agreement definition. Excellent agreement was found between raters for the free recall test, with an ICC of .93 and 95% confidence intervals of .87 to .96 ($F(37,37) = 27$, $p < .001$). The structured question test also demonstrated strong reliability, with an ICC of .94 and 95% confidence intervals of .89 to .97 ($F(37,37) = 32$, $p < .001$). Subsequent analyses were based on the average scores across raters.

5.3.4 Face Recognition

Following the encoding phase, Participants completed a recognition memory task involving actors featured in the video clips. Faces were presented individually in a randomized order and remained on screen until a response was made. Participants were instructed to press a button to indicate if the identity of the face corresponded to any of the actors observed in the previously viewed video. The test included static faces of 10 actors from the video, which were extracted from the Life on Mars TV series, but did not correspond to the exact frames shown in encoding video. Another face from each actor, taken from outside of the Life on Mars TV series, was included in the test. For each target actor, two foil images of different individuals were selected to match age, expression, hairstyle, lighting and overall appearance. Sensitivity (*d′*) was calculated for each participant using hit rates (i.e. correct recognition of faces as being present in the movie) and false alarm rates (i.e. incorrect identification of foils as present in the movie). Data for the recognition memory task was unavailable for two participants in the Original condition.

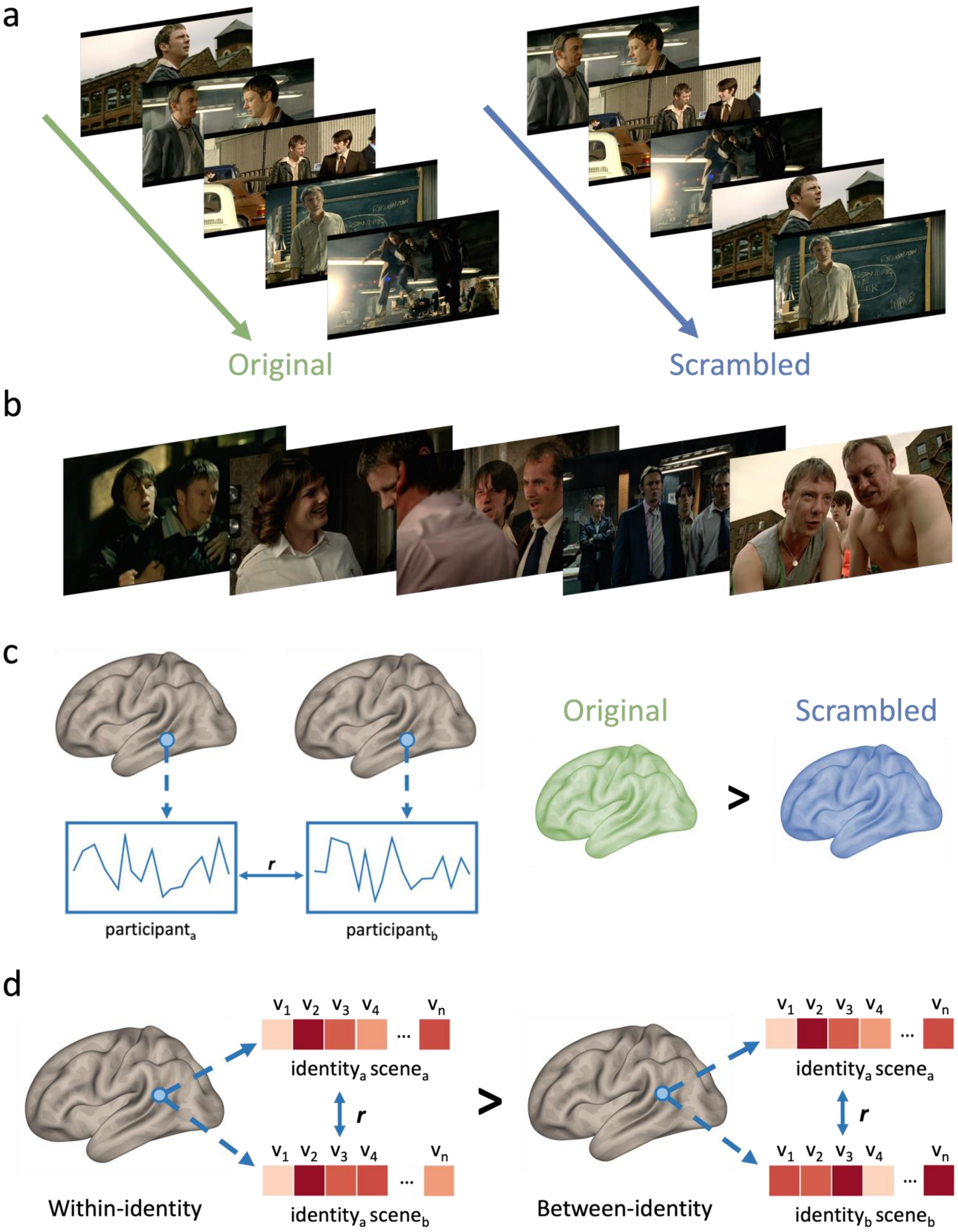


Figure 5.1. Study design and neuroimaging analysis. a) During the learning phase, participants watched an encoding movie from TV show Life on Mars, presented in its Original order or a Scrambled order. Both conditions provided identical visual exposure to the faces of the characters, but the Scrambled condition impaired the ability to accumulate associated conceptual knowledge due to the disordered narrative. **b**) In the recognition phase, participants watched a movie comprising clips from unseen episodes of Life on Mars, while brain activity was measured using fMRI. The clips featured the same characters shown during the learning phase. **c**) Neural responses were analyzed across individuals using inter-subject correlation (ISC, left), in which the time-course of voxel responses were

correlated (r) between individuals. Differences in ISC values were subsequently compared between the Original and Scrambled groups (right). **d**) Patterns of neural response to specific identities in the movie were analysed using multivoxel pattern analysis within each region of interest. The voxelwise pattern of response to the same identity (within-identity) or to different identities (between-identity) were correlated across different scenes. Within-identity correlations were compared to between-identity correlations to identify brain regions showing an identity-specific pattern of response.

5.3.5 Recognition Movie

Approximately four weeks after viewing the encoding movie (mean 31.3 days, range 23-41 days), participants watched a new movie containing previously unseen clips from the first season of Life on Mars while neural activity was recorded using fMRI (Figure 5.1b). The rationale for implementing a delay of 4 weeks was to investigate the enduring effects of narrative structure on recognition memory. Previously, we showed that behavioural differences in face recognition between participants who viewed original or scrambled versions of the encoding video persisted after a similar 4 week interval (Noad & Andrews, 2024). The recognition movie focussed on five main characters from the TV series. The clips were selected from different episodes and, as such, did not form a coherent narrative. The movie was projected onto an in-bore screen at a distance of 57 cm from the participant with the image subtending approximately 38.7 × 22.3 degrees of visual angle. Audio accompanying the movie was played to participants during the scan. The movie was a total of 12 minutes 46 seconds, composed of 14 distinct scenes ranging in length from 4-119 seconds. The movie was presented using PsychoPy (Peirce et al., 2019).

5.3.6 fMRI Data Acquisition

Scanning was conducted using a 3T Siemens Magnetom Prisma MRI scanner equipped with a 64-channel phased array head coil at York Neuroimaging Centre. Functional data were acquired using a gradient-echo echo-planner imaging (EPI) sequence was used to collect data from 60 axial slices, EPI (TR = 2s, TE = 30ms, FOV = 240 x 240 mm, matrix size = 80 x 80, voxel dimensions = 3 x 3 x 3mm, slice thickness = 3mm, flip angle = 80°, phase encoding direction = anterior to posterior, multiband acceleration factor = 2). Additionally, T1-weighted structural images were acquired from 176 sagittal slices (TR = 2300ms, TE = 2.26ms, matrix size = 256 x 256, voxel dimensions = 1 x 1 x 1mm, slice thickness = 1mm, flip angle = 8°). Field maps were collected from 60 slices (TR = 554ms, short TE = 4.90ms, long TE = 7.38ms, matrix size = 80 x 80, voxel dimensions = 3 x 3 x 3mm, slice thickness = 3mm, flip angle = 60°).

fMRI data were analysed using FSL's FEAT v6.0 (http://www.fmrib.ox.ac.uk/fsl; Jenkinson et al., 2012). Preprocessing steps included motion correction, using MCFLIRT (Jenkinson et al., 2002), temporal high-pass filtering (Gaussian-weighted least squares straight line fittings, sigma = 50 s) and slice timing correction. Spatial smoothing was applied at 6mm FWHM Gaussian kernel. Non-brain material was removed using the Brain Extraction Tool (BET; Smith, 2002). Functional data were registered to a high-resolution T1-anatomical image via boundary-based registration (Greve & Fischl, 2009), and subsequently normalized to the standard MNI152 brain template using non-linear registration computed with FNIRT. Field maps were incorporated to correct for distortions in functional images during the registration step.

5.3.7 Intersubject Correlation

To examine brain regions that reflected group differences in conceptual information processing, we measured inter-subject correlations (ISC) in neural response across participants within each group during the Recognition Movie. To compute the ISCs, timeseries from each voxel were converted to % signal change, and 6 head motion parameters were regressed out. The resulting time series were then correlated (Pearson's *r*) with corresponding voxels from other participants in the same group, using a leave-one-out approach. Specifically, for each participant, the timeseries of each voxel was correlated with the average timeseries of the group (N–1) in each corresponding voxel. A Fisher's *z* transform was applied to the correlations.

To compare the Original and Scrambled groups, a permutation test (BrainIAK; Kumar et al., 2021) was used to assess significance of group differences in the ISCs by randomising the group assignment of participants 10000 times to create a null distribution. From this, whole-brain *p*-statistic maps were created for the contrast of Original - Scrambled, which we represented in negative log units. A cluster correction for multiple comparisons was then applied to these maps using an initial cluster forming threshold of $-\log_{10}(p) > 2$ ($p < .01$) and a cluster significance threshold of $p < .05$.

5.3.8 Multivoxel Pattern Analysis

To investigate whether specific brain regions exhibited identity-specific patterns of activity, we compared the pattern of neural response to faces from the 5 main characters (Sam, Gene, Ray, Chris and Annie) in Life on Mars (Figure 5.1d). The movie stimulus was divided into 14 scenes (7 odd, 7 even). The occurrences of the main characters were tagged in the odd and even scenes. For a character to be tagged, it had to include a clear image of the face that was present for at least 2 seconds. To ensure accuracy, two independent raters conducted the tagging prior to resolving any discrepancies in timing. The tagging facilitated the creation of separate regressors for each character in the odd scenes and another set for the even scenes. These regressors, along with their temporal derivatives and head motion regressors were then entered into a first-level GLM analysis (Woolrich et al., 2001). This analysis generated 10 parameter estimates for each participant, which were subsequently normalized by subtracting the mean of the estimates and transforming them into MNI space.

These parameter estimates were then used for multivoxel pattern analysis (MVPA). For each region of interest (ROI), Pearson's correlation coefficients were calculated between the patterns of the parameter estimates for the same versus different identities. These comparisons were always performed between odd and even scenes. Given that the other characters did not feature prominently in the encoding movie, we focused primarily on the two main characters (Sam and Gene). Correlations were performed on the patterns from the core face regions (defined from a localizer scan) and the extended network region (defined from the ISC analysis). The two within-identity correlations (Sam-odd vs Sam-even and Gene odd vs Gene even) were compared against 16 between-identity correlations (odd-even correlations of both main characters with each of the other characters across odd and even scenes). Within- and between-identity correlations were Fisher's *z* transformed and averaged for each participant. To test for identity-specific patterns of activity, the within- and between-identity correlations were compared using paired sample t-tests within each group. Greater correlations for within-identity comparisons relative to between-identity comparisons would indicate a significant identity-specific response.

5.3.9 Localizer Scan

A localizer scan was conducted to delineate face-selective and scene-selective regions of interest. The scan comprised 3 stimulus conditions: faces, scenes, and phase scrambled faces. Face stimuli were presented in three different viewpoints (-45°,0°,45°) and were sourced from the Radbound database of face stimuli (Langner et al., 2010). Faces were displayed against a 1/f amplitude-mask background. Scrambled faces were created by randomising the phase spectra while maintaining the amplitude spectra of the face images including the amplitude mask background. Scene stimuli included indoor and outdoor images sourced from the SUN database (Xiao et al., 2010). Each image subtended approximately 8.4 x 8.4 degrees of visual angle. 4 images from each condition were presented in each block for 600ms with a 200ms ISI for a total of 9 seconds per block. 9 blocks were presented for each condition in a pseudorandomized order, for a total scan time of 244s. To ensure participant engagement, they were required to respond via button press whenever a change in colour of the fixation cross occurred.

Boxcar models of each stimulus block were convolved with a single-gamma haemodynamic response function to create regressors for each condition. These were then incorporated into a first-level GLM analysis (Woolrich et al., 2001) alongside their temporal derivatives and confound regressors for 6 head motion parameters. Individual participant data were subsequently entered into a higher-level group analysis using a mixed-effects GLM using FLAME (Woolrich et al., 2004). Face-selective regions were identified through contrasts of the response to faces against the other conditions (faces > scenes + scrambled face). ROIs were defined using a clustering algorithm that iteratively adjusted the statistical threshold to grow clusters of 250 spatially contiguous voxels (2000 mm^3) around seed voxels within each region. The Fusiform Face Area (FFA), Occipital Face Area (OFA) and Superior Temporal Sulcus (STS) were defined as face-selective regions.

5.4 Results

5.4.1 Conceptual Knowledge

We first investigated whether manipulating the order of events in the encoding phase would affect conceptual knowledge. To assess this, we compared narrative scores between the Original and Scrambled groups on the free recall and structured questions. Consistent with our prior findings (Noad & Andrews, 2024), the Original group demonstrated significantly higher scores on both the free recall task (*t*(33.8) = 10.0, *p* < .001 , *d* = 3.24) and structured question task (*t*(29.2) = 6.3, *p* < .001, *d* = 2.05; Figure 5.2a). These findings suggest that presenting events in their original coherent order fosters a deeper understanding of conceptual knowledge.

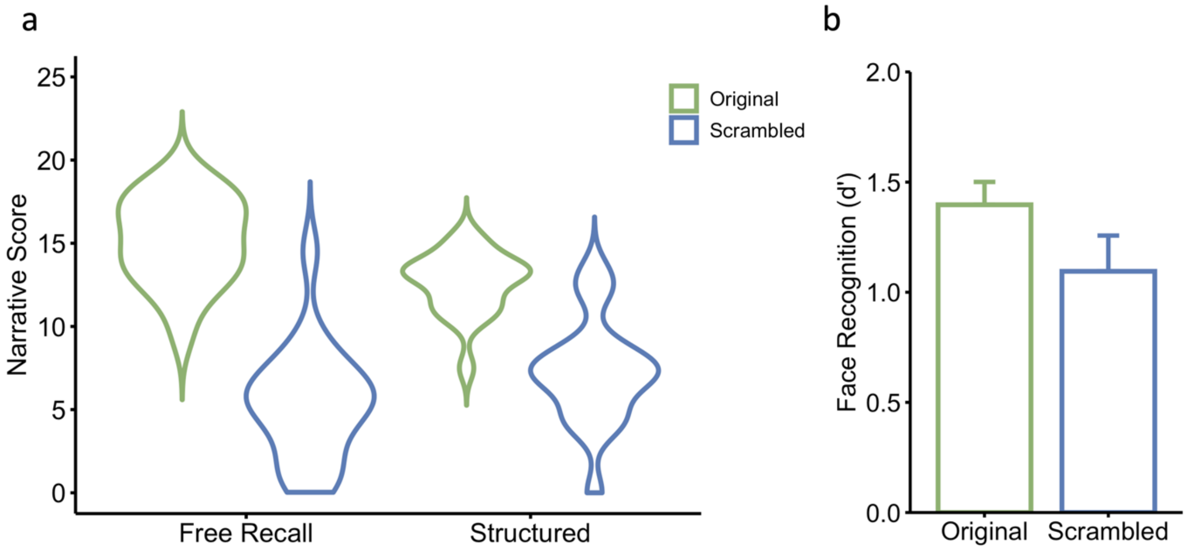


Figure 5.2. Behavioural measures. a) Greater narrative scores on both measures of conceptual understanding were found for participants in the Original group compared to the Scrambled group. **b**) Greater recognition of the faces from the movie was found for participants in the Original group compared to the Scrambled group. However, the difference was not significantly different.

5.4.2 Face recognition

In a previous study, we demonstrated that the level of conceptual knowledge influences face recognition, with higher accuracy observed in the Original condition (Noad & Andrews, 2024). In the current study, we again compared behavioural face recognition scores on the faces from the movie between the Original and Scrambled groups. While participants in the Original group exhibited higher face recognition scores than those in the Scrambled group (Figure 5.2b), this difference did not reach statistical significance (*t*(30.1) = 1.57, *p* = .064, *d* = 0.51). Nevertheless, the trend was in the expected direction and the effect size was comparable (current study: Cohen's d = 0.51; Noad and Andrews, 2024: Cohen's d = 0.33). The difference between studies presumably reflects a difference in sample size (current study: n=38; Noad and Andrews, 2024: n=200).

5.4.3 Inter-subject correlation

To further investigate the effect of conceptual knowledge on face processing, we examined intersubject correlations (ISC) while participants viewed a previously unseen movie containing clips that prominently featured the faces of the main characters. We compared ISCs between participants in the Original and Scrambled groups to assess how narrative coherence during encoding influences neuronal synchronization across subjects when viewing faces during recognition. Regions showing significantly higher ISCs in the Original group were evident across the temporal, parietal and frontal lobes in both hemispheres (red-yellow; Figure 5.3 and Table 5.1). These areas included key regions of the extended face network, such as the amygdala, insula, precuneus, medial prefrontal cortex and the temporal-parietal junction (Gobbini and Haxby, 2007). In contrast, no significant ISCs were found for the Scrambled group compared to the Original group, suggesting that the scrambled narrative impaired the synchronization of the face processing across subjects. The location of the core face-selective regions (blue) defined by an independent localiser scan shows that there was no overlap between face-selective regions and those regions showing higher ISC in the Original group (see Fig. 5.3 and Table 5.2). This indicates that the enhanced ISC associated with conceptual knowledge involves a broader network beyond the core face-selective regions.

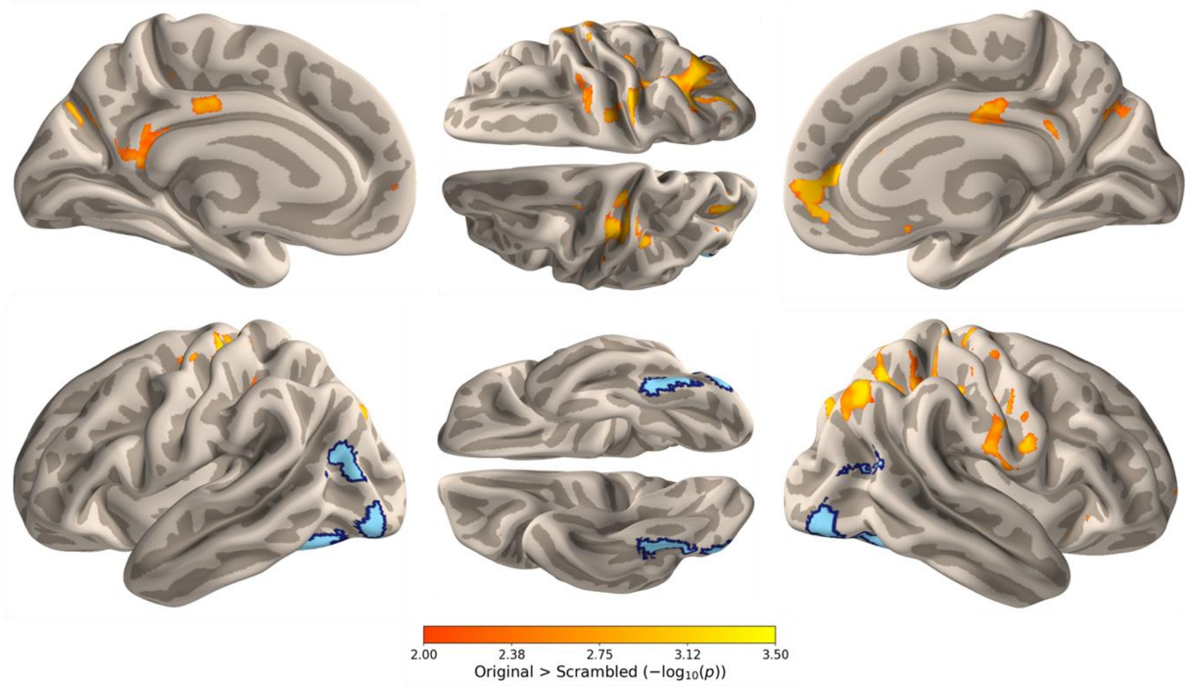


Figure 5.3. ISC comparison between participants in the Original and Scrambled groups when viewing a movie containing the faces of the main characters. Voxels in temporal, parietal and frontal cortex showed higher ISC for the Original group (red-yellow). In contrast, the Scrambled group showed no greater ISCs. The core face-selective regions (blue) were defined by an independent localiser scan. There was no overlap between the core face-selective regions and the regions from the ISC analysis.

Table 5.1. Regions showing greater ISCs for participants in the Original group compared to the Scrambled group.

Region	Hemisphere	*x*	*y*	*z*	*p min (-log)*	*Size*
Accumbens	L	-11	17	-3	2.16	109
	R	10	12	-8	2.30	102
Amygdala	L	-21	0	-16	2.10	102
Anterior Cingulate	R	16	22	30	2.40	100
Frontal Pole	L	-14	68	8	2.00	98
	R	18	68	2	2.40	98
Insula	R	26	15	-11	2.00	93
Mid Cingulate	L	-2	-20	37	2.00	91
	R	6	-11	30	2.70	148
Medial Prefrontal Cortex	L	-15	51	-7	2.00	88
	R	9	53	3	3.00	263
Posterior Cingulate	L	-9	-47	20	2.52	92
	R	5	-42	23	2.40	102
Postcentral Gyrus	L	-31	-26	59	3.00	244
	R	26	-29	71	2.70	109
Postcentral Gyrus 2	R	66	-9	18	2.70	100
Precentral Gyrus	L	-20	-24	64	2.70	218
	R	22	-23	72	2.70	105
Precentral Gyrus 2	R	60	1	24	2.30	111
Precuneus	L	-11	-66	31	2.40	104
	R	14	-62	35	2.52	78
Precuneus 2	L	-21	-78	35	3.00	95
	R	26	-78	35	2.70	117
Superior Frontal Gyrus	L	-19	-9	57	2.00	36
	R	28	-11	60	2.52	105
Superior Parietal Lobule	R	27	-54	48	2.70	175
Supramarginal	L	-34	-37	39	3.00	98
	R	39	-27	38	3.00	124
Supramarginal 2	R	46	-29	48	2.52	149
Temporal Parietal Junction	L	-24	-74	49	2.40	100
	R	41	-63	48	3.00	367

Table 5.2. MNI coordinates of maximum voxel of face-selective regions (occipital face area: OFA; fusiform face area: FFA; superior temporal sulcus: STS) defined by an independent localiser scan (faces > scrambled faces + scenes) with minimum z score from the localiser contrast, and percent overlap of these ROIs with the regions found in the ISC analysis

Region	Hemisphere	*x*	*y*	*z*	Mask size (voxels)	Threshold (z)	Overlap (%)
OFA	L	-42	-84	-10	250	5.71	0
	R	46	-78	-6	250	5.94	0
FFA	L	-42	-48	-22	251	5.05	0
	R	42	-52	-18	250	5.29	0
STS	L	-48	-72	18	250	3.98	0
	R	58	-62	16	249	4.17	0

5.4.4 MVPA

We next examined whether patterns of neural activity could discriminate between the faces of the main characters from Life on Mars. The occurrence of each of the five main characters was tagged across all scenes in the recognition movie (Lally et al., 2023; Milivojevic et al., 2016). The response to each identity was then measured independently across odd and even scenes. To assess identity-specific neural representations, we computed correlations between patterns of response to the same identity (within-identity) across odd and even scenes, and compared them to correlations between responses to different identities (between-identity) across odd and even scenes. The within-identity comparisons were restricted to the two main characters (Sam and Gene) as they appeared prominently in the encoding movie. This analysis was conducted in the core face regions and in the extended network of regions revealed in the ISC analysis. An identity-specific representation is evident if within-identity correlations were significantly higher than between-identity correlations. To test for the presence of identity-specific patterns, we performed a 2 x 2 x 2 mixed ANOVA with Identity (within, between), Group (original, scrambled) and Region (core, extended) as factors. A significant main effect of Identity was found, with within-identity correlations significantly greater than between-identity correlations (within-identity M: 0.13, SE: 0.03; between-identity M: -0.07, SE: 0.01), demonstrating robust identity-specific representations ($F(1,36) = 29.1$, $p < .001$, $\eta^2 = .447$). There was also a significant main effect of Region ($F(1,36) = 19.5$, $p < .001$, $\eta^2 = .351$), with higher correlations in the extended network (M = 0.08, SE = 0.02) compared to core face regions (M = -0.01, SE = 0.02).

To determine whether the identity effects were modulated by conceptual knowledge, we conducted a Group (original, scrambled) x Region (core, extended) mixed ANOVA on the within-identity minus between-identity differences for participants in the Original and Scrambled groups. Although the extended regions exhibited a larger within-between identity difference compared to the core regions (Figure 5.4), the main effect of region was not significant ($F(1,36) = 2.45$, $p = .120$, $\eta^2 = .066$). Similarly, there was no significant main effect of Group ($F(1,36) = 0.1$, $p = .730$, $\eta^2 = .003$), or Group * Region interaction ($F(1,36) = 0.2$, $p = .673$, $\eta^2 = .005$).

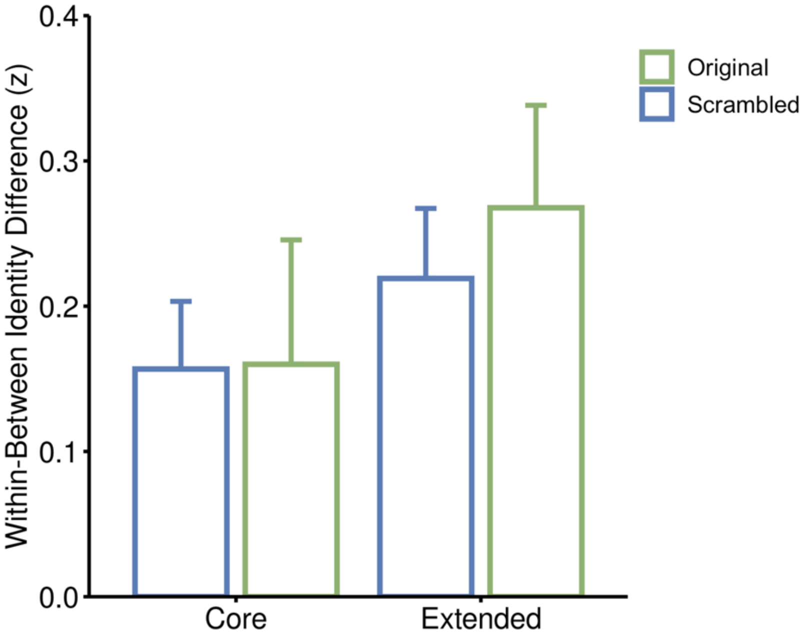


Figure 5.4. Identity-specific neural patterns for the Original and Scrambled groups in core face regions and the extended network found in the ISC analysis. Identity patterns were greater in the extended regions, although this is not significantly different. Error bars denote standard error.

We then examined the effect of identity comparing within-identity and between identity correlations across individual regions within the core face-selective network (Table 5.3) and regions of the extended network identified from the ISC analysis (Table 5.4) for both the Original and Scrambled groups. Additionally, we compared the (within-minus-between) identity effect between the two groups for each region. In the core face-selective regions, only the right and left FFA demonstrated a consistent identity effect across both the Original and Scrambled groups. None of the core regions showed significant differences in identity representation between the Original and Scrambled groups. A consistent identity effect across the Original and Scrambled groups was observed in several regions identified through the ISC analysis. These regions included the accumbens, amygdala, insula, posterior cingulate, post-central gyrus, pre-central gyrus and supramarginal gyrus. However, there was no significant difference in the identity representation between the Original and Scrambled groups in any of these regions.

Table 5.3. Identity-specific representation results for core face-selective areas (occipital face area: OFA; fusiform face area: FFA; superior temporal sulcus: STS). Z denotes mean difference in correlation (Fisher's z) value of within-identity versus between-identity.

		Original (within>between)			**Scrambled (within>between)**			**Original (within – between) > Scrambled (within – between)**		
Region	**Hemisphere**	***z***	***t***	***p***	***z***	***t***	***p***	***z***	***t***	***p***
OFA	L	0.19	1.91	.072	0.13	1.86	.079	0.05	0.45	.657
	R	0.02	0.22	.830	0.02	0.35	.727	0.00	0.01	.991
FFA	L	0.40	3.35	**.004**	0.30	3.89	**.001**	0.10	0.70	.488
	R	0.37	3.26	**.004**	0.26	3.05	**.007**	0.11	0.80	.430
STS	L	0.09	0.77	.448	0.17	1.68	.110	-0.07	-0.47	.645
	R	0.23	2.36	**.030**	0.18	1.63	.120	0.05	0.34	.733

Table 5.4. Identity-specific representation results for extended network of regions found in the ISC analysis. Z denotes mean difference in correlation (Fisher's z) value. P values are uncorrected for multiple comparisons.

		Original (within>between)			Scrambled (within>between)			Original (within – between) > Scrambled (within – between)		
Region	**Hemisphere**	***z***	***t***	***p***	***z***	***t***	***p***	***z***	***t***	***p***
Accumbens	L	0.25	2.46	**.024**	0.25	2.76	**.013**	0.00	-0.03	.973
	R	0.29	2.69	**.015**	0.27	3.15	**.005**	0.02	0.16	.870
Amygdala	L	0.25	2.32	**.032**	0.37	5.10	**.000**	-0.11	-0.87	.392
Anterior Cingulate	R	0.19	1.98	.063	0.12	1.20	.244	0.08	0.55	.583
Frontal Pole	L	0.30	2.26	**.036**	0.00	0.04	.970	0.29	1.56	.127
	R	0.20	1.50	.151	0.02	0.23	.818	0.18	1.14	.263
Insula	R	0.35	4.87	**.000**	0.23	2.79	**.012**	0.12	1.06	.299
Mid Cingulate	L	0.16	1.48	.156	0.25	2.96	**.008**	-0.09	-0.66	.511
	R	0.09	0.75	.464	0.14	1.23	.235	-0.04	-0.26	.797
Medial Prefrontal Cortex	L	0.24	2.08	.052	0.17	2.30	**.034**	0.08	0.55	.589
	R	0.05	0.37	.714	0.13	1.38	.184	-0.08	-0.49	.626
Posterior Cingulate	L	0.28	2.76	**.013**	0.25	3.41	**.003**	0.03	0.24	.813
	R	0.28	2.48	**.023**	0.24	2.21	**.040**	0.04	0.26	.799
Postcentral Gyrus	L	0.25	2.68	**.015**	0.21	2.76	**.013**	0.04	0.33	.743
	R	0.46	3.17	**.005**	0.06	0.47	.641	0.39	1.98	.055
Postcentral Gyrus 2	R	0.20	2.50	**.023**	0.27	2.56	**.020**	-0.07	-0.51	.616
Precentral Gyrus	L	0.39	3.98	**.001**	0.27	2.83	**.011**	0.11	0.84	.407
	R	0.46	2.92	**.009**	0.26	1.98	.063	0.21	1.02	.316
Precentral Gyrus 2	R	0.14	1.22	.238	0.40	4.41	**.000**	-0.26	-1.79	.083
Precuneus	L	0.14	1.11	.280	0.02	0.17	.871	0.11	0.59	.560
	R	0.12	0.96	.349	0.08	0.50	.623	0.04	0.21	.836
Precuneus 2	L	-0.03	-0.19	.851	0.10	1.15	.266	-0.12	-0.77	.445
	R	0.07	0.42	.679	0.17	1.23	.235	-0.10	-0.49	.630
Superior Frontal Gyrus	L	0.60	5.28	**.000**	0.29	1.88	.076	0.31	1.61	.117
	R	0.37	3.66	**.002**	0.09	0.85	.409	0.28	1.92	.063
Superior Parietal Lobule	R	0.24	1.81	.087	0.43	4.97	**.000**	-0.18	-1.16	.255
Supramarginal	L	0.19	1.46	.161	0.21	1.68	.110	-0.02	-0.13	.898
	R	0.26	2.35	**.030**	0.42	5.82	**.000**	-0.17	-1.26	.217
Supramarginal 2	R	0.19	2.37	**.029**	0.40	3.71	**.002**	-0.21	-1.57	.126
Temporal Parietal Junction	L	0.30	1.83	.084	0.25	2.66	**.016**	0.05	0.25	.807
	R	0.32	3.36	**.004**	0.15	1.74	.099	0.17	1.34	.188

5.5 Discussion

Face recognition plays a crucial role in social interaction, yet the neural mechanisms underlying how we become familiar with faces are not fully understood. While existing research has emphasized the role of perceptual experience, face recognition in real-world contexts also involves the integration of conceptual information about the person. In the present study, participants viewed an encoding movie from the TV series Life on Mars. This enabled faces to be encountered in a dynamic, context-rich environment, in which the integration of conceptual knowledge about individuals could occur within an evolving narrative. Conceptual information was manipulated by presenting the movie to participants in either its original sequence, or a scrambled sequence. Both groups were exposed to the same perceptual input, yet this manipulation had a significant effect on the conceptual understanding of events. In previous work, we demonstrated that participants who viewed the original, coherent sequence of the movie exhibited better conceptual understanding of the narrative, which was then associated with enhanced face recognition, persisting for several weeks (Noad & Andrews, 2024).

To investigate the effect of conceptual information on neural responses to faces, participants viewed a previously unseen (recognition) movie featuring the faces of the main characters after a delay of approximately 4 weeks while brain activity was measured using fMRI. To assess how narrative coherence during encoding modulates neuronal activity to faces during the recognition movie, we measured the similarity in response across the brain between participants in each group using inter-subject correlation (ISC). Differences in ISC between the Original and Scrambled groups were found within a network of regions beyond visual cortex which have been previously implicated in familiar face processing (Gobbini & Haxby, 2007; Haxby et al., 2000; Ishai, 2008; Kovács, 2020). For example, higher ISCs were found in the Original group in regions which are associated with theory of mind (Frith & Frith, 1999) and the perception of personality traits (Gobbini et al., 2004; Raykov et al., 2021; Visconti di Oleggio Castello et al., 2017), such as the temporo-parietal junction, anterior cingulate and medial prefrontal cortex. A similar modulation of ISC by conceptual knowledge was observed in the posterior cingulate and precuneus, which have previously been linked to memory retrieval for faces (Dickerson & Eichenbaum, 2010; Rugg et al., 2002; Silson et al., 2019), and the representation of person knowledge (Afzalian & Rajimehr, 2021; Ragni et al., 2021; Thornton & Mitchell, 2017). Additionally, neural responses in the insula, accumbens and amygdala were influenced by conceptual knowledge, likely reflecting affective responses to familiar faces (Gobbini et al., 2004; Harris et al., 2012a; Ramon & Gobbini, 2018).

We also observed effects of conceptual understanding in the precentral and postcentral gyri. Although these regions are typically associated with motor and somatosensory processing, previous studies have reported responses to faces in both the precentral gyrus (Bayer et al., 2021; Rossion et al., 2012; Sarkheil et al., 2013; Taylor et al., 2009) and postcentral gyrus (Cao et al., 2018; Heberlein & Atkinson, 2009; Kragel & LaBar, 2016; Tsantani et al., 2019; Van de Riet et al., 2009). A recent neuroimaging study utilizing a natural viewing paradigm also identified familiarity-related responses in these regions (Noad et al., 2024). These findings suggest that the precentral and postcentral gyri may be involved in a distributed network supporting the representation of faces.

In contrast to our findings in non-visual brain regions, we did not observe any significant effect of conceptual understanding within the core face-selective regions. These regions are primarily involved in the visual representation of faces, yet their precise role in face recognition remains a matter of debate. Some studies have reported that core face-selective regions are capable of distinguishing familiar from unfamiliar faces (Sergent et al., 1992; Weibert & Andrews, 2015), while others find no significant difference in response between familiar and unfamiliar faces (Gobbini et al., 2004; Gorno-Tempini & Price, 2001; Leveroni et al., 2000). This inconsistency suggests that the core face-selective regions may not play a central role in the recognition of familiar faces.

A range of evidence suggests that memory retention is not solely determined by the perceptual exposure, but critically depends on the depth of processing during encoding (Bower & Karlin, 1974; Craik, 2002; Craik & Lockhart, 1972). These findings have been integrated into the levels of processing framework. One potential explanation is that conceptual knowledge may enhance the perceptual processing of stimuli, which in our paradigm could lead to more robust representations of learned faces within the core face-selective regions of the visual cortex (Oh et al., 2021; Winograd, 1981). Alternatively, conceptual knowledge could modulate activity in brain regions directly associated with person knowledge related to a face (Gobbini & Haxby, 2007; Haxby et al., 2000; Ishai, 2008; Kovács, 2020). Our results lend support to this latter hypothesis, consistent with previous research showing that the social evaluation of faces during learning enhances recognition and engages non-visual, social-processing regions of the brain, as compared to when participants perform a purely perceptual task during the learning phase (Shoham et al., 2022).

Unlike previous studies that explicitly explored conceptual processing in face recognition (Bower & Karlin, 1974; Patterson & Baddeley, 1977; Schwartz & Yovel, 2016, 2019a), our design did not include a task during the encoding or recognition movies. Rather, participants engaged with faces in a manner that was more similar to how they encounter faces in real-world settings. Prior research has demonstrated that understanding a narrative can increase the similarity of neural responses across individuals (Hasson, Yang, et al., 2008; Jääskeläinen et al., 2021; Nguyen et al., 2019). Moreover, manipulating narrative coherence during movie watching has been shown to affect the similarity of neural responses in non-sensory regions (Baldassano et al., 2018; Hasson et al., 2010; Hasson, Yang, et al., 2008; Noad et al., 2024; Van Kesteren et al., 2010). In our study, it is likely that participants in the Original group exhibited more synchronized neural activity during the encoding movie due to their exposure to a coherent narrative, which in turn facilitated the consolidation of person knowledge about the characters. In contrast, the recognition phase of our experiment involved a movie that was not narrative driven and was identical for both groups. The segments shown during this phase were drawn from a variety of episodes from the TV series which had not been previously seen. So, while these segments were selected to provide clear views of the characters' faces, there was no coherent storyline to follow. This key feature of our design allowed us to isolate differences in neural processing specifically related to face perception and recognition during this phase of the experiment.

Cognitive models of face recognition propose that faces are initially encoded in an image-dependent code, which is subsequently transformed into a structural or image-invariant code that supports the recognition of familiar faces (Bruce & Young, 1986; Burton, Bruce, et al., 1999; Hancock et al., 2000; Young & Burton, 2017). Activation of these image-invariant representations is thought to underlie the sensation of face familiarity. To investigate whether regions within the face network showed image-invariant response patterns, we compared patterns of neural response to the faces across different scenes during the recognition movie (Lally et al., 2023; Milivojevic et al., 2016). Identity-specific patterns were defined as more similar patterns in response to faces of the same identity compared to those of different identities. We found identity-specific patterns not only in the core face-selective regions, but also in the extended face network. This finding aligns with prior studies demonstrating identity decoding for familiar faces in both the core face network and extended face network (Visconti di Oleggio Castello et al., 2017; Visconti di Oleggio Castello et al., 2021). The presence of identity-specific patterns of response outside the core face network highlights the potential significance of non-visual information and suggests that broader, distributed neural responses may contribute to the cognitive representation of familiar individuals. These non-visual regions may play an integral role in forming invariant representations of faces, supporting the recognition of familiar people across different contexts.

In conclusion, this study investigated the role of conceptual knowledge in processing familiar faces under naturalistic conditions. Our findings demonstrate that conceptual knowledge modulates neural responses to faces in an extended network of regions beyond the core face-selective areas. Additionally, patterns of neural activity within this extended network were able to discriminate between different face identities. These results suggest that non-visual brain regions play a significant role in the recognition of familiar individuals, and that conceptual knowledge is a critical component in the processing of familiar faces.

Chapter 6

Impaired event comprehension during natural viewing in individuals with developmental prosopagnosia

6.1 Abstract

Understanding everyday events is essential for navigating and facilitating successful social interactions. Face recognition is thought to play a critical role in how we associate and interpret events in the real world. In this study, we explored this issue using a natural viewing paradigm in which participants watched a movie containing a rich and detailed narrative. To determine the importance of face recognition in understanding events that occur in natural viewing, we compared neurotypical control participants with participants with developmental prosopagnosia (DP) - a lifelong deficit in the ability to recognize faces. After watching the movie, participants were assessed on their understanding of the events from the movie. We found that DPs showed a significant reduction in their understanding of the events from the movie compared to neurotypical controls. DPs were also impaired in their recognition of the faces from the movie. Together, these results demonstrate the importance of face recognition for understanding naturally unfolding events in everyday life.

6.2 Introduction

The ability to comprehend complex social situations is essential for the formation and maintenance of interpersonal relationships with others. Successfully interpreting everyday events necessitates tracking relevant information about people, locations, objects and actions from a rich and rapidly changing stream of sensory inputs (Baldassano et al., 2018; Milivojevic et al., 2016). Facial recognition is considered particularly important for linking independent yet related events (Milivojevic et al., 2016). Similarly, social interactions play a crucial role in the encoding of events (Dima et al., 2022). Knowing the identity of a person also allows us to access socially-relevant information about them, which can help us to understand their interactions with ourselves and others (Frith & Frith, 2005).

While the recognition of familiar faces is straightforward for most human observers, there are some people who struggle to recognize people from their face. Developmental prosopagnosia (DP) is a neurodevelopmental condition defined by the inability to recognise faces despite otherwise normal visual processing. Unlike acquired prosopagnosia, where individuals experience face recognition deficits following brain damage, DP occurs in the absence of brain injury (Behrmann & Avidan, 2005; Cook & Biotti, 2016; Duchaine & Nakayama, 2006). The prevalence of DP is reported to be around 2% of the general population (DeGutis et al., 2023; Kennerknecht et al., 2006).

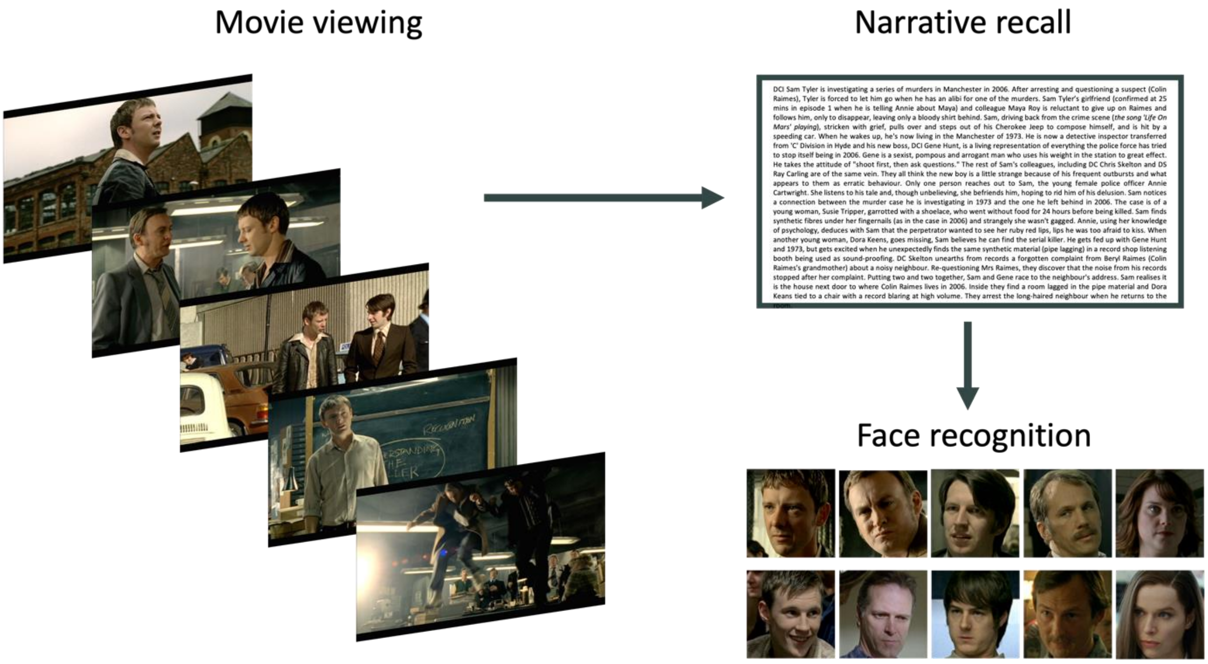
Despite relatively high prevalence rates, the impact of DP beyond face recognition is often overlooked. Nonetheless, a few studies have investigated the negative psychosocial consequences that accompany DP. Individuals with DP often report avoidance of social situations that can lead to a loss of self-confidence and limit employment opportunities (Dalrymple et al., 2014; Yardley et al., 2008). The ability to recognise faces can also affect the size of friendship groups (Dalrymple et al., 2014; Diaz, 2008; Wang et al., 2022) and influence the quality of relationships (Engfors et al., 2024; McKone et al., 2023). In extreme cases, DP can lead to the development of social anxiety disorder (Davis et al., 2011; Yardley et al., 2008). These studies show that DP can have real world effects on social interactions. However, it is not clear whether this deficit in face recognition influences broader aspects of social cognition, such as our ability to understand naturally unfolding events in everyday life.

In this study, we examined the role of face recognition in event understanding using a naturalistic paradigm. These paradigms preserve the rich and detailed sensory input characteristic of everyday experiences while capturing the complexity of social interactions, making them particularly well-suited for investigating real-world event comprehension (Redcay & Moraczewski, 2020; Sonkusare et al., 2019). To determine whether face recognition is important for understanding events that occur during natural viewing, we compared neurotypical participants with DPs. Participants viewed a movie taken from a TV series (Life on Mars), which contained a rich and detailed narrative. Participants were then assessed on their ability to understand the events from the movie. Our hypothesis was that participants with DP would show an impaired ability to understand the events, as a result of their inability to recognise faces.

6.3 Methods

6.3.1 Participants

Twenty-eight developmental prosopagnosic participants (median age: 46 years, age range: 18-72, 13 male, 3 non-binary) and 100 control participants (median age: 19 years, age range: 18-21, 8 male, 4 non-binary, from Noad & Andrews, 2024) completed the experiment online through the Pavlovia platform (https://pavlovia.org). All participants were unfamiliar with the TV show Life on Mars and were fluent English-speakers. They all had normal or corrected-to-normal vision, and had no history of neurological conditions by self-report. Although the control and DP groups differed in age, we found that age did not correlate with the key dependent measures in the DP group (narrative score: *r*(26) = -.14, *p* = .484; BIS score: *r*(26) = .09, *p* = .642), or in the control group (narrative score: *r*(98) = -.03, *p* = .791; BIS score: *r*(98) = .10, *p* = .300). Written informed consent was obtained for all participants and the study was approved by the Psychology Research Ethics Committee at the University of York.



DCI Sam Tyler is investigating a series of murders in Manchester in 2006. After arresting and questioning a suspect (Colin Raimes), Tyler is forced to let him go when he has an alibi for one of the murders. Sam Tyler's girlfriend (confirmed at 25 mins in episode 1 when he is telling Annie about Maya) and colleague Maya Roy is reluctant to give up on Raimes and follows him, only to disappear, leaving only a bloody shirt behind. Sam, driving back from the crime scene (*the song 'Life On Mars' playing*), stricken with grief, pulls over and steps out of his Cherokee Jeep to compose himself, and is hit by a speeding car. When he wakes up, he's now living in the Manchester of 1973. He is now a detective inspector transferred from 'C' Division in Hyde and his new boss, DCI Gene Hunt, is a living representation of everything the police force has tried to stop itself being in 2006. Gene is a sexist, pompous and arrogant man who uses his weight in the station to great effect. He takes the attitude of "shoot first, then ask questions." The rest of Sam's colleagues, including DC Chris Skelton and DS Ray Carling are of the same vein. They all think the new boy is a little strange because of his frequent outbursts and what appears to them as erratic behaviour. Only one person reaches out to Sam, the young female police officer Annie Cartwright. She listens to his tale and, though unbelieving, she befriends him, hoping to rid him of his delusion. Sam notices a connection between the murder case he is investigating in 1973 and the one he left behind in 2006. The case is of a young woman, Susie Tripper, garrotted with a shoelace, who went without food for 24 hours before being killed. Sam finds synthetic fibres under her fingernails (as in the case in 2006) and strangely she wasn't gagged. Annie, using her knowledge of psychology, deduces with Sam that the perpetrator wanted to see her ruby red lips, lips he was too afraid to kiss. When another young woman, Dora Keens, goes missing, Sam believes he can find the serial killer. He gets fed up with Gene Hunt and 1973, but gets excited when he unexpectedly finds the same synthetic material (pipe lagging) in a record shop listening booth being used as sound-proofing. DC Skelton unearths from records a forgotten complaint from Beryl Raimes (Colin Raimes's grandmother) about a noisy neighbour. Re-questioning Mrs Raimes, they discover that the noise from his records stopped after her complaint. Putting two and two together, Sam and Gene race to the neighbour's address. Sam realises it is the house next door to where Colin Raimes lives in 2006. Inside they find a room lagged in the pipe material and Dora Keans tied to a chair with a record blaring at high volume. They arrest the long-haired neighbour when he returns to the room.

Figure 6.1. Natural viewing paradigm and experimental design. Participants watched a 20 minute movie from the TV series Life on Mars. Participants were then tested on their understanding of the events from the clips in two narrative understanding tasks: a free recall of the video, and structured questions about specific events from the video. Recognition of the faces from the video was tested using a face recognition memory test, including (top) target identities and (bottom) foils both from unseen episodes of the show and images from outside the show.

6.3.2 Diagnostic tests

DP participants were recruited through www.troublewithfaces.org and other online sources. To determine diagnostic evidence for the presence of DP, all DP participants completed the PI20 – a 20-item self-report measure of prosopagnostic traits (Shah et al., 2015), and the Cambridge Face Memory

Test (CFMT) – an objective measure of face recognition (Duchaine & Nakayama, 2006). The CFMT is commonly used to show diagnostic evidence for DP, as it has been shown to discriminate between individuals with and without face memory deficits (Duchaine & Nakayama, 2006). To be classified with DP, a participant had to score above the established threshold (>65) on the PI20 (M = 80.3, SD = 8.96), and 2 standard deviations below the typical mean (<65%) on the CFMT (M = 51.3, SD = 8.52; Table 6.1). Combining diagnostic evidence from self-report and objective measures is thought to provide reliable identification of DP (Gray et al., 2017; Tsantani et al., 2021). One participant scored slightly above the CFMT threshold (66.7%) and one participant score slightly below the PI20 threshold (54), but were included in the sample due to showing clear face recognition deficits on the other measure, and also self-reporting problems with face recognition. Control participants all scored within the normal range on the CFMT (>65%) (M = 81.2, SD = 8.1).

Table 6.1. Individual scores on the PI20 questionnaire and Cambridge Face Memory Test (CMFT) used to validate developmental prosopagnosia. High scores on the PI20 indicate more prosopagnosic traits. Low scores on the CFMT show worse face memory performance. Control comparison data (N = 54) for the PI20 and CFMT were taken from (Biotti et al., 2019).

Participant	Age	Gender	PI20 Score	CFMT score (%)	zPI20	zCFMT
1	66	M	92	45.8	5.93	-4.40
2	54	F	85	59.7	5.16	-2.84
3	36	M	73	59.7	3.85	-2.84
4	60	M	91	47	5.82	-4.27
5	50	M	88	48.6	5.49	-4.09
6	50	F	82	55.6	4.84	-3.30
7	44	F	54	51.4	1.76	-3.78
8	56	F	80	52.8	4.62	-3.62
9	42	M	76	62.5	4.18	-2.53
10	34	F	89	47.2	5.60	-4.25
11	56	M	84	51.4	5.05	-3.78
12	25	M	72	44.5	3.74	-4.55
13	51	M	75	45.8	4.07	-4.40
14	29	F	83	59.7	4.95	-2.84
15	58	F	90	52.8	5.71	-3.62
16	21	M	80	48.6	4.62	-4.09
17	44	F	82	62.5	4.84	-2.53
18	27	F	86	41.7	5.27	-4.87
19	41	F	70	29.2	3.52	-6.27
20	51	F	94	55.6	6.15	-3.30
21	58	F	81	44.5	4.73	-4.55
22	22	F	81	51.4	4.73	-3.78
23	58	F	74	58.3	3.96	-3.00
24	29	M	93	45.8	6.04	-4.40
25	45	F	68	62.5	3.30	-2.53
26	29	M	72	66.7	3.74	-2.06
27	61	F	81	36.1	4.73	-5.49
28	25	F	75	50	4.07	-3.93

DPs Mean	80.39	51.34
DPs SD	8.96	8.52
Comparison Mean	38.0	85.0
Comparison SD	9.1	8.9

6.3.3 Stimuli and Experimental Design

Participants viewed a 20-minute (1170s) movie constructed from audio-visual clips from the first episode of BBC TV series Life on Mars (Figure 6.1, left). Participants were asked to watch and attend to the movie for the duration. The movie contained a complex and rich naturalistic narrative involving ten unique characters who appeared across fourteen clips.

6.3.4 Narrative Understanding Analysis

After watching the video, participants were tested on their understanding of the movie (Figure 6.1, top right). Participants were asked to 1) recall the movie in as much detail as possible, providing an unconstrained written response, and 2) answer a set of 8 structured questions about specific events in the video. Each question was accompanied by a static image of the relevant event in the video.

To assess whether the groups differed in understanding of the narrative of the movie, the two narrative understanding tasks were graded by two raters using a predefined marking scheme (see Noad & Andrews, 2024). The free recall test was marked relative to 10 key events that occurred during the encoding video. Raters assigned a mark of 0, 1 or 2 for each point depending on whether the test showed no, partial or a full description of the event, for a possible total of 20 marks. The 8 structured questions were marked in a similar manner, for a possible total of 16 marks. Further analysis was based on the average scores across raters. Differences between groups in narrative measures were tested using Student’s two sample t-tests.

To further explore how natural events are understood in DP, the free recall responses from each participant were compared to a synopsis of Life on Mars using Latent Semantic Analysis (LSA). LSA is a natural language processing technique that can uncover underlying structures in a text by analysing the relationships between words, and can map texts onto a semantic space (Landauer et al., 1998). This technique can be used to compare the semantic similarity between two texts. Here, we compared the free recall of the narrative from each participant to an online synopsis of the first episode of Life on Mars (implemented on http://wordvec.colorado.edu). High similarity of the participant’s free recall response to the synopsis indicates a high similarity in contextual usage of words, which suggests a similar level of understanding to the synopsis.

6.3.5 Face Recognition Analysis

Recognition of the faces from the movie was measured using a face recognition memory task after watching the video clips (Figure 6.1, bottom right). Faces were presented individually in a random order and remained on screen until a response was made. Participants were required to press a button to indicate if the identity of the face corresponded to any of the actors from the video they had watched. Images from the main 10 actors were used in the test. Static images were taken directly from the TV series, but were not images seen in the movie. Another image of each actor was taken from outside of the Life on Mars TV series. Two foil images of different identities were selected to match each of the targets in age, expression, gender, hairstyle and general appearance for both images from the TV series and out of the TV series.

Face recognition performance was calculated using the mean sensitivity (*d'*) for discriminating between faces of characters present in the movie and faces of foils who were not present in the movie. *d'* was calculated based on hit rates (i.e. correct recognition of the face as present in the movie / number of targets) and false alarm rates (i.e. incorrectly responding that foil was present in the movie / number of foils) for each participant (*d' = z hit rate – z false alarm rate*). In cases where the hit rate was 1 and/or the false alarm rate was 0, *d'* was calculated using 0.999 for the hit rate or 0.001 for the false alarm rate to avoid *d'* infinity. A *d'* score of 0 indicates the observer cannot distinguish between target faces and foils (chance performance). Hits and False alarms were also analysed independently to determine if there were differences in response bias.

While accuracy is typically used to classify DPs, it has been shown that they can perform within typical accuracy limits when tasks have an unlimited presentation time (Dobel et al., 2007; Duchaine & Nakayama, 2004). Previous studies have recommended incorporating response time (RT) alongside accuracy (Fysh & Ramon, 2022). Balanced Integration Score (BIS) is a way of integrating an individual's accuracy and response time (Liesefeld & Janczyk, 2019; Liesefeld & Janczyk, 2023). BIS has previously been shown to be a good measure of performance in developmental prosopagnosia, where accuracy is often prioritised over response time (Lowes et al., 2024). A higher BIS score shows better performance while controlling for speed accuracy trade-offs, while a lower BIS score demonstrates poorer performance. BIS is calculated by subtracting a participant's standardised RT on correct trials from their standardised accuracy score (*BIS = z accuracy – z RT*). The control mean (and SD) accuracy and RT on the face recognition memory test were used to calculate Z scores for control and DP participants.

6.4 Results

6.4.1 Impaired Understanding of Narrative in DP

We calculated the narrative understanding score for each participant on the free recall task and structured narrative question task. Narrative understanding scores were compared between the DPs and control participants (Figure 6.2). The DPs had significantly lower narrative understanding scores on both the free recall ($M_C = 15.0$, $SD_C = 3.40$, $M_{DP} = 12.4$, $SD_{DP} = 2.73$, $t(52.9) = 4.33$, $p < .001$, $d = 0.82$) and structured questions ($M_C = 12.1$, $SD_C = 2.35$, $M_{DP} = 10.8$, $SD_{DP} = 2.33$, $t(43.7) = 2.68$, $p = .010$, $d = 0.57$).

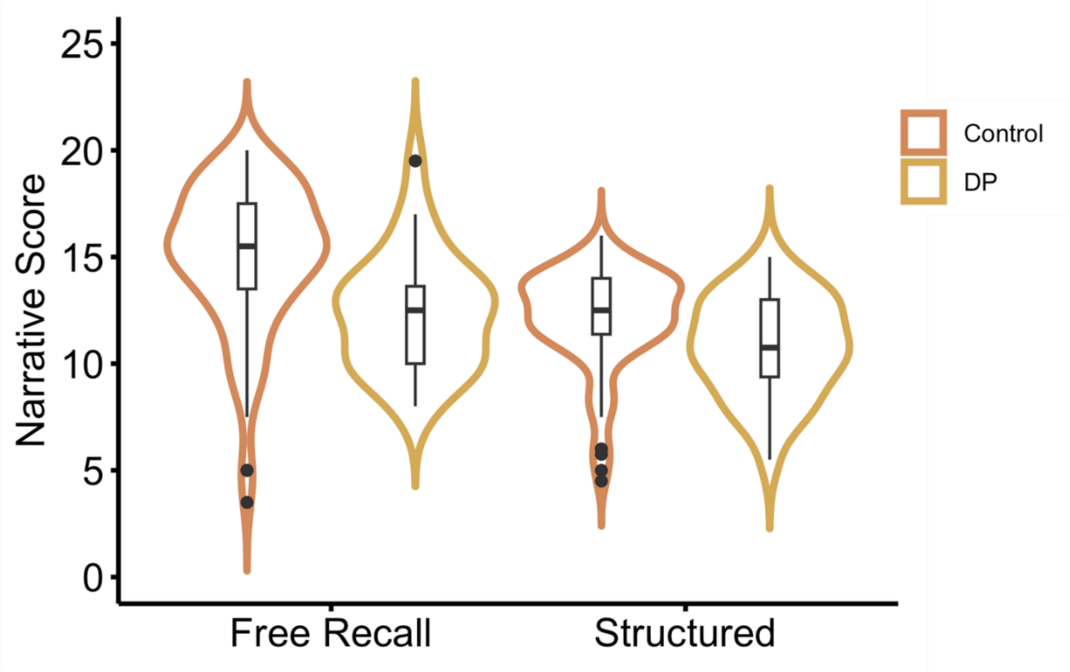


Figure 6.2. Significantly lower narrative understanding scores were found in individuals with DP compared to control participants after watching the movie. A reduction in performance was evident for both the free recall task and on structured narrative questions.

To further explore the understanding of events in the movie, we compared the free recall responses of each participant to a synopsis of the movie using Latent Semantic Analysis. A higher LSA score indicates a greater understanding of the narrative. Having found a large effect of narrative, we performed a one-tailed t-test on LSA scores between groups. DP participants demonstrated a lower LSA similarity score between their free recall response and a synopsis of the video clips (Figure 6.3a). However, this was not significantly different compared to controls ($M_C = 0.70$, $SD_C = 0.04$, $M_{DP} = 0.68$, $SD_{DP} = 0.06$, $t(33.5) = 1.54$, $p = .066$, $d = 0.42$).

Interestingly, the differences in narrative understanding between groups do not appear to be explained by lack of detail or effort, as no significant differences were found between controls and DPs in the word count of the free recall responses (M_C = 372.9, SD_C = 235, M_{DP} = 482.9, SD_{DP} = 307, $t(36.3) = 1.8$, $p = .087$, $d = 0.44$) (Figure 6.3b).

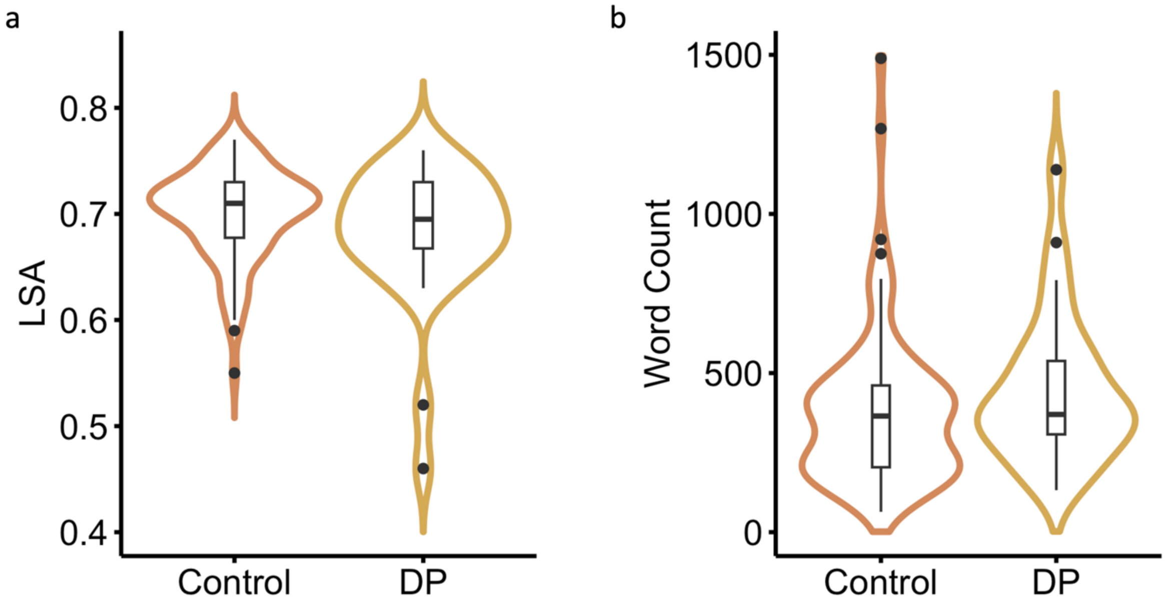


Figure 6.3. Narrative analysis. a) Latent semantic analysis (LSA) showed that Individuals with DP exhibited a lower semantic similarity between their free recall of the narrative and an objective synopsis of the video compared to controls. **b**) DPs did not show any difference in word count on the free recall task, despite showing significantly lower understanding of the narrative. This suggests a similar level of effort across both groups.

6.4.2 Recognition of Faces in DP

To explore learning of faces in naturalistic settings in DP, we calculated performance for each participant on the face recognition memory task. There was no significant difference in *d'* scores ($t(33.9) = 0.25$, $p = .805$, $d = 0.07$) between control participants (M_C = 1.33, SD_C = 0.51) and DPs (M_{DP} = 1.29, SD_{DP} = 0.77). Next, we analysed the hit rate and false alarm rate (Figure 6.4). There was a significant difference in hit rate between groups ($t(42.2) = 4.31$, $p < .001$, $d = 0.94$), with DPs showing a lower hit rate than controls (M_C = 13.1, SD_C = 2.52, M_{DP} = 10.7, SD_{DP} = 2.61). However, there were no significant differences in false alarms between the groups ($t(37.4) = 1.47$, $p = .149$, $d = 0.35$; M_C = 9.29, SD_C = 4.78, M_{DP} = 7.5, SD_{DP} = 5.92).

To further explore face recognition in DP, we compared response times (RT) for correct trials (Figure 6.5a). A t-test showed significant differences between groups ($t(31.9) = 4.30$, $p < .001$, $d = 1.25$), with DPs having longer reaction times (M_C = 1.66, SD_C = 0.50, M_{DP} = 2.41, SD_{DP} = 0.89). Given the significantly increased response times in DP, we used Balanced Integration Score (BIS) to incorporate the response time with accuracy on the face recognition test (Figure 6.5b). We then compared BIS scores using a t-test. There were significant differences between groups ($t(31.9) = 3.29$, $p = .002$, $d = 0.95$), which reflected lower BIS scores in the DP group ($M_C = 0.00$, $SD_C = 1.37$, $M_{DP} = -1.58$, $SD_{DP} = 2.44$).

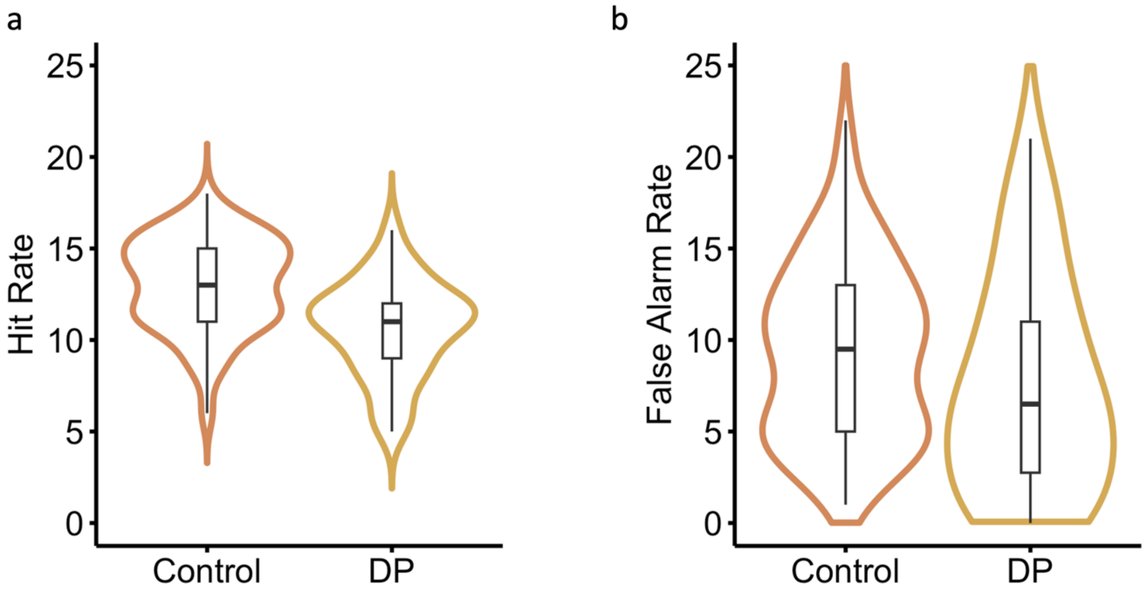


Figure 6.4. Face recognition sensitivity. a) Individuals with DP had a lower hit rate on the face recognition memory test compared to control participants. **b**) DPs also showed a lower false alarm rate, but this difference was not statistically significant.

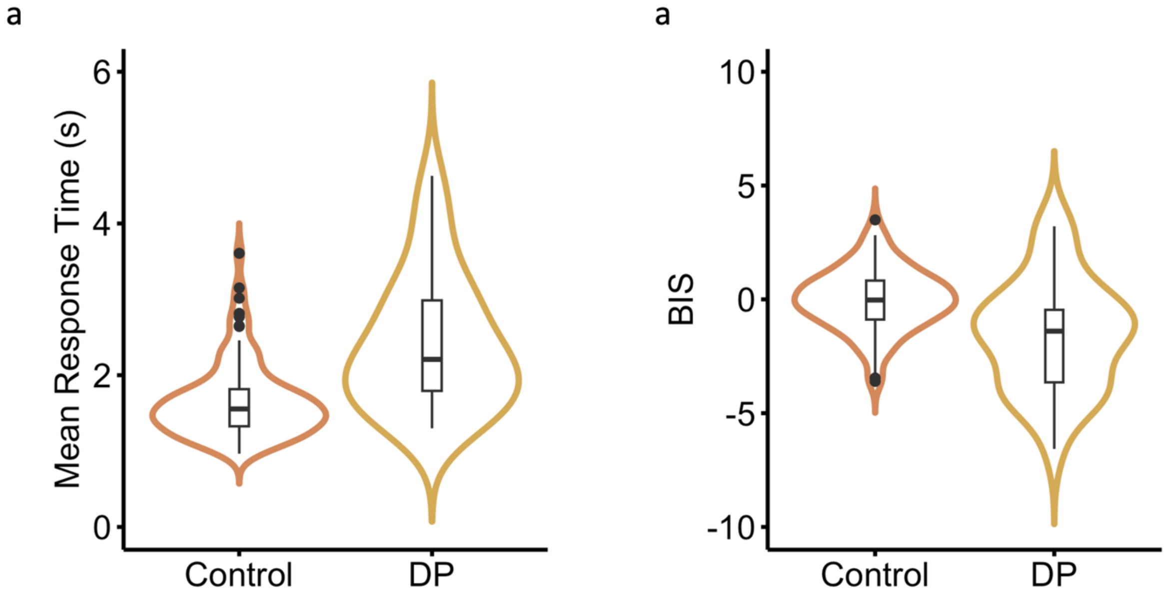


Figure 6.5. Face recognition. a) DPs showed significantly longer response times compared to control participants in the face recognition task. **b**) Balanced Integration Scores (BIS) incorporated the response time with accuracy on the face recognition test. DPs showed a significantly lower BIS.

6.5 Discussion

The ability to track information, such as the presence of individuals, is considered crucial for understanding events in everyday life (Baldassano et al., 2018). This study aimed to investigate the role of face recognition in event comprehension during naturalistic viewing. We employed a natural viewing paradigm to examine narrative comprehension in neurotypical individuals and those with developmental prosopagnosia (DP). Our results demonstrated a reduction in narrative understanding in individuals with DP, suggesting that facial recognition is crucial for interpreting naturally unfolding events.

Social interactions are dynamic and complex, requiring not only the recognition of individuals, but also the tracking of relationships between people (Karagoz et al., 2023). The findings of this study suggest that the deficits in DP may extend beyond face recognition, potentially impacting broader aspects of social cognition. This aligns with previous research showing that individuals with DP often avoid social situations and experience social anxiety (Dalrymple et al., 2014; Yardley et al., 2008). Our results further support these insights by demonstrating that reduced narrative comprehension in movies may reflect a more generalized difficulty in understanding everyday events in individuals with DP.

Previous research has shown that non-visual, conceptual information about individuals, such as who a person is, what they do and where we usually see them, is important for learning new faces (Noad & Andrews, 2024; Schwartz & Yovel, 2016). Neuroimaging studies provide further support for the role of non-visual information, demonstrating that the processing of familiar faces activates brain regions typically associated with conceptual knowledge (Gobbini & Haxby, 2007; Kovács, 2020; Noad et al., 2024; Visconti di Oleggio Castello et al., 2017; Visconti di Oleggio Castello et al., 2021). In this study, we demonstrate the reverse effect; impairments with face recognition can disrupt the acquisition of conceptual knowledge about people and events. Given the importance of this information for becoming familiar with a face (Noad & Andrews, 2024), this may exacerbate difficulties in learning new faces in individuals with DP.

The findings from this study hold significant implications for the rehabilitation of DP. While substantial efforts have been made to understand the processes underlying DP, comparatively less attention has been directed toward effective rehabilitation strategies (Bate & Bennetts, 2014; J. M. DeGutis et al., 2014). Previous attempts at remediation have primarily focussed on visual processing abilities (Corrow et al., 2019; J. DeGutis et al., 2014; DeGutis et al., 2007). These techniques involve training individuals on visual strategies, such as relying on specific facial features or distinguishing characteristics (Adams et al., 2020). These visual rehabilitation methods are predicated on the hypothesis that the face processing network has the potential for functional reorganisation (DeGutis et al., 2007). However, the efficacy of these interventions has yielded mixed results, with only modest success in the most promising cases. The current study introduces an alternative approach, highlighting the potential of focussing on non-visual information associated with a person as a novel intervention strategy. Strengthening the conceptual representation of a person may facilitate face recognition in individuals with DP. Interestingly, improvements in overt recognition of individuals with acquired prosopagnosia has been shown when familiar faces that shared conceptual information were also presented (De Haan & Campbell, 1991).

In real world environments, faces are typically learned within rich, social contexts. Thus, replicating these conditions in the lab is crucial for studying face processing. Natural viewing paradigms, such as movie watching, offer a unique opportunity to examine face learning under conditions that closely mirror real-world experiences (Redcay & Moraczewski, 2020). To our knowledge, no prior studies of DP have investigated learning of new faces in natural viewing conditions. Our findings reveal significant differences in face recognition between individuals with DP and control participants. DPs exhibited a lower hit rate than controls, along with a lower, albeit not significant, false alarm rate. This more conservative response pattern fits with previous research on newly learned face recognition in DP (Epihova et al., 2023). Response times were also significantly greater for DPs, indicating a more prolonged decision process compared to control participants. The extended response times may explain the relatively preserved d’ scores in DPs, as these individuals may reach the correct answer through a more effortful visual analysis of images. This aligns with previous research which has shown that DPs can perform within typical accuracy limits when tasks have unlimited presentation time (Duchaine & Nakayama, 2006; Lowes et al., 2024). In this study, integrating response time with accuracy revealed a clear and significant reduction in face recognition performance among DPs. The difficulty in achieving effortless recognition in DP may impair their ability to comprehend social events, particularly in dynamic, natural viewing contexts where sensory input is constantly changing.

While numerous studies have proposed that deficits in face recognition occur in isolation from other impairments (Barton et al., 2019; Bate, Bennetts, et al., 2019; Garrido et al., 2018), growing evidence suggests that individuals with DP can have co-occurring deficits in non-face object recognition (Barton et al., 2019; Barton & Corrow, 2016; Biotti et al., 2017; Duchaine et al., 2007; Epihova et al., 2022, 2023) and even in broader cognitive abilities, such as topographical navigation (Bate, Adams, et al., 2019; Corrow et al., 2016; Klargaard et al., 2016). Consequently, the observed reduction in narrative understanding among individuals with DP may reflect a more generalized difficulty in information processing that extends beyond face recognition deficits. This raises the possibility that deficits in face recognition may not be the sole contributor to impairments in narrative understanding. Future work could explore this hypothesis by examining event comprehension in contexts that do not contain faces, such as audio-based narratives, or movie sequences without face-related content.

In conclusion, this study provides the first empirical evidence for impaired event comprehension in individuals with DP. The observed reduction in event understanding was not due to differences in effort or detail, as indicated by comparable word counts in the recall of events between groups. These findings align with a growing body of literature emphasizing the interaction between visual and non-visual information in the recognition of familiar faces, particularly in naturalistic viewing conditions. These results underscore the broader, everyday impact of DP and suggest potential avenues for future interventions targeting non-visual aspects of face processing.

Chapter 7

General Discussion

7.1 Aims

Humans are proficient at quickly and accurately recognising familiar faces (Young & Burton, 2017). Although the ability to recognize familiar individuals is critical for guiding social interactions, the underlying cognitive and neural mechanisms are not fully understood. Previous work has focussed on the importance of visual properties in familiar face recognition in highly controlled laboratory settings. While these approaches have yielded significant insights, a growing body of research suggests that the non-visual, conceptual information associated with faces when they are encountered in the real world might also be important. To address this gap, the empirical studies in this thesis have used natural viewing paradigms to investigate the role of conceptual information in familiar face recognition. The primary objectives of this work were to explore the neural correlates of familiar face perception under ecologically valid conditions, and to determine the influence of naturally occurring conceptual information in familiar face processing.

First, the importance of visual and non-visual brain regions in familiar face processing was investigated using a natural viewing paradigm in fMRI (Chapter 2). To assess whether these neural responses are critical for face processing, the neural response was investigated in individuals with developmental prosopagnosia (Chapter 2) and in a case study of an individual experiencing hyperfamiliarity for faces (Chapter 3). Building on evidence showing the importance of non-visual brain regions in familiar face processing, Chapter 4 explored the role of non-visual, conceptual information in becoming familiar with a face. To address how conceptual information modulates the neural response to faces, the response to faces in visual and non-visual regions of the brain was again investigated with a natural viewing paradigm in fMRI (Chapter 5). Finally, the relationship between naturally occurring conceptual and perceptual information in face recognition was further explored by investigating whether individuals with developmental prosopagnosia have difficulties in acquiring conceptual information during naturalistic events (Chapter 6). Together, the findings presented in this thesis highlight the critical role of conceptual knowledge, processed in a network of non-visual brain regions, in facilitating the visual recognition of a familiar face.

7.2 An alternative framework for familiar face processing

Cognitive models of face processing emphasize the critical role of invariant visual representations in the recognition of familiar faces (Bruce & Young, 1986; Burton, Bruce, et al., 1999). These models propose a sequential process whereby a face is first structurally encoded in an image-based representation. This representation is subsequently processed by face recognition units (FRUs) which maintain an image-invariant representation of identity for familiar faces. Empirical evidence for an image-invariant visual representation includes the robust ability to recognize familiar faces across a range of visual changes in the image (Bruce, 1982). Activation of the FRU then triggers the corresponding person identity node (PIN), which contains identifying information. Activation of the FRU is necessary for a sense of familiarity. This is then followed by activation of the PIN to allow full recognition. Support for this process comes from observations that we can perceive a face as being familiar, but not remember who it is. However, remembering a person is always accompanied by a sense of familiarity (Young et al., 1985).

In neural models of face processing it is proposed that visual areas of the brain contain image-dependent and image-invariant visual representations of a face (Haxby et al., 2000). These visual regions roughly correspond to cognitive models, with the occipital face area (OFA) proposed to encode an image-dependent representation, and the fusiform face area (FFA) encoding an image-invariant representation analogous to the FRU. However, neuroimaging experiments show inconsistent support for an image-invariant visual representation for familiar faces (Davies-Thompson et al., 2009; Davies-Thompson et al., 2013; Ewbank & Andrews, 2008; Rotshtein et al., 2005; Weibert et al., 2016). In contrast, a network of regions beyond the visual brain consistently show responses to familiar compared to unfamiliar faces (Gobbini et al., 2004; Gorno-Tempini & Price, 2001; Leveroni et al., 2000; Natu & O'Toole, 2011), and even demonstrate identity-specific patterns of response (Visconti di Oleggio Castello et al., 2017; Visconti di Oleggio Castello et al., 2021). This suggests that non-visual brain regions may play an important role in the recognition of familiar faces (Gobbini & Haxby, 2007; Kovács, 2020).

In Chapter 2, a network of regions beyond the visual brain were shown to be involved in processing familiar compared to unfamiliar faces. These regions are typically associated with representing the conceptual information, or person knowledge, related to a face (Gobbini and Haxby, 2007; Kovacs, 2020). The neural response in this network of extended regions was significantly reduced in people with developmental prosopagnosia. This suggests that the response in these regions may be critical for familiar face recognition. These findings align with a growing body of evidence highlighting the recruitment of these non-visual regions in familiar face processing (Visconti di Oleggio Castello et al., 2017; 2021). In contrast to these regions, limited differences were observed in the neural response of the core face-selective regions for familiar compared to unfamiliar face processing. These findings suggest that the key neural mechanisms underlying familiar face recognition occur beyond the visual brain. This diverges from traditional neural models of face processing that emphasize the importance of visual regions, such as the FFA (Haxby et al., 2000).

The pivotal role of non-visual brain regions in familiar face processing raises an important question: does the conceptual information processed in these regions directly contribute to face recognition? Emerging evidence suggests that learning faces in conjunction with conceptual information enhances subsequent recognition compared to purely perceptual experience (Schwartz & Yovel, 2016, 2019b; Shoham et al., 2024). However, a potential limitation of these studies is their reliance on controlled laboratory paradigms, which do not accurately capture how conceptual knowledge is encountered in the real-world. To address this gap, Chapter 4 employed a natural viewing paradigm to familiarize participants with faces, while manipulating the conceptual information provided to different groups of participants. The findings revealed superior face recognition in individuals who had greater conceptual understanding about the narrative. Complementary findings in Chapter 6 demonstrated the reverse relationship, as individuals with developmental prosopagnosia exhibited a diminished understanding of conceptual information while viewing naturalistic events when compared to neurotypical controls. Together, these findings underscore the integral role of conceptual knowledge in supporting the recognition of familiar faces.

A theoretical framework for understanding how conceptual information enables the visual recognition of faces is the level of processing framework (Bower & Karlin, 1974; Craik, 2002; Craik & Lockhart, 1972). This framework proposes that memory traces depend on the depth of processing during encoding, rather than perceptual exposure alone. According to this framework, faces associated with conceptual information undergo deeper processing than those presented solely visually, resulting in an enhanced representation in memory. However, such a framework does not explain where the modulation of processing occurs. One hypothesis is that conceptual information strengthens sensory representations, such as in visual regions of the brain. Support for this comes from findings which show that the representations of individual faces become more perceptually similar when two individuals are deemed to be more similar in their personalities (conceptual information) (Oh et al., 2021). This perspective aligns with models of face processing, which emphasize the importance of invariant visual representations for recognition. Alternatively, conceptual information could modulate the neural response directly in regions associated with processing conceptual information. Support for this possibility is evident in a study showing that making social evaluations of faces during learning leads to better recognition, and engages regions in the non-visual brain when compared to a purely perceptual task (Shoham et al., 2022).

In Chapter 5, these alternative explanations were investigated by determining which brain regions are modulated by conceptual information when new faces are learnt. The findings from this study revealed that conceptual knowledge modulated the neural response to faces in non-visual regions of the brain. This supports the hypothesis that conceptual information enhances face recognition in regions beyond the visual brain. This explanation challenges existing models of face processing as it implies that the critical response to familiar faces involves conceptual information processed in non-visual regions, rather than an invariant visual representation.

The findings presented in this thesis underscore the critical role of conceptual information in shaping cognitive and neural representations of familiar faces. This has significant theoretical relevance as it departs from arguments made in most classic models of face processing, which posit that conceptual knowledge simply supplements familiar face processing following recognition (Bruce & Young, 1986). The findings from this thesis lend support to the possibility that the critical computation in familiar face recognition may not stem from an image-invariant visual representation. Prior evidence has demonstrated that both familiar and unfamiliar face recognition may rely on the same set of critical visual features (Abudarham et al., 2021; Abudarham et al., 2019; Abudarham & Yovel, 2019), suggesting that different visual representations may not underpin the differences in familiar and unfamiliar face recognition. While visual encoding of a face is certainly necessary for recognition, an image-invariant visual representation may not be necessary.

Evidence for an image-based (rather than an image-invariant) representation of familiar faces is apparent in behavioural studies. For example, face learning experiments show that recognition is linked to the learned image (Longmore et al., 2008; Dunn, Ritchie, Kemp & White, 2019), repetition priming of familiar faces is greater for the same image relative to a different image of a person (Ellis et al., 1987) and it is known that some images of familiar faces are easier to recognise than others (Burton et al., 2005). Similarly, neuroimaging evidence indicates that responses to familiar faces in visual cortex are image-dependent (Davies-Thompson et al., 2009; Davies-Thompson et al., 2013; Weibert et al., 2016). These findings also align with advances in computational vision, where deep learning models trained for the recognition of faces retain image-based information in the fully-connected layers (O'Toole & Castillo, 2021). This suggests that familiar face recognition may not involve a visual image-invariant representation analogous to structural face recognition units.

Despite the evidence for image-dependent visual representations, humans demonstrate robust recognition of familiar individuals across diverse images. Our proposal is that this capacity may rely on mechanisms outside the visual domain. Specifically, different images of familiar face could activate different patterns of response in face-selective regions, but converge on a common pattern of response in non-visual regions of the brain. Evidence from Chapters 2 and 5 supports this framework, demonstrating that the key neural responses to familiar faces occur outside of visual regions. Chapter 5, in particular, shows that the pattern of response in these extended regions of the brain can discriminate the identity of a face, fitting with findings from recent studies showing identity decoding in non-visual regions (Visconti di Oleggio Castello et al., 2017; Visconti di Oleggio Castello et al., 2021).

Disorders of face perception provide additional evidence against the necessity of an image-invariant visual representation. Evidence for this comes from autonomic responses found in prosopagnosic participants who show no overt recognition of familiar faces, but exhibit physiological responses to familiar compared to unfamiliar faces (Bauer, 1984; Burton et al., 2005; Tranel & Damasio, 1985). This has led to the suggestion that emotional responses to familiar faces are processed in an independent pathway (Bauer, 1984; Schweinberger & Burton, 2003). The opposite is found in individuals with Capgras syndrome, who can recognise familiar others but believe they have been replaced with an unfamiliar person (Devinsky, 2009). In this syndrome, there is no difference in physiological response between familiar and unfamiliar faces, demonstrating that affective response is an important component of familiar face processing. In Chapter 3, the neural correlates of hyperfamiliarity for faces (characterised by the sense that unfamiliar faces are familiar) were evident in altered response in the medial temporal lobes. Again, this suggests that post-perceptual mechanisms are an important factor in processing familiarity of faces.

Functional connectivity between core face regions and the extended face network may play a critical role in face recognition. While neural models of familiar face processing propose extensive connectivity between visual and non-visual brain regions (Gobbini & Haxby, 2007; Haxby et al., 2000), empirical evidence for the role of these connections in processing familiar faces is limited. Previous work mapping connectivity in the face processing network has demonstrated connectivity between face-selective regions in the visual brain and the extended face network (Levakov et al., 2023; Wang et al., 2020), but it has not shown how this connectivity is affected by familiarity. However, evidence from developmental prosopagnosia has shown disrupted connectivity between face-selective regions and visual regions in the extended face network (Avidan et al., 2014; Lohse et al., 2016; Rosenthal et al., 2017).

In Chapter 2, familiar face recognition was associated with significantly greater connectivity between visual, face-selective regions and the extended face network. This connectivity was reduced in people with developmental prosopagnosia, suggesting that it is critical for familiar face processing. Consistent with these results, in Chapter 3 the connectivity between these visual and non-visual regions was enhanced in an individual with hyperfamiliarity for faces. These novel findings demonstrate the importance of connectivity between visual and non-visual brain regions in familiar face processing.

These findings support that idea that connecting the visual representation of a face with the conceptual knowledge associated with it is an important mechanism in familiar face recognition. Evidence from behavioural work shows that conceptual information such as a name is important for binding different instances of a face into a single robust representation (Dunn et al., 2021; Menon et al., 2015). Accordingly, we propose that the significant difference in recognition performance for familiar and unfamiliar faces may be due to an invariant conceptual representation of a familiar face. This representation is similar in concept to the FRU in that each familiar identity has a unique invariant representation. However, rather than being a visual representation, it reflects a distributed representation of conceptual knowledge associated with the face. This distributed but invariant conceptual response to familiar faces is the hallmark of familiar face processing. Familiar and unfamiliar faces undergo similar visual processing, but the invariant conceptual representation enables recognition across visually different images of the same identity for familiar faces only.

These findings suggest a distributed model of familiar face processing, in which conceptual and perceptual information are connected without a central hub, such as a FRU. This concept aligns with Damasio’s (1989) “higher-order convergence zones”, which propose that perceptual experience (familiarity) modulates neural activity in multiple regions simultaneously. This construct aligns with the distributed neural profile found for familiar faces (Chapter 2 & 5; Visconti di Oleggio, 2017; 2021). Similar distributed models of conceptual representation (Gainotti, 2011) argue for direct connections between sensory and semantic information without a central hub. If familiar face recognition works in a similar way, this could explain the robust recognition of faces across image changes.

This thesis provides converging evidence that conceptual information plays a pivotal role in familiar face processing. The response to familiar faces occurs in a distributed network of regions beyond the visual brain (Chapter 2; Chapter 5). Connectivity between visual and non-visual regions is critical for familiar face recognition (Chapter 2; Chapter 3). Conceptual information is important in becoming familiar with a face (Chapter 4), and is disrupted in disorders of face processing (Chapter 6). Finally, conceptual information modulates the neural response to faces in non-visual regions (Chapter 5). These findings offer significant refinement to theoretical models, emphasizing the role of distributed, conceptually driven processes in familiar face recognition.

7.3 The neural basis of disorders of familiar face recognition

Disorders of face recognition provide a unique framework for understanding the neural mechanisms underlying familiar face processing. In this thesis, the neural correlates of two different disorders of familiar face processing were investigated: developmental prosopagnosia (DP) and hyperfamiliarity for faces (HFF). DP is characterised by a severe impairment in the inability to recognise a familiar individual from their face (Duchaine & Nakayama, 2006). By examining deficits in DP, we can identify the neural substrates critical for familiar face recognition. In contrast, HFF involves the inappropriate sensation of familiarity when viewing unfamiliar faces, despite normal recognition of familiar faces (Vuilleumier et al., 2003). This condition could therefore offer insights into the mechanisms underpinning the sensation that a face is familiar. Together, these disorders can demonstrate whether core face-selective regions in visual cortex are sufficient for familiar face recognition, or whether regions beyond the visual cortex are also necessary.

In Chapter 2, individuals with DP were compared to neurotypical control participants. A key question was whether neural deficits in DP were confined to visual processing in core face-selective regions or extended to non-visual regions. Familiar face processing in neurotypical controls engaged an extended network of regions beyond core face-selective regions in visual cortex. When comparing familiar controls to familiar DPs, a significant attenuation was found in non-visual regions of DPs. These findings underscore the necessity of these non-visual regions for familiar face processing, and aligns with previous evidence showing reduced neural responses to faces in the extended face network in DPs (Avidan & Behrmann, 2009; Rivolta et al., 2014; Zhao et al., 2022). However, the core face-selective regions also showed a deficit in the processing of unfamiliar faces in DP. A comparison of unfamiliar

DPs with unfamiliar controls in the movie watching paradigm revealed significant effects in the core face regions. There was also a reduced selectivity for unfamiliar faces in face-selective regions. This difference in the processing of unfamiliar faces in DP suggests an inability to encode visual information about a face.

Chapter 3 focused on HFF, examining neural responses and connectivity to identify mechanisms underlying the sensation of face familiarity. The approach used in this study was to determine brain regions in which a patient with HFF showed more similar responses to familiar participants compared to unfamiliar participants. Again, the core face regions failed to demonstrate any neural correlates of HFF. In contrast, the neural response of the medial temporal lobe (MTL) in an individual with HFF was more similar to familiar than unfamiliar participants. This was despite the fact that the individual with HFF was unfamiliar with the faces. This aligns with findings from other studies showing a disruption of processing in the MTL is associated with HFF (Amlerova et al., 2012; Bujarski & Sperling, 2008; Michelucci et al., 2010). The role of the MTL in familiar face recognition is well documented, with neural responses showing selective and invariant responses to familiar identities (Nielson et al., 2010; Quiroga et al., 2009; Weibert et al., 2016). These findings suggest that the sensation of familiarity for faces is generated after perceptual processing. This diverges from traditional models of face processing which suggest that a sense of familiarity is achieved when the image is matched to internal stored visual representation of a familiar face in a FRU.

Differences in connectivity between visual and non-visual brain regions were found in both DP and HFF. There was reduced connectivity between core face-selective regions and the extended face network for familiar faces in DPs compared to controls. This is consistent with the idea that a disruption in the interaction between core and extended face regions may underlie the deficit in face recognition evident in DP (Avidan et al., 2014; Rosenthal et al., 2017; Thomas et al., 2009). Conversely, in Chapter 3, connectivity between visual and non-visual brain regions was increased in HFF. Together, these results suggest that functional connectivity between visual and non-visual regions of the face processing network are important for familiar face processing. Thus, the ability to link visual information to a conceptual representation could be an important component of familiar face recognition, and may be disrupted in disorders of face processing.

Chapter 6 showed that DPs exhibit reduced conceptual understanding of naturalistic events that was presumably linked to their impaired face recognition. Given the importance of conceptual information in becoming familiar with a face (Chapters 4 & 5), the reduced acquisition of conceptual knowledge in

DPs may exacerbate difficulties in learning new faces in individuals with DP. The exact mechanism underpinning the relationship between conceptual information and face recognition in DP remains unclear. One possibility is that the reduction in conceptual understanding may reflect an inability to relate the visual instance of a face to the conceptual information associated to it. Such an explanation would suggest that visual-conceptual connections are a key contributor to familiar face recognition, and is supported by the reduced connectivity between visual and non-visual regions in DPs found in Chapter 2. An alternative possibility is that there may be a broader issue with processing conceptual information in DP. This broader issue may reflect acquisition of person knowledge specifically, or it may reflect an overall disruption in conceptual information acquisition which is independent of face processing. Future work could test this by investigating whether DPs have lower conceptual understanding of visual naturalistic narratives in the absence of faces. Audio or written narratives could also be recruited to test whether person-specific knowledge can be acquired in the absence of a visual image of a face. Including narratives with and without person-related knowledge could further disambiguate whether the issue with conceptual information stems from general conceptual difficulties, is specific to person processing, or is a result of face recognition difficulties. If person knowledge specifically is impaired, it may be of relevance to investigate whether other aspects of social cognition, such as social working memory (Krol et al., 2018; Meyer et al., 2012), could also be impaired in DP.

Although DP is considered a face-selective impairment, evidence suggests co-occurring deficits in other cognitive abilities, such as object recognition (Barton et al., 2019; Barton & Corrow, 2016; Biotti et al., 2017; Duchaine et al., 2007; Epihova et al., 2022, 2023) and topographical navigation (Bate, Adams, et al., 2019; Corrow et al., 2016; Klargaard et al., 2016). In Chapter 2, we found lower selectivity for scenes in the parahippocampal place area (PPA) in DPs compared to controls, and also lower neural similarity between DPs during movie watching in scene-selective regions. Recent research has also demonstrated the reduced category selectivity in DPs is not limited to face-selective regions, and that DPs may also show reductions in scene- and body-selective regions (Jiahui et al., 2018). It is not clear why DPs show this reduction in scene processing, but it may provide evidence for a broader impairment in DP. Future research should utilise naturalistic stimuli to help gain a better understanding of the wider impairment associated with DP.

7.4 Challenges and advantages of natural viewing paradigms

Traditional experimental approaches in face recognition often involve presenting participants with a randomized sequence of discrete, static face images, typically in the absence of context. This methodology offers significant advantages, including precise control over confounding variables and straightforward statistical analysis. Although these controlled paradigms have yielded insights into the fundamentals of face recognition, they diverge substantially from the conditions in which we encounter faces in real-world environments. Real-world face perception involves a dynamic integration of sensory inputs over time, during which there is accumulation of visual and conceptual information about a person. This real-world information is ignored in typical experimental paradigms, but may play an important role in visual cognition. Indeed, there is evidence that neural responses can differ between artificial and naturalistic contexts, even at early levels of processing in visual cortex (Hasson et al., 2010).

Naturalistic viewing paradigms provide an opportunity to bridge the gap between laboratory conditions and real-world experience. For instance, movie-watching paradigms simulate the social complexity of natural environments. Because face recognition and other aspects of social cognition are inherently dynamic and context-dependent, ecological validity is particularly crucial. However, the richness of naturalistic stimuli can introduce challenges; it can be difficult to identify which elements from the stimuli are affecting face recognition. Nonetheless, carefully designed paradigms can balance ecological validity with experimental control to address these challenges.

One strategy for minimizing confounds involves presenting all participants with the same stimulus, while recruiting distinct groups to address specific theoretical questions. Using techniques such as intersubject correlation (ISC), it is possible to measure differences across groups. For example, in Chapters 2, 3, 5 and 6, participants with differing familiarity or neurocognitive profiles viewed the same video stimulus. This approach ensures consistent sensory input while enabling comparisons based on group-specific response. It also avoids the need for a control stimulus, with the potential confounds that can be introduced. In Chapter 2, comparison of participants familiar or unfamiliar with the stimulus revealed responses to familiarity, while the inclusion of individuals with DP enabled the examination of the neural correlates of a disorder of face recognition.

Another approach to maintain experimental control during natural viewing is to manipulate the participant's experience of the stimulus without changing the overall sensory input across participants. This method allows experimental manipulation of conceptual understanding while controlling for overall perceptual experience. In Chapters 4 and 5, this approach was used to familiarise participants with faces alongside different levels of conceptual understanding. All participants viewed the same set of video clips, but one group watched them in the original chronological order, while the other group viewed a scrambled sequence. This manipulation preserved perceptual consistency while altering conceptual comprehension of the stimuli. These strategies show how naturalistic viewing paradigms can maintain control over potential confounds while exploring real-world cognitive processes.

Despite these strengths, natural viewing paradigms present unique challenges. For instance, during movie-watching participants are free to move their gaze across the stimulus, introducing variability in fixation patterns. A critical question is whether individual differences in eye movements contribute to observed neural and behavioural differences. Prior studies suggest that naturalistic stimuli elicit remarkably consistent eye movements across observers, even in the presence of substantial manipulations of the stimulus (Hasson, Landesman, et al., 2008; Shepherd et al., 2010; Wang et al., 2012). Moreover, temporal scrambling of movie clips or altering prior contextual knowledge have a minimal effect on gaze patterns (Hutson et al., 2017; Wang et al., 2012). These findings suggest that individual differences in gaze behaviour are unlikely to account for the results presented in this thesis.

7.5 Future directions

The work in this thesis has largely focussed on group differences in face recognition. However, this ignores individual differences in face recognition ability (White & Burton, 2022). Another approach is to investigate whether similarities in one measure between participants relate to similarities in other measures. Individual approaches can provide a more nuanced understanding of mechanisms underlying face recognition. For example, in Chapter 4, we adopted this approach to show that the similarity in conceptual knowledge predicted faces that were recognized. Research in other fields of social cognition has demonstrated that similarities between participants' behavioural profile relate to neural response. For example, similarities in the understanding of a narrative or political views across individuals have been related to similarities in neural response during naturalistic viewing paradigms (Nguyen et al., 2019; van Baar et al., 2021). Extending such approaches to face recognition could illuminate the relationship between behavioural and neural responses. For example, future work could investigate whether more similar conceptual representations of a face correspond to more similar neural responses, and whether this occurs in visual or non-visual regions of the brain. Furthermore, it remains unclear how these effects differ during encoding compared to recognition. Chapter 5 demonstrated modulation of non-visual regions during the recognition of faces associated with conceptual information, but did not provide direct evidence of differences at encoding. The levels of processing framework would predict that non-visual regions would likewise be more engaged during encoding of faces associated with conceptual information. One way of testing this would be to see if similarity between participants in the faces they recognised from the video related to similarity in neural response in non-visual brain regions during encoding.

While the importance of conceptual information in familiar face recognition has been established, questions still remain regarding which elements are most critical. This thesis grouped conceptual information under a broad category encompassing semantic, episodic and affective information. However, isolating and independently assessing these dimensions could clarify their respective roles. For instance, participants' descriptions of identities learned during natural viewing could be analysed for episodic, semantic and affective content. This approach could determine if identities with richer representations in any specific domain are better recognised or have more distinct neural profiles. These findings might have implications for remedial treatments in disorders of face processing. For example, Chapter 6 highlighted reduced conceptual understanding in individuals with DP. This aligns with recent work showing that DPs struggle with names but not occupations of newly learned faces (Palsamudram et al., 2024). Identifying the types of information that are important for developing a strong representation of a face could help tailor recognition strategies in people with face recognition difficulties.

Future work could explore the contributions of perceptual and conceptual information in other aspects of face recognition. The other race effect, characterised by the better recognition of own race than other race faces, has been attributed to both perceptual (Meissner & Brigham, 2001; Wang et al., 2023) and social mechanisms (Levin, 1996, 2000). Recent research shows that learning other race faces while making social evaluations leads to better recognition than when faces are learnt solely through perceptual experience (Schwartz et al., 2023). Indeed, it may be that conceptual information could lead to a reduction in the other race effect. Might the other race effect also extend to conceptual information associated with others; for instance, are individuals worse at recalling person knowledge associated with other race faces? Similarly, in autism spectrum condition, face recognition difficulties (Weigelt et al., 2012) have been attributed to both perceptual (Jones et al., 2008) and social mechanisms (Dawson et al., 2002). Neuroimaging studies have revealed disruptions in connectivity between visual and non-visual regions of the brain in autistic individuals during face processing (Koshino et al., 2008; Thomas et al., 2011). The connectivity findings in this thesis suggest that these disruptions may reflect challenges in integrating perceptual and conceptual information. Future research could investigate whether the ability to acquire conceptual information mediates face recognition performance in autistic individuals, shedding light on potential therapeutic interventions.

The importance of connectivity between visual and non-visual brain regions in familiar face recognition warrants further exploration. For example, while Chapter 2 highlighted the role of connectivity between visual and non-visual regions, it remains unclear whether these contributions were primarily feedforward or feedback. Existing evidence suggests feedback (Fan et al., 2023) and feedforward processes (Karimi-Rouzbahani et al., 2021) during familiar face recognition. Investigating the directionality of information flow during natural viewing could clarify the active role of conceptual information in face recognition. Previous work has demonstrated that functional connectivity differences relate to differences in behaviour across people (Finn & Bandettini, 2021; Liu et al., 2019), and that individuals even have a functional connectivity fingerprint which relates to individual differences in behaviour (Finn et al., 2015). An individualistic approach to functional connectivity could be used to investigate how differences in face recognition behaviours relate to underlying connectivity patterns.

The duration of exposure to faces during familiarization may significantly influence recognition performance and neural responses. In Chapter 2, prolonged exposure (8 seasons of TV show) yielded large behavioural and neural effects compared to individuals who had no exposure. By contrast, Chapters 4 and 5 used relatively brief exposures (20 minute movie) resulting in much smaller, albeit significant, effects. Future work could extend the exposure to faces by showing participants a whole TV series, either in the original order or a scrambled order, to provide stronger support for the hypothesis that conceptual knowledge influences face recognition in the real world.

7.6 Conclusions

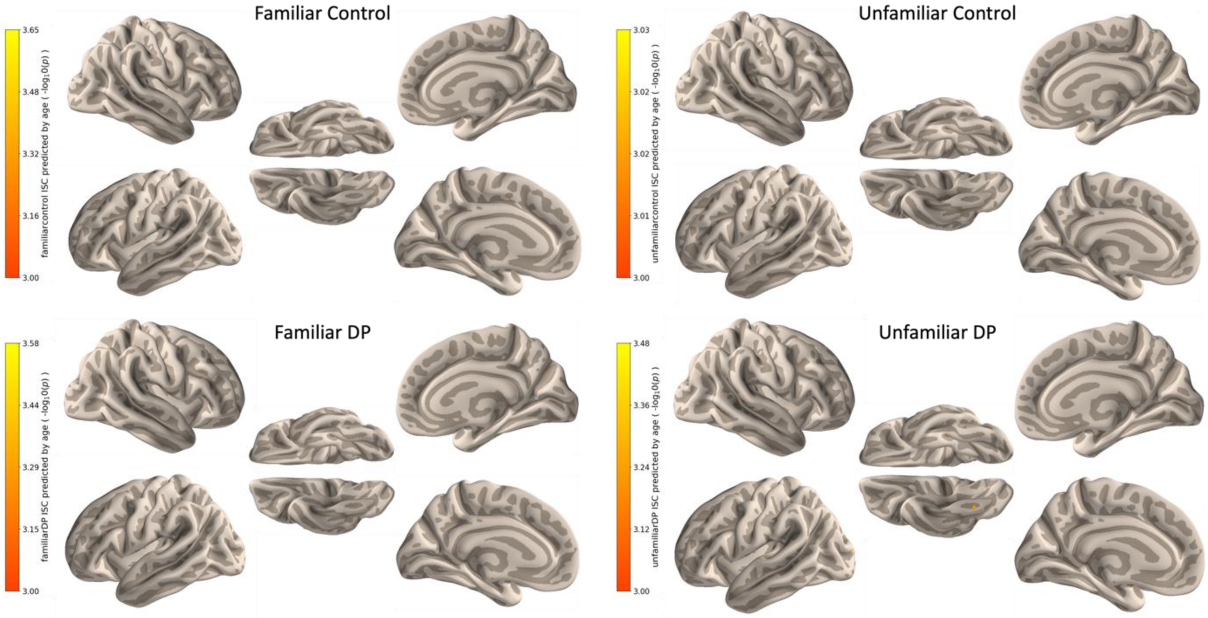
The primary aim of this thesis was to investigate the neural correlates of familiar face processing under naturalistic conditions, and to elucidate the role of conceptual information in this process. A key question in understanding the neural basis of familiar face processing is whether the critical processes involved in recognition occur within core face-selective regions in the visual brain, or in the extended face network. In Chapter 2 and 3, a natural viewing paradigm using fMRI revealed differences in the neural response to familiar compared to unfamiliar faces occur in a distributed network beyond visual cortex. This extended network demonstrated stronger activation in neurotypical controls compared to individuals with developmental prosopagnosia. The findings in Chapter 2 and 3 also show that connectivity between core face-selective regions in visual areas of the brain and this extended network in non-visual regions is increased for familiar face recognition. Moreover, this connectivity profile was significantly reduced in DPs, and significantly increased in hyperfamiliarity for faces, suggesting it may a critical mechanism supporting familiar face recognition.

Traditional theories of familiar face recognition propose that an invariant visual representation underpins recognition. However, the observed involvement of non-visual brain regions raises the question of whether the conceptual information processed in these regions contributes to face recognition. To address this, Chapter 4 explored the interplay of conceptual and perceptual information in becoming familiar with a face during natural viewing. The results demonstrated that faces are more accurately recognised when learned alongside naturally occurring conceptual information. Chapter 5 further revealed that this conceptual information alters the neural response during recognition in non-visual regions of the brain. In Chapter 6, individuals with DP showed reduced conceptual understanding during natural viewing, providing further evidence for a relationship between conceptual information and familiar face processing. Together, these findings highlight the integral role of conceptual information in shaping the neural representation and recognition of familiar faces.

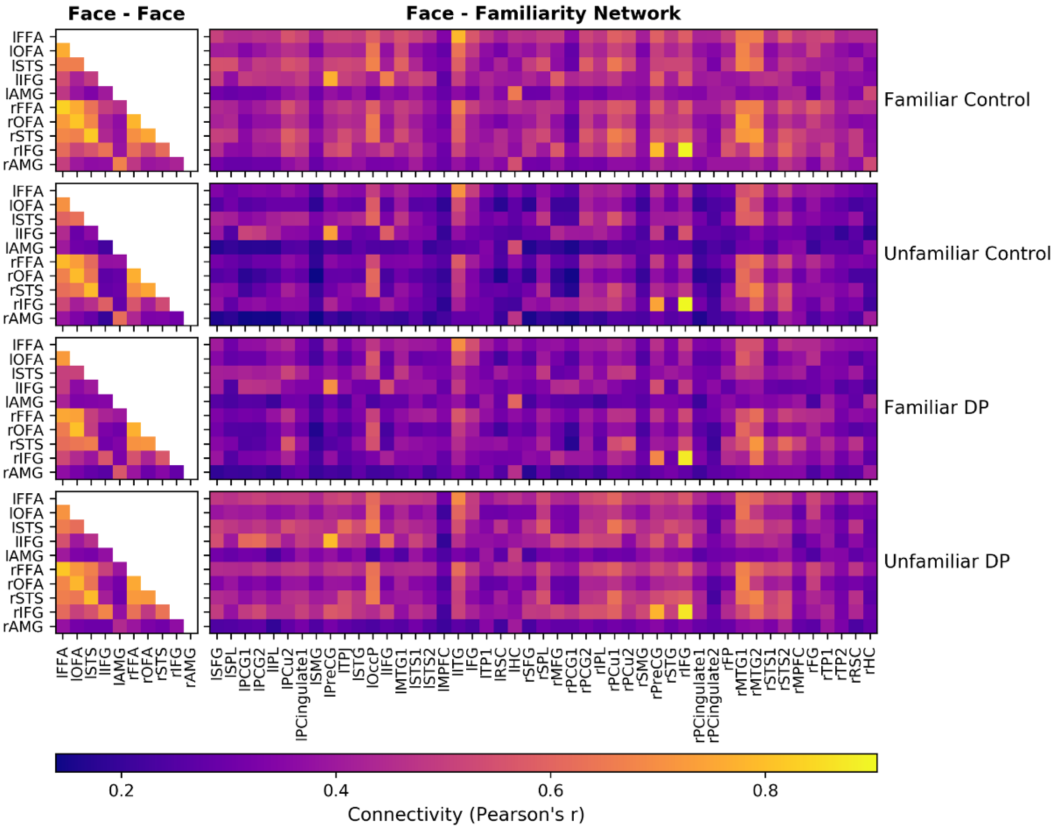
In conclusion, this thesis has investigated the neural mechanisms underlying familiar face processing during natural viewing. The findings underscore the importance of non-visual brain regions in supporting the visual recognition of familiar faces, and show how disruption to these regions occurs in disorders of face processing. Moreover, the results establish conceptual information as a critical component in the process of familiarization and recognition, influencing neural responses beyond visual cortex. These findings contribute novel insights to theoretical models of face recognition and provide a new framework for understanding the interaction between perceptual and conceptual processes in social cognition.

Appendices

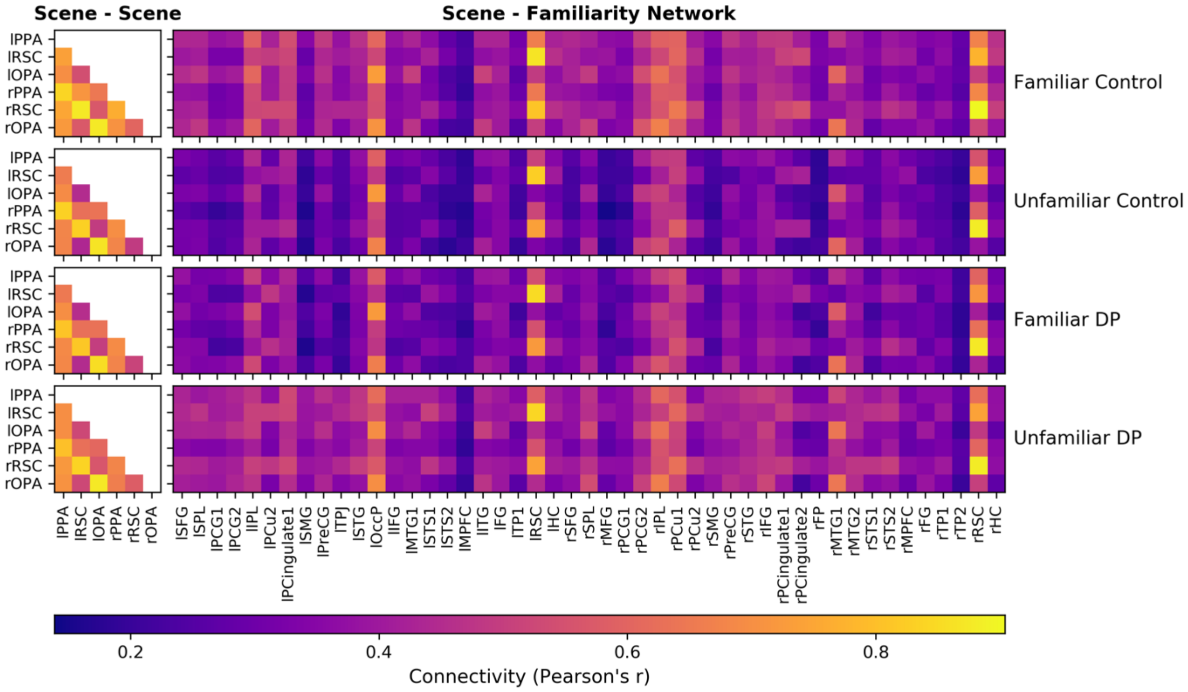
Appendix A1: Chapter 2



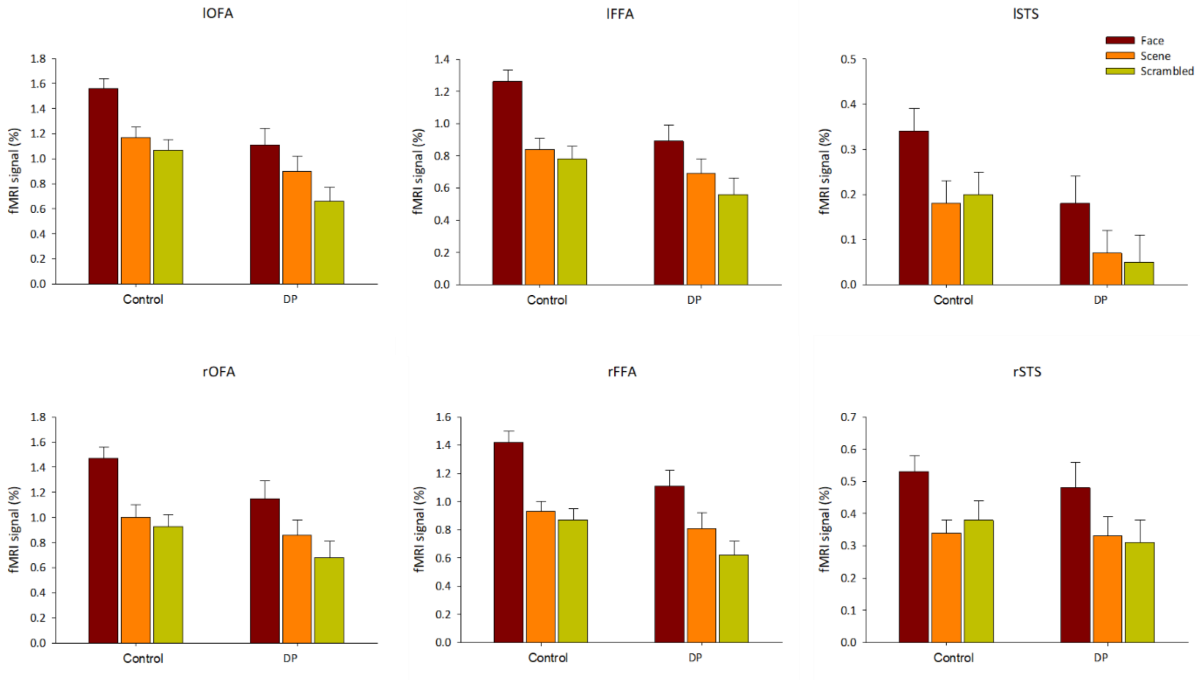
Supplementary Figure 2.1. Age did not predict inter-subject correlations (ISC). Prediction of intersubject correlations by age are shown for each group of participants, uncorrected and thresholded at $p < .001$ ($-\log_{10}(p) > 3$).



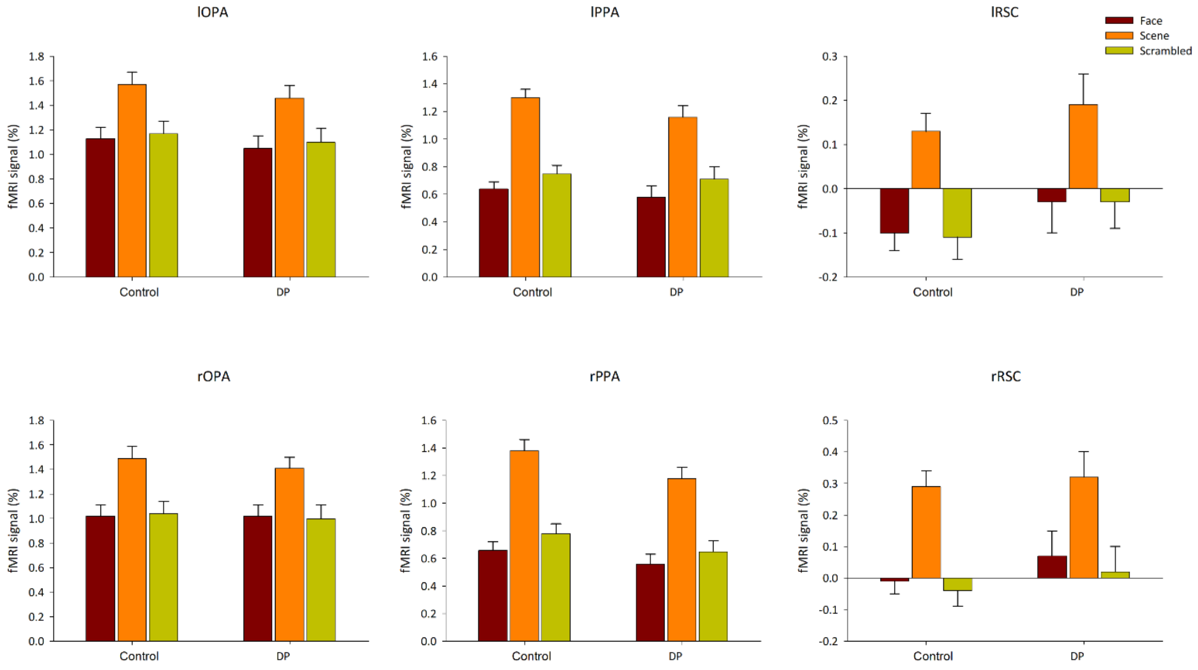
Supplementary Figure 2.2. Functional connectivity for familiar and unfamiliar controls and DPs in (left) face-selective regions and (right) between face-selective regions and the familiarity network. Patterns of connectivity are similar across groups.



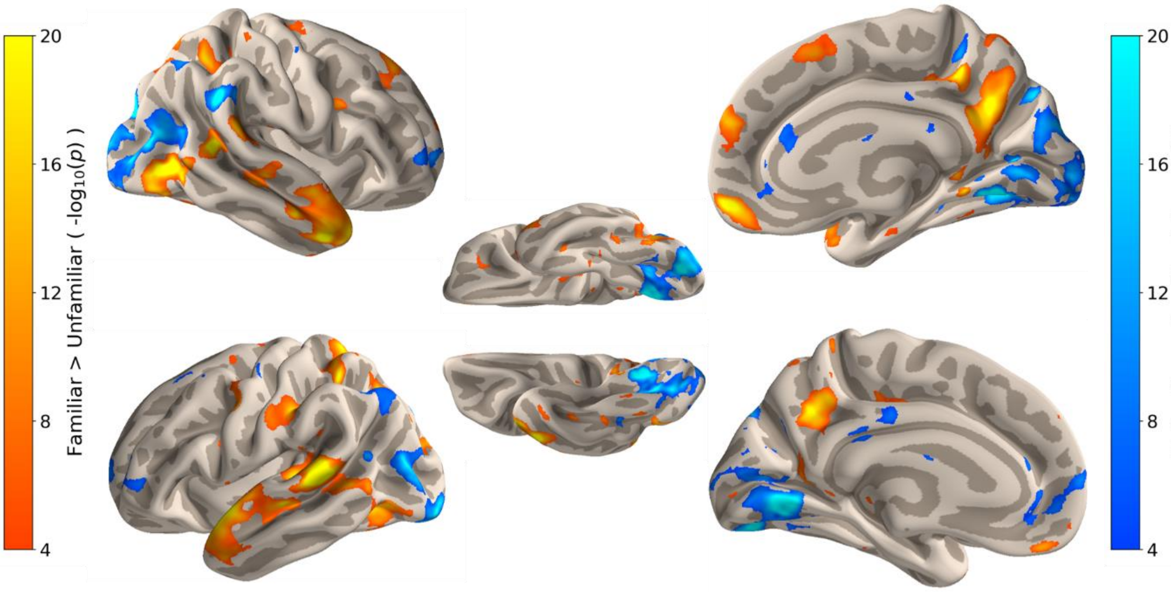
Supplementary Figure 2.3. Functional connectivity for familiar and unfamiliar controls and DPs in (left) scene-selective regions and (right) between scene-selective regions and the familiarity network. Patterns of connectivity are similar across groups.



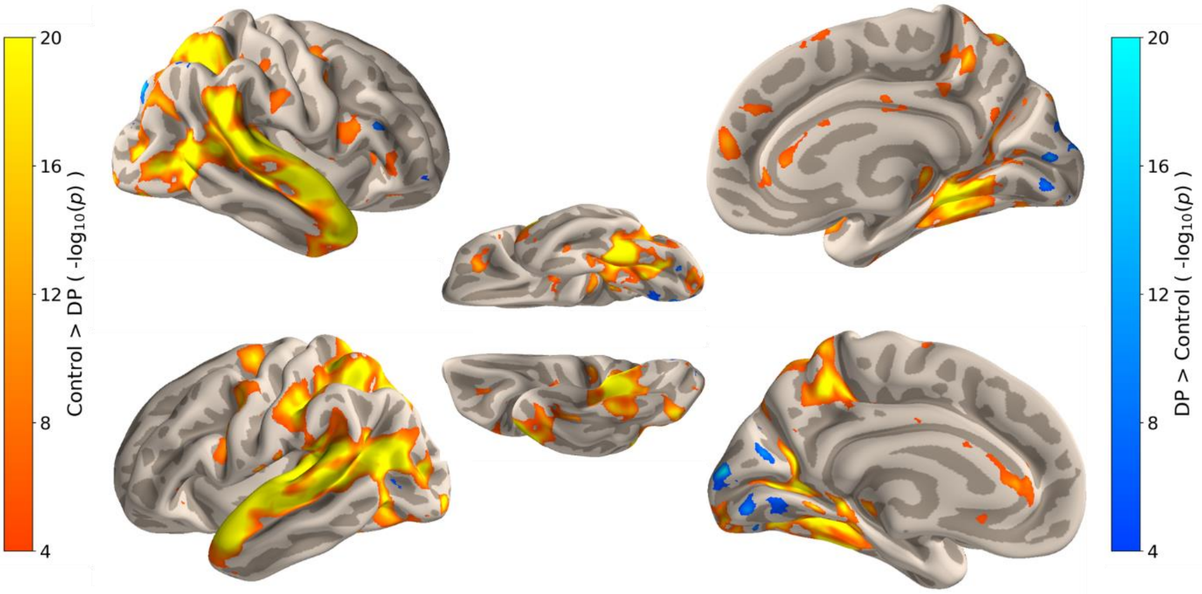
Supplementary Figure 2.4. Response to faces, scenes and scrambled faces in face regions in the control and DP groups.



Supplementary Figure 2.5. Response to faces, scenes and scrambled faces in scene regions in the control and DP groups.



Supplementary Figure 2.6. Regions showing a main effect of familiarity (control familiar + DP familiar > control unfamiliar + DP unfamiliar).



Supplementary Figure 2.7. Regions showing a main effect of group (control familiar + control unfamiliar > DP familiar + DP unfamiliar).

Supplementary Table 2.1. Individual scores on the PI20 questionnaire and Cambridge Face Memory Test (CMFT) used to validate developmental prosopagnosia. High scores on the PI20 indicate more prosopagnosic traits. Low scores on the CFMT show worse face memory performance. Control comparison data (*N* = 54) for the PI20 and CFMT were taken from Biotti et al., (2019).

Participant	Age	Gender	Familiarity	Handedness	PI20 Score	CFMT score (%)	zPI20	zCFMT
1	56	F	N	R	74	58.33	3.96	-3.00
2	40	M	N	R	76	62.5	4.18	-2.53
3	49	F	N	R	87	44.44	5.38	-4.56
4	27	F	N	R	83	59.72	4.95	-2.84
5	53	F	N	R	84	54.17	5.05	-3.46
6	69	M	N	L	65	48.6	2.97	-4.09
7	55	M	N	R	84	51.39	5.05	-3.78
8	50	F	N	R	86	62.5	5.27	-2.53
9	48	M	N	R	77	56.94	4.29	-3.15
10	48	M	N	R	88	48.61	5.49	-4.09
11	53	M	N	R	87	58.3	5.38	-3.00
12	54	M	N	R	80	43.1	4.62	-4.71
13	55	F	N	R	83	51.4	4.95	-3.78
14	39	F	N	R	75	45.8	4.07	-4.40
15	33	M	N	R	75	48.6	4.07	-4.09
16	50	F	Y	R	81	63.89	4.73	-2.37
17	42	F	Y	R	80	56.9	4.62	-3.16
18	60	F	Y	R	90	44.4	5.71	-4.56
19	32	F	Y	L	89	47.22	5.60	-4.24
20	55	F	Y	R	92	54.1	5.93	-3.47
21	23	M	Y	R	85	27.8	5.16	-6.43
22	46	M	Y	R	79	59.7	4.51	-2.84
23	38	F	Y	R	83	43.1	4.95	-4.71
24	29	F	Y	R	74	61.1	3.96	-2.69
25	28	F	Y	R	78	52.8	4.40	-3.62
26	23	M	Y	R	72	44.5	3.74	-4.55
27	43	F	Y	R	54	51.4	1.76	-3.78
28	25	M	Y	R	78	61.1	4.40	-2.69
DPs Mean					79.96	52.23		
DPs SD					8.00	8.15		
Comparison Mean					38.0	85.0		
Comparison SD					9.1	8.9		

Supplementary Table 2.2. MNI coordinates of the centre of face- and scene-selective region masks from the face > scrambled face + scene, and scene > face + scrambled face contrasts from the localiser for control participants.

Region	Hemisphere	Coordinates			Mask size (voxels)	Threshold (z)
		x	*y*	*z*		
Occipital face area	R	47	-77	-4	250	6.47
	L	-44	-79	-8	250	5.82
Fusiform face area	R	42	-50	-18	250	6.25
	L	-39	-51	-20	249	5.99
Superior temporal sulcus	R	50	-61	14	249	4.88
	L	-44	-68	16	250	4.38
Inferior frontal gyrus	R	40	11	30	250	3.85
	L	-41	6	35	250	3.26
Amygdala	R	21	-4	-14	227	3.11
	L	-20	-3	-15	250	3.17
Occipital place area	R	34	-83	17	250	7.95
	L	-29	-90	16	250	7.54
Parahippocampal place area	R	26	-44	-9	250	8.91
	L	-24	-52	-10	250	8.19
Retrosplenial Cortex	R	18	-52	10	250	5.98
	L	-18	-55	8	250	5.05

Supplementary Table 2.3. MNI coordinates of maximally responding voxel of cluster regions revealed in the familiar control > unfamiliar control whole brain contrast

Region	Hemisphere	Coordinates			Mask size (voxels)	Threshold (-log$_{10}$(p))
		x	*y*	*z*		
Superior Frontal Gyrus	R	18	-4	62	100	9.65
	L	-28	-6	68	100	7.98
Superior Parietal Lobule	R	26	-44	54	100	14.3
	L	-20	-50	60	100	17.8
Medial Frontal Gyrus	R	6	16	62	67	4.02
Postcentral Gyrus 1	R	52	-32	52	100	6.61
	L	-44	-42	52	100	8.18
Precuneus 1	R	4	-46	50	100	11.1
Intraparietal Lobule	R	22	-70	48	100	8.12
	L	-18	-68	44	100	7.92
Postcentral Gyrus 2	R	26	-40	48	100	8.16
	L	-42	-42	50	100	15.3
Precuneus 2	R	2	-58	34	100	14.5
	L	-2	-56	42	100	11.1
Posterior Cingulate 1	R	16	-34	42	94	4.01
	L	-12	-20	40	100	6.41
Supramarginal Gyrus	R	60	-28	26	100	6.83
	L	-54	-24	32	100	11.2
Precentral Gyrus	R	44	4	28	100	4.20
	L	-50	2	34	92	5.43
Temporoparietal junction	L	-60	-50	22	100	10.1
Superior Temporal Gyrus	R	50	-32	22	100	11.1
	L	-48	-36	30	100	5.85
Occipital Pole	L	-18	-84	18	102	5.33
Inferior Frontal Gyrus	R	34	12	24	100	8.75
	L	-44	6	20	100	8.22
Posterior Cingulate 2	R	2	-36	18	70	4.03
Frontal Pole	R	4	58	30	100	5.21
Retrosplenial Cortex	R	18	-52	14	63	4.14
	L	-20	-58	14	77	4.00
Middle Temporal Gyrus 2	R	54	-46	6	100	9.14
Middle Temporal Gyrus 1	R	48	-62	0	100	14.2
	L	-58	-62	2	99	6.03
Superior Temporal Sulcus 1	R	54	-10	-2	100	7.76
	L	-44	-26	2	100	6.56
Superior Temporal Sulcus 2	R	54	-2	-10	100	5.61
	L	-68	-36	8	100	14.6
Medial Prefrontal Cortex	R	6	54	-12	100	5.75
	L	-2	48	-20	90	4.03
Hippocampus	R	18	-26	-10	39	4.03
	L	-26	-22	-8	83	4.01
Inferior Temporal Gyrus	L	-44	-42	-14	100	8.34
Fusiform Gyrus	R	44	-34	-20	94	4.01

	L	-32	-28	-24	100	4.44
Temporal Pole 1	R	54	16	-16	75	6.20
	L	-58	10	-10	100	7.68
Temporal Pole 2	R	38	8	-44	90	4.01

Supplementary Table 2.4. Percentage overlap and maximum t-value of face- and scene-selective regions with the unfamiliar control > unfamiliar DP contrast. There is an overlap with the core face regions and regions that showed greater ISCs in unfamiliar controls than unfamiliar DPs.

Region	**Hemisphere**	**% overlap**	***t***
Occipital face area	R	30.4	7.93
	L	20	7.17
Fusiform face area	R	28.8	8.10
	L	32	10.2
Superior temporal sulcus	R	1.6	-9.64
	L	0	3.70
Inferior frontal gyrus	R	0	-3.73
	L	0	2.95
Amygdala	R	0	4.04
	L	0	4.01
Occipital place area	R	10	5.05
	L	30	6.40
Parahippocampal place area	R	83.6	10.4
	L	20.8	6.09
Retrosplenial Cortex	R	12.4	6.52
	L	29.6	7.68

Supplementary Table 2.5. MNI coordinates of the maximum responding voxels of the regions from the control > developmental prosopagnosia face > scene and scene > face contrast from the localiser

		Coordinates			
Contrast	**Hemisphere**	***x***	***y***	***z***	**Z value**
Face > Scene + Scrambled Faces	L	-38	-58	-22	3.25
Scene > Face + Scrambled Faces	R	16	-38	-14	3.77
	L	-34	-42	-9	3.77

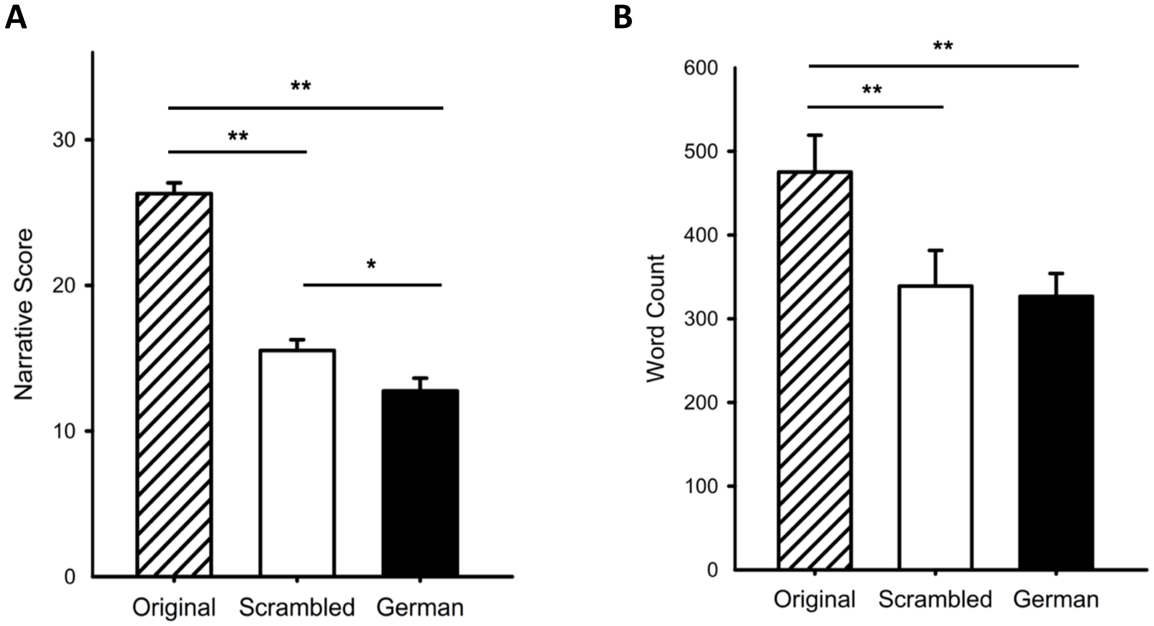
Supplementary Table 2.6. One-tailed Welch's t-tests (assuming unequal variances) to show the difference in signal for controls vs DPs from the localiser scan for faces, scene and scrambled faces.

Region	Hemisphere	Face		Scene		Scrambled faces	
		t	*p*	*t*	*p*	*t*	*p*
Occipital face area	R	1.86	.034	0.87	.194	1.57	.061
	L	2.87	.003	1.91	.030	2.85	.006
Fusiform face area	R	2.14	.018	0.97	.169	1.94	.029
	L	3.02	.002	1.33	.094	1.78	.040
Superior temporal sulcus	R	0.49	.313	0.14	.444	0.77	.221
	L	1.94	.028	1.71	.046	2.00	.025
Occipital place area	R	-0.00	.498	0.62	.270	0.24	.404
	L	0.66	.257	0.77	.223	0.42	.338
Parahippocampal place area	R	1.17	.122	1.86	.033	1.23	.112
	L	0.72	.237	1.33	.094	0.37	.355
Retrosplenial Cortex	R	-0.92	.180	-0.38	.352	-0.57	.284
	L	-0.87	.194	-0.69	.246	-1.07	.144

Appendix A2: Chapter 4

Pilot Study

We performed an exploratory online pilot study with 156 (82 completed both time points) participants to investigate the interaction between perceptual and conceptual information in face recognition. The results validate the experimental design for the main experiment and generate estimated effect sizes for a sample size computation. The methods and design are identical to the proposed study, except an additional condition was included. Participants in the additional German condition watched the movie clips in the original order but with the soundtrack dubbed in German, meaning that the narrative was incoherent.

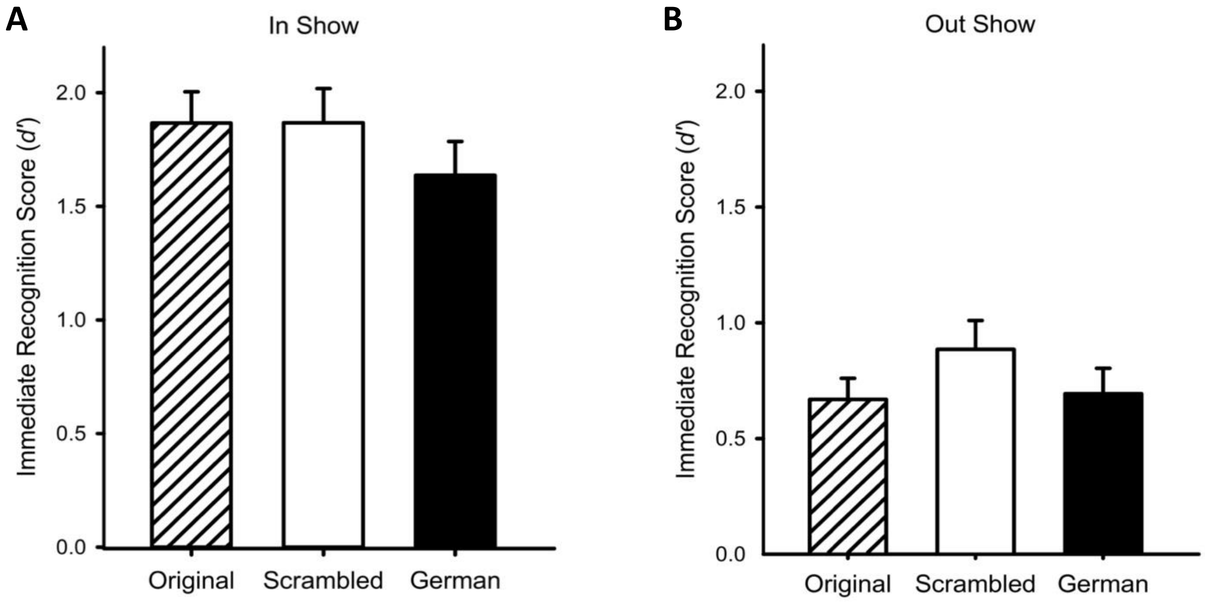


Supplementary Figure 4.1. Performance on narrative tests of conceptual understanding across the different experimental conditions in pilot study a) and difference in word count in the free recall task between conditions b). This shows that conceptual understanding was greater in the Original condition compard to the Scrambled or German conditions. Error bars indicate standard error. ** p < .001, * p < .05

Suppl. Fig. 4.1 shows the differences in contextual understanding across the different conditions (Original, Scrambled, German). A one-way ANOVA revealed a significant difference in narrative score between the conditions ($F(2,153) = 88.82$, $p < .001$, $\eta^2 = 0.54$). Planned comparisons showed that the narrative score for the Original condition was significantly greater than for the Scrambled ($p < .001$), and the German condition ($p < .001$). The Scrambled and German group were significantly different (p

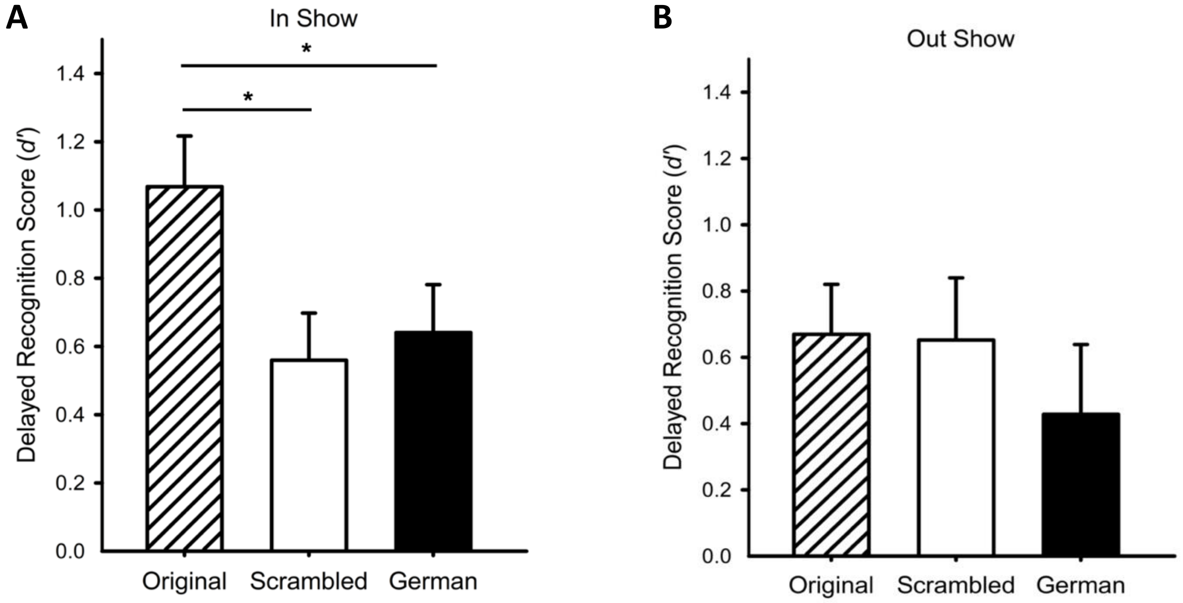
= .013). Agreement between raters for the conceptual understanding tests was calculated using intra-class correlation coefficient (ICC) with a two-way mixed model and Agreement definition. Excellent agreement was found between raters in the free recall test with an ICC of .91 and 95% confidence intervals of .88 to .94 ($F(155,155) = 22$, $p < .001$) and in the structured question test with an ICC of .93 and 95% confidence intervals of .90 to .95 ($F(155,155) = 27$, $p < .001$). We also measured the total word count across the conditions in the Free Recall task. A one-way ANOVA revealed significant differences in word count between the conditions ($F(2,153) = 4.77$, $p = .010$, $\eta^2 = 0.06$). The mean score for the Original condition was significantly higher than for the Scrambled ($p = .012$) or German ($p = .006$) conditions. This indicates a more detailed response in the Original condition. There was no significant difference between the Scrambled and German group in mean word count ($p = .827$). Together, these findings show that the contextual understanding of the stimulus was greatest in the Original condition.

Next, we investigated the extent to which differences in conceptual understanding affected face recognition. First, we measured face recognition immediately after participants had watched the movie. Suppl. Fig. 4.2 shows differences in recognition across the different conditions. A one-way ANOVA showed that there was no significant effect of condition on the In Show ($F(2,153) = .901$, $p = .409$, $\eta^2 = 0.01$) or Out of Show ($F(2,153) = 1.25$, $p = .288$, $\eta^2 = 0.02$) faces. This implies that differences in contextual information did not influence the recognition of faces. Rather, it would appear that recognition is based on the overall visual or perceptual experience of the faces.



Supplementary Figure 4.2. Immediate face recognition performance (d') for each condition for pilot study. a) shows d' for In Show faces stimuli and **b**) shows d' for Out of Show faces. Error bars indicate standard error.

We then repeated the face memory task after approximately 4-weeks to explore how the consolidation of the events influenced face recognition. Although all of the 156 participants were invited to take part, only 82 completed the task (Original N = 27, Scrambled N = 27, German N = 28). The average delay between the immediate and delayed tasks was 65.4 + 33.2 days, which was equivalent across groups. In contrast to the pre-registered study, the same images were used in both the immediate and delayed face recognition tests. Suppl. Fig. 4.3 shows the mean face recognition scores for each condition. There was a significant difference in the recognition of In Show faces across the conditions (F(2,79) = 4.51, p = .014, $\eta 2$ = 0.103). This difference for In Show faces reflects a significant difference between the Original condition and both the Scrambled (p = .005) and German (p = .032) conditions. There was no difference between the Scrambled and German conditions for In Show faces (p = .474). In contrast, there was no effect of condition for the Out of Show faces (F(2,79) = .58, p = .560, $\eta 2$ = 0.016). This suggests a consolidation of contextual and perceptual knowledge leads to increased face recognition. However, this is only evident for faces from the In Show condition. This suggests that the effect of consolidation is restricted to face images that are similar to those seen at encoding.



Supplementary Figure 4.3. Long-term face recognition performance (d') for each condition for pilot study. a) shows d' for In Show faces stimuli and **b**) shows d' for Out of Show faces. Error bars are standard errors. * p < .05

To investigate the role of conceptual information and consolidation on subsequent face recognition, two-tailed independent groups t-tests were run on the difference in face recognition score at the immediate and delayed time-point for the In Show and Out of Show images separately. There was no significant difference in recognition of In Show faces after a delay between the Original (M = 0.81, SD

= 1.03) and German (M = 0.95, SD = 1.01) groups (*t*(52.8) = 0.52, *p* = .608, d = 0.139). There was no significant difference in recognition of Out of Show faces after a delay between the Original (M = -0.02, SD = 0.79) and Scrambled (M = 0.27, SD = 0.97) groups (*t*(49.9) = 1.2, *p* = .235, d = 0.327) or the Original and German (M = 0.07, SD = 1.06) groups (*t*(49.9) = 0.36, *p* = .723, d = 0.095). However, there was a near significant difference in recognition of In Show faces after a delay between the Original and Scrambled (M = 1.3, SD = 1.03) groups (*t*(52) = 1.75, *p* = .086, d = 0.476), suggesting that conceptual understanding and consolidation under some conditions may be important for subsequent recognition of faces with a similar visual context.

To investigate how the appearance of the image at encoding affects face recognition, one-tailed independent groups t-tests were run on the In Show and Out of Show average d prime scores over both time points for the Original condition and Scrambled condition separately. A significant difference between the In Show (M = 1.47, SD = 0.75) and Out of Show (M = 0.66, SD = 0.67) images was found for the Original condition (*t*(51.3) = 4.23, *p* < .001, d = 1.150). Similarly, a significant difference between the In Show (M = 1.15, SD = 0.67) and Out of Show (M = 0.79, SD = 0.69) images was found for the Scrambled condition (*t*(51.9) = 1.9755, *p* = .028, d = 0.538). This is consistent with the idea that suggests face memory is dependent on the specific perceptual experience (Juncu et al., 2020; Ritchie & Burton, 2017).

To investigate if, after consolidation, conceptual knowledge has a greater effect on recognition of faces that are similar to the appearance at encoding, two-tailed independent groups t-tests were run on the difference in face recognition scores for the In Show and Out of Show images for each condition at the immediate and delayed time-point. There was no significant difference in recognition of In Show and Out of Show faces at the immediate time point between the Original (M = 1.23, SD = 1.22) and German (M = 1.1, SD = 0.97) conditions (*t*(49.6) = 0.45, *p* = .656, d = 0.122) or between the Original and Scrambled (M = 0.88, SD = 1.1) conditions (*t*(51.4) = 1.10, *p* = .276, d = 0.299). There was no significant difference in recognition of In Show and Out of Show faces at the delayed time point between the Original (M = 0.4, SD = 0.92) and German (M = 0.21, SD = 1.21) conditions (*t*(50.3) = 0.64, *p* = .523, d = 0.173). However, there was a significant difference in recognition of In Show and Out of Show faces at the delayed time point between the Original and Scrambled (M = -0.15, SD = 0.78) group at the delayed time point (*t*(50.5) = 2.37, *p* = .022, d = 0.644), showing that recognition of In Show faces was greater than Out of Show faces after a delay for the Original group compared to the Scrambled group. This shows the importance of consolidation of conceptual knowledge for recognition of faces, but only for faces that are similar in appearance to those at encoding.

Supplementary Table 4.1. Hypotheses, sampling and analysis plan for each of the research questions

Hypothesis		Sampling plan	Analysis Plan	Interpretation given different outcomes	Theory that could be shown wrong by the outcomes
1. Manipulating the order of the events in the movie will affect understanding of the narrative or context	1.1. A greater understanding of the narrative as shown in the free recall test will be found in the Original condition than the Scrambled condition.	A sensitivity analysis has been computed for a one-sided independent t-test with a power of 0.9 and alpha level of 0.02. Our proposed sample size of 100 participants per condition (Original and Scrambled) is sufficient to detect the effect size for hypothesis 1.1 (d = 1.96 [upper CI: 2.43, lower CI: 1.49]), for hypothesis 1.2 (d = 1.55 [upper CI: 1.99, lower CI: 1.12]) and for hypothesis 2 (d = 0.476 [upper CI: 1.03, lower CI: -0.078]) found in the pilot study (see figure 4.1).	A one-tailed independent groups t-test will be performed to determine if conceptual understanding scores in the free recall test are greater in the Original compared to the Scrambled condition. A statistical effect of condition at *p*<.02 will confirm hypothesis 1.1.	A significant effect of condition would show that the movie manipulation has successfully affected conceptual understanding. A lower score for the Scrambled condition compared to the Original condition will show that a coherent context leads to better understanding. Successful manipulation of movie context understanding will be concluded only if both hypothesis 1.1 and 1.2 are confirmed. A higher score for the Scrambled condition compared to the Original condition would disconfirm the hypothesis.	A null result would suggest that the movie manipulation did not affect conceptual understanding as intended. The outcome of experimental hypotheses 2 and 4 cannot be interpreted as due to the effects of context.
	1.2. A greater understanding of the narrative as shown in the structured question test will be found in the Original condition than the Scrambled condition.		A one-tailed independent groups t-test will be performed to determine if the structured question test scores are greater in for the Original compared to the Scrambled conditions. A statistical effect of condition at *p*<.02 will confirm hypothesis 1.2.		
2. The recognition of faces after a delay will depend on the context in which they were originally presented			The difference between the immediate and delayed face recognition scores (immediate – delayed) will be calculated separately for the Original and Scrambled conditions using the In Show images. A one-tailed independent groups t-test will then be performed to determine if the difference scores are greater in the Scrambled compared to the Original condition. A statistical difference at *p*<.02 will confirm hypothesis 2.	A larger difference in face recognition between the immediate and delayed timepoints in the Scrambled compared to the Original condition would show that the context in which a face is presented influences subsequent recognition, if it has been consolidated into memory. If there is no difference or a larger difference in recognition in the Original compared to the Scrambled condition, then this would disconfirm the hypothesis.	A null result for In Show images would suggest that consolidation of conceptual information does not have a role in face learning and recognition. This would challenge models of memory consolidation (Lewis & Durrant, 2011), which posit that consolidation is necessary. for extraction of contextual information into memory. A significant result would support the role of contextual understanding and consolidation in face learning, which is not central to current models of face learning.

3. Recognition of faces images will be greater if they are consistent with the appearance at encoding	Based on the sensitivity analysis (see figure 4.1), our proposed sample size of 100 participants per condition (Original and Scrambled) is sufficient to detect the effect size found in the pilot for hypothesis 3 (d = 1.15 [upper CI: 1.7, lower CI: 0.56]).	Recognition of In Show faces and Out of Show faces will be averaged across the immediate and delayed timepoints in the Original condition. A one-tailed independent groups t-test will be performed to assess if recognition of In Show faces is greater than Out of Show faces. A statistical effect of condition at $p<.02$ will confirm hypothesis 3.	Higher recognition of In Show compared to Out of Show images would show that face memory is dependent on visual experience at encoding. A non-significant effect or greater recognition of Out of Show images than In Show images would disconfirm hypothesis 3.	A significant result would support theory that suggests face memory is dependent on perceptual experience at encoding (Juncu et al., 2020; Ritchie & Burton, 2017). A null result would challenge current theory about the importance of experience with within-person variability in face recognition.
4. The effect of context on the recognition of faces after consolidation will be greater if the images are consistent with the appearance at encoding	Based on the sensitivity analysis (see figure 4.1), our proposed sample size of 100 participants per condition (Original and Scrambled) is sufficient to detect the effect size found in the pilot for hypothesis 4 (d = 0.64 [upper CI: 1.2, lower CI: 0.08]).	The difference between In Show and Out of Show face recognition scores (In Show – Out of Show) will be calculated for the Original and Scrambled groups at the delayed timepoint. A one-tailed independent groups t-test will determine if the difference scores in the Original condition are greater than in the Scrambled condition. A statistical effect at $p<.02$ will confirm hypothesis 4.	A greater difference between In Show and Out of Show face recognition in the Original compared to the Scrambled condition at the delayed timepoint would show that the effect of context on face recognition following consolidation is greater when the face images are consistent with the way that they appeared at encoding. A non-significant result would imply that the effect of context on face recognition following consolidation does not depend on whether the face images are consistent with the appearance at encoding.	A null result would challenge current theory about the importance of experience with within-person variability in face recognition. A significant result would support theory that suggests face memory is dependent on perceptual experience at encoding (Juncu et al., 2020; Ritchie & Burton, 2017), and support the role of conceptual understanding and consolidation in face learning, which is not central to current models of face learning.

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