Understanding variability in processing facial expressions: Behavioural and neuroimaging studies

A thesis submitted for the degree of Doctor of Philosophy

By

Thomas Oliver Murray

Department of Life Sciences

Brunel University London

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I, Thomas Oliver Murray, declare that the work presented in this thesis is my own and will not be submitted to another institution for the award of any other degree. It is clearly stated within the thesis where information or data has been derived from other sources.

Abstract

The ability to perceive and recognise facial expressions of emotion is an important part of social communication. These processes are subject to influence from several internal and external sources of variance. The aim of the research within this thesis is to explore the relative contribution of some of these sources of variance on the processing of facial expressions. Under this broad aim, two main problems are addressed, using a combination of behavioural and neuroimaging methods in each.

The first concerns the effect of observer age on the recognition of emotions from facial expressions. We showed that (1) older adults have poorer recognition of certain facial expressions than younger adults, and that these differences are explained by differences in several cognitive and visual measures, and (2) that the neural response to facial expressions attenuates across the lifespan.

The second problem concerns the relative influence of stimulus-based cues and conceptual knowledge of emotions on behavioural and brain representations of emotion. Within this set of studies, we showed that perceptual similarity and confusability of facial expressions of emotion are explained by the similarity of face shapes, surface textures, and similarity of emotion concepts. In addition to behavioural measures, we found that these cues can explain representational similarity within several regions of the brain involved in the perception of facial expressions.

Together, the results highlight several sources of variance affecting the processing of facial expressions of emotion in adults. These studies also pave the way for future research to investigate age differences from the perspective of differences in the role of conceptual and stimulus-based cues.

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1 Literature review

1.1 Facial Expressions of Emotion

The experience of an emotion can cause physiological changes to a person's face, conveying information about their emotional state to others. As observers, therefore, we are able to infer the emotional state that an individual might be experiencing based on their facial expression. Early research into the identification of emotions from facial expressions concluded that the expressions associated with each emotional state are largely consistent across individuals, and across cultures (Ekman, 1970; Ekman & Oster, 1979). For example, smiling is associated with the emotion happiness, whereas a lowered brow and pursed lips are associated with anger. Furthermore, Ekman's research concluded that there are six universal expressions of emotion: anger, disgust, fear, happiness, sadness, and surprise. Although this has since been the subject of debate (e.g. Barrett, 2006; Cowen & Keltner, 2017; Skerry & Saxe, 2015), these six categories of facial expression have been used extensively in subsequent research.

Despite the relative consistency of the correspondence between an expression and an emotion, there are numerous factors that can affect how people identify the emotion that another person might be experiencing. For example, individuals with some clinical disorders (e.g. schizophrenia), and patients with damage to certain regions of the brain, often experience difficulty correctly identifying the emotion of another individual based on their facial expression (e.g. Adolphs, Tranel, Damasio, & Damasio, 1994; Premkumar et al., 2008). Even considering non-clinical samples, the ability to recognise emotions from facial expressions varies considerably across individuals and ages.

This thesis aims to examine several of the contributing factors that can influence the recognition of emotions from facial expressions. Two main research areas will be addressed. One set of studies concern the effect of observer age on recognition ability, and the cognitive and behavioural measures that may account for these age-related changes. A second set of studies examines the contribution of the observer's internal knowledge of emotion concepts, and physical properties of the facial expression stimulus, to the processing of facial expressions.

In either case, the behavioural studies of recognition performance are supplemented by neuroimaging experiments looking at the neural basis of facial expression processing, with the common aim of understanding the relative contribution of several factors to the processing of facial expressions.

1.2 Facial expression processing in the brain

A distributed network consisting of a number of regions of the brain is involved in the processing of facial expressions of emotion. Several regions (for example, some temporal regions including the amygdala and superior temporal sulcus) are suggested to be involved in the general processing of emotions from expressions (Adolphs et al., 1999; Engell & Haxby, 2007), whereas other regions have been reported to respond to specific expressions. First, this subsection will explore the regions that are implicated in the processing of specific expressions. Next, research into the regions that are involved in the general processing of expressions will be reviewed.

When assessing which regions are involved in the processing of specific expressions using fMRI, the activation in response to each emotion can be contrasted against the response to baseline or a fixation cross. Such analysis may highlight the regions involved in processing the expression alongside the network of regions involved in processing faces. Alternatively, the activation in response to a specific emotion may be contrasted against the response to neutral faces. This method identifies the expression-specific regions without the network of face-responsive regions. Here, we focus on the latter method of analysis.

Contrasting the response to angry faces to the response to neutral faces revealed significantly higher activation in the bilateral fusiform gyri (Kesler-West et al., 2001) left medial temporal gyrus (Sprengelmeyer, Rausch, Eysel, & Przuntek, 1998), left insula (Fusar-Poli et al., 2009), bilateral amygdala (Fischer et al., 2005; Whalen et al., 2001; Yang et al., 2002), right occipital gyrus (Fusar-Poli et al., 2009; Kesler-West et al., 2001), and bilateral cingulate cortices (Jehna et al., 2011; Sprengelmeyer et al., 1998). Data from a patient with a large frontal legion covering areas including the orbitofrontal cortex further suggests that this area is also involved in the processing of angry faces (Blair & Cipolotti, 2000).

For fearful faces, greater activity in the bilateral amygdala (Breiter et al., 1996; Fusar-Poli et al., 2009; Whalen et al., 2001; Yang et al., 2002), right fusiform gyrus (Fusar-Poli et al., 2009; Sprengelmeyer et al., 1998), left inferior frontal gyrus (Kesler-West et al., 2001), bilateral medial frontal gyri (Fusar-Poli et al., 2009) and left dorsolateral frontal cortex (Sprengelmeyer et al., 1998) compared to neutral has been reported. The role of the amygdala in the processing of facial expressions of fear has been well documented in numerous lesion studies, in which patients with amygdala damage are impaired at the processing of fearful faces (e.g. Adolphs, Tranel, Damasio, & Damasio, 1994, 1995; Adolphs et al., 1999; Fine & Blair, 2000).

Facial expressions of disgust have been reported to evoke greater activity in the right putamen (Sprengelmeyer et al., 1998), right thalamus (Fusar-Poli et al., 2009), bilateral occipital cortices

(Jehna et al., 2011) and left insula cortex (Fusar-Poli et al., 2009; Jehna et al., 2011; Sprengelmeyer et al., 1998), compared to neutral faces.

Compared to neutral faces, sad faces show greater activity in the left fusiform gyrus (Kesler-West et al., 2001), right amygdala (Fusar-Poli et al., 2009; Yang et al., 2002) and left lingual gyrus (Fusar-Poli et al., 2009). Support for the role of the amygdala in the processing of sad faces comes from Adolphs and Tranel (2004), who reported that patients with bilateral amygdala damage performed more poorly at the recognition of sad faces than controls.

For happy faces compared to neutral faces, higher activation in the bilateral amygdala (Fusar-Poli et al., 2009; Yang et al., 2002), left fusiform gyrus (Fusar-Poli et al., 2009), medial frontal/cingulate sulcus (Kesler-West et al., 2001) and right anterior cingulate cortex (Fusar-Poli et al., 2009) has been reported.

Subtracting the response to neutral faces from the response to negative (a mix of angry and disgusted) faces revealed significantly higher activation in the right middle and bilateral superior temporal gyri, the left amygdala, and the right orbitofrontal cortex (Iidaka et al., 2001). Furthermore, the researchers reported that activity in the left amygdala correlated with activity in the left prefrontal cortex, suggesting an interaction between these areas in response to negative facial expressions.

Support for the role of the amygdala in the processing of emotions from facial expressions comes from lesion studies, where patients with bilateral amygdala damage are impaired at the recognition of emotions from facial expressions, particularly fear and anger (for a review, see Fine & Blair, 2000). There are some suggestions that the functional role of the amygdala is to evaluate the affective significance of stimuli, and contribute to prioritising attention to the stimuli where appropriate (Pessoa & Adolphs, 2010).

In sum, frontal, temporal, and some occipital regions are associated with the processing of different expressions. Some temporal regions such as the superior and medial temporal gyri, and some frontal regions such as the prefrontal and orbitofrontal cortices appear to be involved in the processing of negative expressions. While the amygdala is commonly reported to respond to negative expressions, there is some evidence (e.g. Yang et al., 2002) to suggest that it also responds to facial expressions of happiness. Similarly, regions of the cingulate cortex appear to respond to both happy and angry faces.

Next, research into the regions involved in the general processing of facial expressions will be reviewed. A key model of face perception (Haxby, Hoffman, & Gobbini, 2002, 2000) proposes 3 core regions, within a distributed network, that are implicated in the processing of faces. The original model proposes that early processing of facial features occurs in the inferior occipital gyrus (Occipital Face Area; OFA), invariant aspects of faces (e.g. identity) are processed in the lateral fusiform gyrus (Fusiform Face Area; FFA), while variable aspects of faces (e.g. facial expressions) are processed in the superior temporal sulcus (STS). Evidence from an fMRI-adaptation study supports this functional dissociation of the FFA and STS, in that reduced signal in the anterior STS was associated with repeated instances of expression, while repeated identities led to reduced signal in both a region of the fusiform cortex and the posterior STS (Winston, Henson, Fine-Goulden, & Dolan, 2004).

There is, however, research to suggest that all three of these regions may be involved in the processing of facial expressions. When attending to either the identity or expression of faces, the response in the FFA is larger when attending to expression, and is sensitive to changes in expression (Ganel, Valyear, Goshen-Gottstein, & Goodale, 2005). Similarly, Fox, Moon, Iaria, and Barton (2009) used an fMRI-adaptation paradigm to assess the involvement of the FFA, OFA, and STS in the processing of both identity and expression. The OFA was sensitive to both changes in identity and expression, even when participants were not aware of a change. The FFA and pSTS were also sensitive to these changes. Together, these studies suggest that all three of the core face regions are involved in the processing of expressions, in addition to identity. In support of this, research using Multivariate Pattern Analysis (MVPA; Haxby et al., 2001) has reported that these 3 regions represent facial expressions in the form of decodable patterns of activation. Contrary to more standard univariate analysis of fMRI data, which assesses the signal change within each voxel between experimental conditions, MVPA uses distributed patterns of activation across voxels within a region of interest to determine whether that region contains information about different stimuli. For example, early research using MVPA reported dissociable patterns of activation in response to different stimuli belonging to the same sub-category of objects (e.g. different images of shoes) within the ventral visual cortex (Haxby et al., 2001). Research using MVPA has been used to study representations of different facial expressions within face-responsive regions.

Research using machine-learning classifiers has reported that patterns in response to 7 different facial expressions can be successfully decoded above chance in the bilateral superior temporal sulci (Said, Moore, Engell, Todorov, & Haxby, 2010; Said, Moore, Norman, Haxby, & Todorov, 2010). Similarly, binary classifiers have been used to discriminate between pairs of patterns elicited by different facial expressions within the FFA (Harry, Williams, Davis, & Kim, 2013) and OFA (Zhang et al., 2016). Together, this suggests that the core regions of the face processing network (Haxby et al., 2002, 2000) may all contain discriminable representations of facial expressions, to some extent.

In addition to the 3 regions in the core face network, regions in the ‘extended’ face network (the intraparietal sulcus, amygdala, insula, and anterior temporal; Haxby et al., 2000) are also suggested to contain decodable representations of facial expressions. Wegrzyn et al (2015) used a classifier to decode patterns of activation in response to happy, angry, fearful and neutral faces within these 4 regions, in addition to the 3 core face regions. Together, this research suggests that regions within both the core and extended face network represent of facial expressions.

A research question that is subject of debate is whether facial expressions are processed categorically or continuously. There is seemingly contradictory evidence that the perception of expressions and associated neural representations are based either on the allocation of expressions to distinct emotion categories, or that expressions vary continuously across several dimensions. Behavioural evidence that facial expression are processed categorically comes from studies showing that participants are better able to detect differences between morphed facial expressions that cross a categorical boundary than those that do not (Calder, Young, Perrett, Etcoff, & Rowland, 1996; Etcoff & Magee, 1992). Alternatively, the relatively consistent patterns of confusions made between expressions (Young et al., 1997), and the ability of participants to detect differences in intensity of expressions (Calder, Young, Rowland, & Perrett, 1997) suggests a continuous perception of facial expressions.

Some studies have addressed whether facial expressions are represented continuously or categorically in the brain. For example, Harris, Young, and Andrews (2012) presented participants with morphed facial expressions that varied either within- or between-emotion category. Results showed that the posterior STS was sensitive to both within- and between-emotion category changes in facial expressions, suggesting that facial expressions are represented continuously in this region. Conversely, the amygdala was only sensitive to between-category changes in expressions, suggesting that this regions facial expressions categorically.

Similarly, Said, Moore, Norman, et al. (2010) presented participants with a series of morphed facial expressions from along the Anger-Fear continuum, measuring neural response with fMRI. The researchers trained a classifier to discriminate between the responses in the left- and right-STS to the two end points of the continuum (i.e. the response to 100% angry faces and the response to 100% fearful faces), then tested the classifier to discriminate between the intermediate morphed faces. Under the hypothesis that facial expressions are represented categorically, the performance of the classifier at classifying the responses to the intermediate steps would best be modelled as a step function, whereas under the hypothesis that facial expressions are represented continuously, the performance of the classifier would be linear. Results showed that the left-STS represented facial expressions continuously (i.e. performance of the classifier showed a linear relationship with the percentage of an emotion in the morph). However, in the right-STS, performance of the classifier was modelled both linearly and with a step function, suggesting that this region represents both subtle stimulus-gradations and distinct emotion categories.

1.3 Thesis content

There are several sources of variance that can affect the recognition of emotions from facial expressions. Here, the literature review (and subsequent research within the thesis) will focus on two main areas of research that examine some of these sources of variance.

The first research area examines the effect of observer age on the recognition of emotion from facial expressions, and the cognitive, behavioural, and neural measures that may account for any age-related changes. Below is a review of the literature surrounding the contribution of several sources of variance that may account for any age-related changes in expression recognition. The review covers both behavioural measures, and age-differences in neural response to expressions.

The second area of research examines the relative contribution of stimulus-based cues and conceptual knowledge of emotions on the perception, recognition, and neural representations of facial expressions. As before, research into the contribution of these cues to both behaviour and neural representations will be covered.

1.4 Ageing and the recognition of emotions from facial expressions

The recognition of emotions from facial expressions is an important part of social communication, and age-related changes in the ability to recognise emotions has been a focus of research over the past three decades (Malatesta, Izard, Culver, & Nicolich, 1987). Research into this area has assessed the ability of older adults to recognise the six basic emotions in comparison to younger adults. The observed pattern of impairments is that older adults experience difficulty recognising negative emotions; particularly anger (Isaacowitz et al., 2007; Sullivan, Ruffman, & Hutton, 2007), sadness (Calder et al., 2003; Horning, Cornwell, & Davis, 2012) and fear (Calder et al., 2003; Horning et al., 2012; Sullivan et al., 2007). Some research has suggested an age-related improvements in the recognition of disgusted facial expressions (Calder et al., 2003; Horning et al., 2012; Suzuki, Hoshino, Shigemasu, & Kawamura, 2007; Wong, Cronin-Golomb, & Neargarder, 2005), however a meta-analysis reviewed effect sizes between the accuracies of younger and older participants from 17 datasets, and reported that the mean effect size between the two groups for the recognition of disgust failed to reach statistical significance (Ruffman, Henry, Livingstone, & Phillips, 2008).

Several cognitive processes are associated with the normal recognition of emotions from facial expressions. Changes in these processes that occur across the lifespan may explain the age differences in emotion recognition that have been observed in behavioural research. Several of these cognitive processes are claimed to account for the young-old differences in expression recognition. While there is research reporting that young-old differences can be explained by age differences in (for example) low-level visual processes, face processing, working memory and fluid intelligence, there is little research into the relative contribution of these potential covariates on the young-old differences that have been observed. Below is an outline of several cognitive processes that are associated with the recognition of emotions from facial expressions, and research into the contribution of these processes to the age-related changes in recognition that occur. In addition to cognitive processes as measured behaviourally, there is evidence to suggest that age-differences in expression recognition may be in part due to changes in structure and function of several regions of the brain. This neuropsychological account, and surrounding research, is also explained below.

1.4.1 Low-level visual processing

There is evidence to suggest that low level visual processing may account for the effects of age on emotion recognition from facial expressions. The processing of visual information recruits complex visual pathways, so any age-related deterioration to these pathways (Spear, 1993) may account for deficits in the recognition of facial expressions.

Two measures of low-level visual processing are visual acuity and contrast sensitivity. Visual acuity is a measure of the clarity of vision, where individuals with better visual acuity are better able to process smaller changes in shapes (for example when reading small print). Contrast sensitivity is a measure of the ability to detect differences in shading and textures, where individuals with better contrast sensitivity are better able to tell apart subtle changes in shading. This ability to detect subtle changes in shape and surface textures is an important part of facial expression recognition (Bruce & Young, 1998; Sormaz, Young, & Andrews, 2016), as these are two properties of face stimuli that aid in the recognition of emotions (this is discussed in more detail later in the chapter). Both visual acuity and contrast sensitivity typically decline across the lifespan (Rubin, Roche, Prasada-Rao, & Fried, 1994), so it is possible that this reduction in visual processing may account for some of the age-related changes in emotion recognition.

Adults with age-related macular degeneration (AMD; a condition that is associated with poorer visual acuity and contrast sensitivity; Bellmann, Unnebrink, Rubin, Miller, & Holz, 2003) perform more poorly than age matched controls when deciding whether a face was expressive or neutral (Boucart et al., 2008). This could suggest that differences in visual acuity and contrast sensitivity may account for some young-old differences in expression recognition.

Murphy and Isaacowitz (2010) tested a group of younger and older adults on the recognition of angry, sad, fearful, and happy facial expressions, and measured contrast sensitivity, visual acuity, and several other cognitive and affective measures. Contrast sensitivity was correlated with the recognition of only angry and fearful faces, whereas visual acuity was not correlated with the recognition of any facial expression. Furthermore, age differences in the recognition of anger and sadness were still present after controlling for the visual, cognitive, and affective control measures, suggesting a specific age-related impairment in the recognition of these emotions.

Research has yet to investigate the independent contribution of the decline in visual processing on the deficits in emotion recognition observed in ageing. While it is clear how deficits in visual processing can result in difficulties processing facial expressions, it is not clear how visual impairments can account for the specific pattern emotion recognition observed in ageing. As there are specific impairments in the recognition of anger, sadness, and fear, and reported improvements in the recognition of disgust, it is possible that there are more contributing factors to the young-old differences in facial expression recognition than a general decline in low-level visual processing.

1.4.2 General face processing deficit

Research into ageing and emotion recognition seems to suggest that the age-related decline in facial expression recognition is independent from any changes in general face processing ability. The processing of faces activates a large network of brain regions, with the recognition of facial identity and facial expressions occurring along separate neural pathways (Haxby et al., 2002). Identity and expression processing do, however, share some common perceptual processes (Palermo, O'Connor, Davis, Irons, & McKone, 2013), so research has investigated whether the age-related decline in facial expression processing is completely independent from any changes in face identity processing.

The processing of face identity has been shown to decline with age (Crook & Larrabee, 1992), alongside the processing of facial expressions. . This has led some researchers to question whether the decline in emotion recognition is emotion-specific, or symptomatic of a more general decline in face processing. To test this, research into ageing and emotion recognition has often included a face identity processing task as a control measure, however most studies suggest that the young-old differences in emotion recognition are independent from any differences in face identity processing (Orgeta & Phillips, 2008; Sullivan & Ruffman, 2004; Suzuki et al., 2007).

1.4.3 Working Memory and Fluid Intelligence

Both working memory and fluid intelligence are suggested to play a role in facial expression processing. The terms ‘working memory’ and ‘fluid intelligence’ are often used to refer to the same cognitive process, although some argue that working memory is a more general process that encompasses the short-term maintenance of information, while fluid intelligence is the flexible knowledge required to solve novel problems, and that these two processes are distinct but highly correlated (Salthouse & Pink, 2008).

The role of these processes in emotion recognition has been demonstrated via the interference on task performance that occurs, while simultaneously using emotion recognition processes and processes of working memory. For example, Phillips, Channon, Tunstall, Hedenstrom, and Lyons (2008) found that participants performed more poorly during an emotion recognition task when under working memory load (while completing a 2-back task), than when they were not. In a second experiment, they found that this effect was greatest when participants had higher numbers of emotion labels to choose from.

The relationship between working memory and emotion processing was further demonstrated by Stiernströmer, Wolgast, and Johansson (2016). Participants were required to complete a 2-back task, where they indicated if a presented facial expression displayed the same emotion as the facial expression two trials previously. There was an effect of emotional valence on performance, as participants matched negative facial expressions more accurately than positive. Such interference on task performance suggests the involvement of at least partially overlapping cognitive processes.

Frontal regions of the brain including the medial prefrontal cortex have been suggested to be recruited during both emotion processing (Phan, Wager, Taylor, & Liberzon, 2002) and tasks requiring the use of fluid intelligence (Gong et al., 2005). These frontal regions of the brain are reported to undergo substantial structural changes across the normal adult lifespan (Allen, Bruss, Brown, & Damasio, 2005) alongside changes in working memory and fluid intelligence (Salthouse & Davis, 2006). Taking this structural change together with the decline in both working memory and emotion processing that occurs during ageing has led to the view that changes in working memory or fluid intelligence may account for the age-related impairments in facial expression recognition

(Suzuki & Akiyama, 2013). This neuropsychological account is discussed in more detail in the next subsection.

The research into the contribution of working memory to the decline in emotion processing, however, has not been entirely consistent with this position. There is research suggesting that the recognition of emotions from facial expressions is only partially dependent on fluid intelligence. Some research uses measures of emotion recognition, averaged across the different expressions used in the tasks. For example, Sullivan and Ruffman (2004) used an emotion recognition task where a presented facial expression morphed into a second expression, and participants were required to identify the second expression. Young-old differences were still present after covarying reaction time and fluid intelligence, suggesting that age differences in emotion processing are partially independent from these control measures. It was not reported, however, whether these measures accounted for a significant amount of variance in the emotion processing task.

Similarly, Phillips, MacLean and Allen (2002) measured emotion recognition across several modalities in a group of younger and older adults, and reported that performance on the facial expression recognition task was correlated with performance on the Matrix Reasoning test (Wechsler, 1997), a measure of fluid intelligence. This suggests that there is some overlap between emotion recognition from facial expressions and fluid intelligence, however the measure of facial expression recognition in this study only used 4 examples of each facial expression, and accuracy was averaged across the six expressions.

When examining the influence of fluid intelligence on the ability to process specific expressions however, the research is not entirely consistent. For example, Horning et al. (2012) measured accuracy at the recognition of the 6 basic emotions, fluid intelligence (using the Matrix Reasoning subtest of the WASI; Wechsler, 1999), speed of processing (using a reaction time task; Teng, 1990), and verbal memory (using the Rey Auditory Verbal Learning Test; Rey, 1964), in a sample of participants aged 5-89. Using multiple linear regression, the researchers showed that these control measures accounted for variance shared between age and recognition accuracy of anger, disgust, and surprise, for participants aged 46-89. Age was not a significant predictor of accuracy, but fluid intelligence was, suggesting that differences in fluid intelligence can account for the age differences in the recognition of anger, disgust and surprise.

However, Suzuki and Akiyama (2013) performed principle components analysis on speed of processing and fluid intelligence scores to create a ‘general cognitive ability’ variable, and found that this measure can account for young-old differences in the recognition of the 6 basic emotions except for anger and disgust. Furthermore, using the raw fluid intelligence scores in the model (instead of the general cognitive ability variable), only age differences in the recognition of happiness were accounted for.

Suzuki et al. (2007) measured emotion recognition accuracy from the facial expressions of the 6 basic emotions, and measures of fluid intelligence (WAIS-R Picture completion subtest), crystallised intelligence (WAIS-R Information subtest), face identity processing, and general affect. These control measures fully accounted for the age-related decline in the recognition of sadness, but did not fully account for the age-related improvement in the recognition of disgust. Despite this, their measure of fluid intelligence accounted for a significant amount of variance in the recognition of disgust, further suggesting that there is a partial overlap between fluid intelligence and the recognition of this expression.

In sum, age differences in working memory and fluid intelligence may account for some differences in emotion recognition, but examining the role of fluid intelligence on the recognition of specific expressions produces some mixed results. Research has yet to explore the distinction between working memory and fluid intelligence as contributors to the age-related decline in facial expression processing.

1.4.4 Neuropsychological account

Evidence suggests that the brain undergoes structural and functional changes across the adult lifespan. For example, a linear reduction in global grey matter volume across age was reported in a large-scale study (n=465, age range = 61 years) using voxel-based morphometry (Good et al., 2001). It was also reported that some parietal regions (superior parietal gyri, pre- and post- central gyri), and the insula/frontal operculum undergo a relatively accelerated decline in volume across the lifespan. Similarly, Allen et al. (2005) reported an age-related reduction in grey matter volume, with particular reduction in the frontal and temporal lobes. A direct comparison of grey matter volume between middle-aged and older adults revealed significant reductions in volume in some frontal areas including the middle and frontal gyri, and some temporal areas including the right superior temporal and left posterior-superior temporal gyri (Ramanoël et al., 2018). While it has been reported that the volume of some medial temporal structures, including the amygdala and hippocampus, may not decline as rapidly as other areas (Good et al., 2001; Grieve, Clark, Williams, Peduto, & Gordon, 2005), some research suggests that these structures are still subject to age-related reductions in volume (Mu, Xie, Wen, Weng, & Shuyun, 1999).

In sum, there appears to be some overlap between the regions that undergo structural changes, and the regions that are involved in the processing of facial expressions of emotion. The reduction in volume of the amygdala may account for the general age-related decline in expression recognition, but the accelerated structural changes to some frontal and temporal regions may account for age differences in the recognition of some negative emotions. To examine whether structural changes to these regions affects the ability to process emotions, the next step is to identify any age-related changes in functional response to facial expressions.

Several studies have examined the effect of age on functional response to facial expressions. A common result of this research is an age-related reduction in amygdala response to facial expressions. For example, Iidaka et al. (2002) examined young-old differences in functional response to positive, negative, and neutral faces compared to a baseline condition (blocks of rectangles). Older adults had reduced activation in the amygdala in response the negative faces than younger adults. For positive faces, older adults had reduced activation in the parahippocampal, lingual, and angular gyri. Similarly, Fischer et al. (2005) reported reduced amygdala activation in older adults compared to younger adults in response to angry versus neutral faces. Conversely, older adults showed greater response than younger adults in a region of the insula cortex. One explanation for the age-related impairment in the recognition of anger, therefore, could reflect this reduced involvement of the amygdala or increased involvement of the insula. As with the processing of angry faces, it has been reported that older adults show reduced amygdala response to happy faces than younger adults (Keightley, Chiew, Winocur, & Grady, 2007; Williams et al., 2006). In addition to angry and happy faces, fearful faces are reported to evoke a greater response in the amygdala for younger and middle-aged adults than older adults (Williams et al., 2006). Mather et al. (2004) reported greater amygdala activity in younger adults than older adults in response to negative emotionally valenced stimuli (International Affective Picture System; Lang, Bradley, & Cuthbert, 1997), suggesting that the young-old differences in amygdala response to facial expressions may reflect age differences in a more general response to emotional stimuli.

In addition to the amygdala, an age-related reduction in activation has been reported to occur in other parts of the limbic system. For example, Fischer et al. (2005) reported that older adults have reduced activation in response to angry faces in the bilateral hippocampi compared to younger adults. Similarly, Iidaka et al (2002) reported that older adults show reduced activation in the parahippocampal gyrus in response to positive faces than younger adults. Gunning-Dixon et al. (2003) compared the activation during an emotion discrimination task to the activation during an age-discrimination task, in groups of younger and older adults. While the researchers did not directly compare the neural activity of younger and older adults, they reported that younger adults recruited regions of the superior temporal lobe and parts of the limbic system (the amygdala, hippocampus and parahippocampal gyrus) during the emotion discrimination task whereas older adults did not. The general decline in expression recognition could reflect this attenuated activity in the amygdala or other parts of the limbic system. However, as there is a relative sparing of the recognition of happy faces, and there is a similar age-related attenuation of amygdala and parahippocampal response to happy faces, this may not solely account for the specific age-related impairments in the recognition of anger, sadness and fear.

Considering that some frontal regions are both involved with the processing of emotions, and are subject to accelerated age-related changes, it may be the case that these regions show age differences in functional response to expressions. Keightly et al. (2007) reported that younger and older adults recruit different regions when processing happy faces, but there is an overlap between the groups in the recruitment of the ventromedial prefrontal cortex. Notably, activation was found in the amygdala for younger adults but not older adults. Surprisingly, however, little difference was found between the groups when comparing the activation in response to angry, disgusted, or sad faces. This result is not necessarily consistent with the neuropsychological account, as it would be expected that the behavioural group differences in the recognition of negative expressions would be reflected by group differences in neural activation.

However, Williams et al. (2006) reported that increasing age is associated with greater response to fearful faces in the medial prefrontal cortex, and reduced response to happy faces. Importantly, participants' subjective ratings of emotional intensity could be predicted by activity in the MPFC. This result links neural activity to behaviour, and provides support for the neuropsychological account. As older adults show reduced amygdala response to fearful faces than younger adults, it may be the case that the medial prefrontal cortex takes on a role in the processing of negative expressions.

It is worth noting that the reduced activation in older adults compared to younger adults may not necessarily directly reflect reduced behavioural recognition of an emotion. Group differences in activation could reflect, for example, age-related dedifferentiation, a process whereby neural representations become less distinct across the lifespan. Processes of dedifferentiation have been studied in areas of the ventral visual cortex, where reduced neural specialisation for different object categories was reported to occur across age (D. C. Park et al., 2004). In addition to these areas, age-related dedifferentiation has been studied in areas of the face processing network, where activation in the FFA and areas of the extended network (Haxby et al., 2000) became less face-selective across the lifespan (J. Park et al., 2012). It is possible, therefore, that the age-related reduction in response to facial expressions might reflect reduced specificity to different expression categories, or reduced selectivity for emotional faces in comparison to neutral.

Alternatively, differences in activation in response to facial expressions between younger and older adults might reflect compensatory mechanisms, or poorer neural efficiency. Some studies have reported age-related increases in activation in lateral, medial, and inferior frontal regions in comparison to younger adults for emotion processing tasks (Gunning-Dixon et al., 2003; Keightley et al., 2007; Williams et al., 2006). These increases in activity in some regions, and concurrent decreases in other regions, have been argued to reflect some reorganisation of the cortical networks recruited during the perception of facial expressions (Gunning-Dixon et al., 2003). According to neurocognitive models of ageing, concurrent increases and decreases in activation in response to (e.g.) tasks requiring working memory could reflect some compensatory mechanisms, where some frontal regions take on some of the processing load to account for the decline in other neural structures (D. C. Park & Reuter-Lorenz, 2009). While these accounts are not necessarily incompatible with the neuropsychological account, the association between measures of dedifferentiation or neural compensation and behaviour have not yet been examined.

In sum, older adults have less activation than younger adults in a network of regions, including the medial prefrontal cortex, and the amygdala and other areas of the limbic system. This age-related attenuation is suggested to account for the young-old differences in the behavioural recognition of expressions, although research has yet to examine whether this reduction in activity is associated with measures of expression recognition accuracy.

Together, there are several contributing factors to the age-related decline in expression recognition. Although there is research suggesting that these age differences can be accounted for by several cognitive and behavioural measures, we have yet to determine the relative contribution of these measures to the age-related changes in expression recognition. Furthermore, the neuropsychological account offers a compelling account of these age-differences, although there are some results that are not necessarily consistent with the explanation. Research has yet to examine the relationship between neural response to expressions and the behavioural recognition of the emotion.

1.5 Alternative accounts of age-differences in expression recognition

Of course, the accounts listed above are not an exhaustive list of explanations for age differences in expression recognition, and several alternative accounts have been proposed. One such account suggests that older adults experience positivity effects (Carstensen & Mikels, 2005), where older adults experience a processing bias towards positive stimuli and/or a reduction in the processing of negative stimuli. Support for this account comes from a study showing that older adults have poorer recall and recognition accuracy for negatively valenced emotional stimuli than younger adults, suggesting a processing bias towards the positively valenced stimuli (Charles, Mather, & Carstensen, 2003). In relation to age differences in the processing of facial expressions, this account suggests that the age-related reduction in the processing of negative facial expressions (i.e. anger, fear, and sadness), and the sparing of any age differences in the processing of positive facial expressions (i.e. happy), are a result of a bias in processing towards positive stimuli in general. On study showed that older adults displayed an attentional bias (measured using reaction time to indicate the position of a dot-probe placed over one of two faces) away from sad and angry faces, and towards happy faces (Mather & Carstensen, 2003). Additionally, eye-tracking studies have shown that older adults spend longer looking at negative facial expressions than positive expressions (Mather & Carstensen, 2003; Sullivan et al., 2007), suggesting that any positivity bias might not reflect an avoidance in processing negative facial expressions rather a difficulty processing them. However, a test of the positivity bias account of age differences would be to examine the emotions that older adults find difficult to recognise in other modalities (e.g. voices or body postures). Any age differences in the recognition of happiness from (e.g.) voices, or the lack of any difference in the recognition of emotions from negative voices, would be contradictory to an account suggesting a processing bias towards positive stimuli. The meta-analysis provided by Ruffman et al., (2008) showed that older adults are frequently poorer at recognising happiness from voices, and that there is no significant difference between younger and older adults in the recognition of fearful voices, suggesting a positivity bias cannot be the sole explanation of any age differences in expression recognition.

Another account for the age differences in expression recognition suggests that there is an own-age bias. Studies showing age differences in expression recognition tend to use databases of emotional faces that typically comprise younger adult models, and so the age differences that have been observed may simply reflect a reduction in the ability to process expressions belonging to other age groups. In support of an own-age bias in the processing of faces Rhodes and Anastasi (2012) conducted a meta-analysis and reported that memory for (and discrimination between) face identities is superior for ones own age group as opposed to other age groups. However the results surrounding the perception of emotions from faces in own/other age groups is not as clear. For example, Ebner and Johnson (2009) presented younger and older adults with happy, angry and neutral younger and older faces, and found no evidence for an own-age bias in expression recognition or memory of faces. In a subsequent study, Ebner, He and Johnson (2011) reported that both younger and older adults had better emotion identification for younger faces in comparison to older faces, suggesting that facial expressions displayed by older adults may be more difficult to identify, regardless of observer age. However the researchers reported age differences in gaze behaviour, with both age groups spending longer looking at faces from their own age group, suggesting there may be some own age bias in how emotional faces are processed. Using fMRI, Ebner et al. (2013) examined neural response to happy, angry, and neutral facial expressions displayed by younger and older models, in groups of younger and older participants. In the medial prefrontal cortex, insula, and amygdala, activity was higher for expressions displayed by own-age models, across all expressions. Examining the response to individual expressions, this own-age effect remained for happy and neutral faces, but disappeared for angry faces (i.e. there was no greater response to own-age vs other-age for angry faces). This result is interesting given the relative difficulty in the processing of negative facial expressions, and suggests that any age differences in the processing of angry facial expressions are not simply a result of an own-age bias. As reported in previous studies (Ebner et al., 2011; Ebner & Johnson, 2009), both groups of participants were more accurate at identifying emotions displayed by younger faces than older faces. Together these results suggest that behaviourally, little own-age effects are observed, but the eye-tracking and fMRI results suggest some own-age effects in the processing of facial expressions.

1.6 Top-down and Bottom-up processing

Visual perception is not a solely feed-forward, stimulus-driven process. Instead, we apply expectations, derived from memories and associations, to make predictions of the visual input. There is an interaction between internal models and visual stimuli that shape conscious visual perception (O’Callaghan, Kveraga, Shine, Adams, & Bar, 2017). A key theory proposed by Gregory (1980) compares perceptions to scientific hypotheses, suggesting that visual perception tests our predictions, and that our predictions are updated if they are not consistent with the visual input. This interaction between top-down and bottom-up information is biologically supported as there are both feed-forward and feed-back connections between V1 and other higher-order cortical areas of the visual system (Bullier, 2001a, 2001b).

Top-down predictions facilitate visual perception, and aid in the recognition of stimuli across multiple domains including objects, words, and social categories (Bar et al., 2006; O’Callaghan et al., 2017; Stolier & Freeman, 2016). In the domain of social perception, there is research suggesting that judgements of gender and race is biased by expectations based on internal concepts of stereotypes (Levin & Banaji, 2006; Macrae & Martin, 2007). Similarly, there is evidence suggesting an interaction between top-down and bottom-up mechanisms within the face processing system (Li et al., 2009), including the recognition of emotions from facial expressions. In other words, internal representations of emotion concepts likely predict and shape the visual perception of facial expressions of emotion.

The following literature review (and research within the thesis) aims to explore the interaction between bottom-up mechanisms (that process properties of the face stimuli) and top-down mechanisms (that utilise knowledge of emotion concepts) in the visual perception of facial expressions of emotion. The relative roles of stimulus-properties and emotion concepts in both behaviour and neural representations of facial expressions will be explored.

1.6.1 Behavioural Studies

The recognition of emotions from facial expressions requires the perceptual processing of the visual stimulus. In addition to the stimulus-based cues, higher-level conceptual information may play a role in the recognition of emotions. For example, an emotion labelling task (where participants select the best label to match the presented facial expression, e.g. Young, Perrett, Calder, Sprengelmeyer, & Ekman, 2002) requires participants not only to process the visual input but also to have some semantic knowledge of the emotion labels. The recognition of emotions, therefore, is reliant on both conceptual and stimulus-based sources of information. This integration of stimulus-based cues and conceptual knowledge may also occur in perceptual tasks, which do not require the explicit labelling of an expression.

Palermo et al. (2013) distinguish between perceptual tasks (e.g. same/different, 3 alternate forced choice, etc.) and labelling tasks, by suggesting that labelling tasks require initial perception plus additional cognitive processes needed to assign an emotion label. Palermo and colleagues reported that performance on a perceptual matching task was correlated with performance on a labelling task. Furthermore, performance on the labelling task was correlated with performance on a vocal emotion labelling task, whereas performance on the perceptual matching task was not. Together, this suggests that the perceptual and labelling tasks share perceptual processes, whereas the labelling task also taps into a cognitive process used to assign emotion labels to a stimulus, regardless of the stimulus modality. These results suggest that perceptual tasks and labelling tasks may recruit different processes, or rely to different extents on different processes. Below, we review evidence of the use of stimulus-based cues and/or conceptual cues in perceptual and categorical tasks.

1.6.1.1 Integration of high- and low- level information in perceptual tasks

Facial expressions are associated with specific musculature movements which physically change the appearance of the face and are consistent across individuals (Ekman & Friesen, 1971). These movements allow for changes in the overall shape of the face, such that both the shape and position of individual features may vary. For example, a smile changes the shape of the mouth, whereas a surprised face may change the position the eyebrows. Muscular movements also create differences in what is referred to as surface information, i.e. the texture of the face (Bruce & Young, 1998). As the shape changes, the pattern of light and shadow across the face too changes. For example, an angry scowl is associated with a heavy brow which causes a darker shadow above the eyes than other expressions.

The importance of shape cues in emotion perception tasks has been shown in studies using contrast-negated faces. By negating the contrast of face images, surface cues become disrupted but information about face shape remains intact. It has been shown that there is no difference in error rates between pairs of normal faces and pairs of contrast negated faces during same/different expression judgement tasks, suggesting that the perceptual processes required for these task make little use of surface information and instead primarily rely on shape cues (Harris, Young, & Andrews, 2014; White, 2001).

Pallet and Meng (2013) measured thresholds at which an emotion can be detected in a face, using a psychophysical paradigm to adjust the weighting of the emotion in expressive-neutral warps. Contrast negation had little effect on the thresholds of detection, in a task where participants were required to choose the expressive (warped) face from a pair containing a neutral face, further suggesting that the perception of expressions is unaffected by disruption to surface information.

Benton (2009), however, reported that surface information may in fact also be used during the perceptual encoding of expressions. The author used an adaptation paradigm, in which the presentation of the adapter caused the perception of the expression of the test face to shift away from the expression of the adapter. When participants viewed a contrast-negated adapter, the shift in perception was smaller than when the adapter face was normal. This suggests that surface cues may play a role in the perceptual encoding of faces.

Sormaz, Watson, et al. (2016) investigated the usage of both shape and surface information in a perceptual task involving pairwise similarity of pairs of expressions. After computing the pairwise similarities of the shape (using Procrustes analysis) and surface (using correlation between pixel intensities) properties of the face images, the authors showed that the pairwise perceived similarity could be predicted by the pairwise shape and surface distance measures. The mean beta for surface was larger than the mean beta for shape as predictors of perceptual similarity, although statistical inference on this difference was not reported.

In addition to low-level information based on shape of facial muscles and texture of faces, there is some evidence that conceptual information may also influence these perceptual tasks that do not require the labelling of facial expressions. For example, some studies have shown that performance on perceptual tasks could be altered after access to emotion concepts was disrupted, via a process called ‘semantic satiation’. When a word is read aloud a high number of times, access to the meaning of the word becomes temporarily attenuated (Smith & Klein, 1990). In the context of emotion concepts, participants who verbally repeat an emotion label (e.g. “anger”) aloud a high number of times experience a temporary attenuation of access to the concept of anger.

Lindquist, Barrett, Bliss-Moreau, and Russell (2006) reported that participants were both slower and less accurate at matching pairs of facial expressions (a task conducted in the absence of emotion labels), and Gendron, Lindquist, Barsalou and Barrett (2012) reported reduced effects of repetition priming, after access to the semantic meaning of emotion labels had been disrupted via this process of ‘semantic satiation’. Together, this could suggest that perception of expressions can be altered if an individual does not have access to the concept of the emotion.

Further evidence for the role of concepts in the perception of expressions comes from Nook, Lindquist and Zaki (2015), in which participants used a slider to indicate which of a set of morphed facial expressions they believed they had previously seen in a trial. When the facial expression in the trial was paired with an incongruent emotion label (e.g. a sad face paired with the emotion label “anger”), participants indicated that they had viewed an expression (using the slider) that was closer along the morphed continuum to an expression corresponding to the label (e.g. an angry face) than was actually presented in the trial. Importantly, this shift in perception was larger for incongruent emotion labels (e.g. a sad face paired with the label “anger”) than for congruent labels (e.g. an angry face paired with the label “anger”).

A similar shift in perception was reported by Halberstadt and Niedenthal (2001). Participants were presented with ambiguous morphs (a 50-50 blend of two facial expressions) alongside an emotion label corresponding to one of the two faces used to create the morph. Using a slider to choose a morphed expression that they believed they had seen, participants chose faces displaying an expression that was closer to the corresponding label than had been presented in the trial. Taken together, this suggests the activation of concepts via emotion labels can influence the perception of the expression.

Fugate, Gouzoules, and Barrett (2010) tested the hypothesis that concepts shape perception by investigating whether conceptual knowledge can affect categorical perception of chimpanzee facial expressions. Categorical perception was measured using an ABX task, where participants were presented with 2 morphed faces sequentially (A and B) followed by a test face (X) that was a repetition of either A or B. Categorical perception is demonstrated when participants are more accurate at discriminating between faces A and B if they cross a categorical boundary in the morphed continuum than if they do not. Participants who were trained to pair chimpanzee facial expressions with arbitrary nonsense labels demonstrated categorical perception more so than those who had been trained without the labels, providing support for the role of concepts in the perception of facial expressions.

A recent study by Brooks and Freeman (2018) showed further the influence of concepts on a number of emotion perceptual tasks, using a representational similarity analysis approach (this method of analysis is summarised in the next subsection (1.4.2.1) and is explained in more detail in Chapter 4). Across three experiments the researchers showed that pairwise measures of conceptual similarity of emotions predicted measures of perceptual similarity of the corresponding facial expressions. Conceptual similarity was measured using subjective ratings of the similarity of emotion categories, and the overlap between ratings of the association of emotions with more specific feelings (i.e. emotion categories that were more conceptually similar had common feelings attributed to them).

Perceptual similarity of the images was measured using two approaches. The first was the deviation in mouse-tracking trajectory, during a two-choice categorisation task. Participants were presented with a facial expression and two emotion labels, and were required to drag the face towards one of the labels. The size of the deviation in trajectory towards the non-target category label is argued to reflect the degree to which that category was activated by the perception of the face (Freeman, 2018).

The second approach was a reverse-correlation paradigm. In this task, participants were presented with two identical neutral faces, overlaid with different patterns of noise on each trial, and were required to choose which face was (e.g.) “more angry”. ‘Classification images’ were then generated by averaging the patterns of noise that participants had previously indicated displayed a given emotion. Two independent groups of participants then provided the measures of perceptual similarity; the first rated classification images on a 7-point scale with each emotion category at the end points (e.g. 1= Angry, 7 = Disgusted), or as subjective ratings of how similar pairs of the classification images look (i.e. 1 = “Not at all similar”, 7 = “ Extremely similar”).

These results suggest that conceptual information may influence performance in perceptual tasks. However, the explicit use of emotion labels in all these experiments could have led participants to rely more on, or make explicit use of, conceptual information (Brooks & Freeman, 2018; Halberstadt & Niedenthal, 2001; Nook et al., 2015). For example, in the mouse tracking task from Brooks and Freeman (2018), the changes in mouse trajectories could be affected by the conceptual similarity of the labels, not of the facial expressions *per se*. Similarly, the perception of the classification images may have been influenced by the presence of the labels on the 7-point scale.

As perception likely involves the interaction between multiple bottom-up and top-down processes, it is unlikely that any perceptual task (e.g. a 3AFC task) will fully isolate the use of perceptual processes from any higher-level cognition. Despite this, ideally a perceptual task designed to assess the ability to discriminate between facial expressions using perceptual processes would avoid the use of any emotion labels.

1.6.1.2 Integration of high- and low- level information in labelling tasks

A commonly used task within facial expression research requires participants to choose which of several (typically 6) labels best describes the emotion of a presented facial expression (e.g. Young et al., 2002). This labelling task requires the perceptual processing of the stimulus-based cues, in addition to knowledge of the semantic meaning associated with the emotion labels. Recognition accuracy was significantly reduced when participants freely labelled a facial expression than when they undertook a forced-choice labelling task (Widen, Christy, Hewett, & Russell, 2011), suggesting that the presence of emotion labels aids in the recognition of emotions from facial expressions during forced-choice labelling tasks. Furthermore, participants had higher false recognition rates when they indicated if facial expressions matched an emotion label than if they matched the expression of another face (Fernández-Dols, Carrera, Barchard, & Gacitua, 2008), again showing how the presence of a label affected the recognition of the emotion. It has been argued that emotion labels provide more clearly defined emotion categories than faces do (Nook et al., 2015), so the presence of labels in multiple-choice recognition tasks aids in reducing ambiguity over the emotion category that the facial expression falls into.

As with perceptual tasks, categorical tasks also involve the processing of shape and surface information. A number of studies have reported that participants are still able to recognise emotions from line drawings of facial expressions (Etcoff & Magee, 1992; Katsikitis, 1997; Mckelvie, 1973). These line drawings remove surface information from the face and leave only shape information available, so these results could suggest that the processes involved in recognition do not make use of surface information. However, in order to claim that surface cues are unimportant, recognition must be tested for faces that remove shape information and leave only surface information available. Evidence that the processes involved in labelling emotions make use of both shape and surface cues comes from Sormaz, Young, and Andrews (2016) who created a set of facial expression stimuli that varied in either shape or surface information only. The surface-varying stimuli were created by warping an original set of facial expression images (Ekman & Friesen, 1976) to the average shape, whereas the shape varying stimuli were created by finding the average surface texture and warping this to the original shapes. The recognition accuracy for both sets of stimuli was well above chance but was significantly improved for original unedited images (that varied in both shape and surface information), highlighting how the processes involved in emotion labelling tasks make use of both shape and surface information.

1.6.2 Neuroimaging Studies

There is currently little research investigating the regions of the brain that may be involved in this integration of conceptual and stimulus-based information. Below, we review research suggesting that representational structure of emotions in the face processing network may make use of stimulus properties, while regions involved in processing theory of mind may contain modality-independent representations of emotions.

1.6.2.1 Representations of facial expressions in regions explained by stimulus-properties

To investigate whether the representational structure of emotions within a given region is organised around high- or low- level information, previous research has often used Representational Similarity Analysis (RSA; Kriegeskorte, Mur, & Bandettini, 2008). RSA is a method of predicting the representational structure within a given region with use of theoretical models.

In short, the representational distance of each pair of experimental conditions is calculated, then the relationship between these representational distances and the distances as measured within a different modality is assessed, typically using a correlational approach. If a significant association is found between them, then it is inferred that the representational structure of the stimuli within the region is (at least partially) explained by the information used to construct the model. For example, RSA has been used to show that the pairwise dissimilarities of patterns of neural response to different object categories in the ventral visual pathway is strongly associated with the pairwise dissimilarities of low-level image properties (Rice, Watson, Hartley, & Andrews, 2014). RSA is explained in more detail in Chapter 4.

This type of analysis has been used in the context of facial expression processing to predict the representational structure of facial expressions in the core face network from properties of face stimuli. For example, Weibert, Flack, Young and Andrews (2018) measured the similarity of low-level properties of images of facial expressions by measuring the correlation between GIST descriptors (Oliva & Torralba, 2001). Briefly, this method finds the spatial frequency distributions of an image after passing the image through a series of Gabor filters, then creating a vector (the GIST descriptor) from the filtered image after windowing it. The researchers found that the similarity of this low-level image property predicted representational distances of facial expressions in all three of the core face regions. While this result suggests that the representational distances within these regions can be explained by similarities of low-level image properties, it does not necessarily mean that the representational structure is organised around the similarities of shape and surface properties of the facial expressions.

Some researchers have used shape and surface information, alongside perceived perceptual similarity of expressions, to study the representational structure of emotions within the core face regions. Sormaz, Watson, et al. (2016) presented participants with blocks of angry, disgusted, fearful, happy and sad faces. Using RSA, the perceptual similarity of expressions (as measured behaviourally) was predicted by the similarity of neural representations in the STS and OFA, but not the FFA. Furthermore, perceptual similarity of expression pairs was also predicted by the pairwise similarity of the face shapes and surface textures. While the researchers did not use the stimulus-models to predict the similarity of neural representations, together these results might suggest an association between the representational structure within the OFA and STS, and the shape and surface properties of the stimuli.

Similarly, Said, Moore, Engell, et al. (2010) found that the representational structure of facial expressions within the posterior STS was associated with behavioural ratings of the perceptual similarity of expression pairs. Together, these studies suggest that perceived similarity of pairs of expressions is associated with the similarity of neural representations, within some of the core face processing regions. As the results from Sormaz, Watson, et al (2016) suggest that this perceived similarity is associated with the similarity of shape and surface information, it is possible that these stimulus-based properties play a role in explaining the representational structure of expressions within these regions.

1.6.2.2 Regions that contain modality-independent representations of emotion

There is research to suggest that some areas associated with theory of mind may contain representations of emotion concepts, that may be activated in response to expressions. For example, there are studies that suggest that regions of the Medial Prefrontal Cortex (MPFC) may represent modality independent emotion concepts. Skerry and Saxe (2014) presented participants with facial expressions or animations of a situation that were either positively or negatively valenced. The researchers used the multivoxel patterns of activation in the MPFC to train a classifier using the response to one set of stimuli (e.g. animations), and tested the classifier using the other set of stimuli (i.e. faces). The classifier performed above chance when discriminating between valence of the second set of stimuli, suggesting that the representations of the valence within this region of the brain are cross-modal.

Similarly, Peelen, Atkinson, and Vuilleumier (2010) used this method of training and testing a classifier using different stimulus modalities, to discriminate between the emotions of faces, voices, and body postures. Using a whole-brain searchlight analysis, the classifier was reported to perform above chance using voxels in the MPFC and left STS. Together, these studies show that the patterns of neural activation within the MPFC is common across different modalities and stimulus sets. While this region is not typically responsive to faces, these studies showed that faces can elicit dissociable patterns of activation in response to different valences and expressions. As the patterns are cross-modal, it is likely that the representational structure of expressions within the MPFC can be explained by emotion concepts rather than anything specific to the stimulus.

Skerry and Saxe (2015) required participants to read short stories that described an event that happened to a character, who would experience one of 20 ‘fine grained’ emotions. The researchers trained a classifier to discriminate between the patterns of activation in response to each of the subtle emotion categories, using voxels within several areas involved with theory of mind (the MPFC, bilateral temporoparietal junctions, the precuneus, and right STS). The classifier successfully decoded the emotion categories above chance in all regions, suggesting that these regions may represent different emotion categories with subtle distinctions.

Although the MPFC is not typically face-responsive, there is research to suggest that the MPFC is involved in processing facial expressions. Research using TMS over frontal areas including the MPFC and dorsolateral prefrontal cortex has reported disruption of priming effects for facial expression recognition (Mattavelli, Cattaneo, & Papagno, 2011), improvement facial affect recognition in schizophrenia (Wölwer et al., 2014), interference with the recognition of angry facial expressions (Harmer, Thilo, Rothwell, & Goodwin, 2001) and interference with the in-group advantage in expression recognition (Gamond & Cattaneo, 2016). In sum, both the MPFC and STS are involved in the processing of facial expressions of emotion, and both regions contain representations of emotion categories with subtle distinctions. The work of Peelen et al. (2010) and Skerry and Saxe (2014) suggest that the MPFC may represent emotion concepts independently from any stimulus modality, so it is possible that the representational structure of facial expressions within the MPFC and STS may be best explained by the similarities of emotion concepts.

A key result comes from Brooks, Chikazoe, Sadato and Freeman (2019) who investigated whether the structure of the neural representations of facial expressions can be explained by emotion concepts. In the MRI scanner, participants were presented with facial expressions displaying the 6 basic emotions. A neural Representational Dissimilarity Matrix (RDM) was constructed by taking the squared Euclidean distance between the patterns of activation associated with each facial expression category. Offline, participants also rated the relationship between each of the 6 emotions and 40 word/phrase stimuli (e.g. “On a scale from 1 = not at all to 7 = extremely, how related is ‘tension’ to the emotion Sadness?”, Brooks et al., 2019, page 8). A conceptual similarity matrix was constructed by taking the correlation of these ratings, between each pair of the 6 emotions.

Multiple linear regression was used to assess the correspondence between the conceptual model and neural RDM, using searchlight to select the voxels used in the analysis. Searchlight analysis centres a sphere on each voxel in the brain, and repeats the statistical test (in this case, multiple linear regression RSA) using the voxels within this region to construct the RDM, then maps the result of the statistical test (i.e. regression coefficient for the conceptual model) back to the centre voxel in the searchlight. Three measures of visual similarity were controlled for in the regression model at each location, by constructing separate matrices that measured the similarity of the silhouettes of the faces, the pixel intensities, and the representations from a computational model of object recognition (HMAX).

The results showed that the representational structure of expressions within a region of the right fusiform gyrus could be explained by the conceptual model, after controlling for the 3 measures of visual similarity of the stimuli. These results suggest that information about emotion concepts may shape the representational structure of facial expressions in the right fusiform gyrus, adding to the understanding of its role in the perceptual processing of faces.

In sum, the MPFC and right STS have been reported represent both facial expressions and stimulus-independent representations of emotions. In addition to this, emotion concepts shape representations of facial expressions in the right FFA. Taken together, these results suggest that emotion concepts play a role in explaining the representational structure of expressions within these regions.

1.7 Aim of research in this thesis

The broad aim of the set of studies reported here is to explore the relative contribution of different sources of variance on the processing of facial expressions of emotion. This thesis covers two main research areas; the first examines the effects of observer age on the processing of facial expressions of emotion, and the second examines the contribution of stimulus-based cues and conceptual knowledge. Within both research areas, both behavioural methods and fMRI are used.

Within the ageing research, first behavioural methods are used to explore the relative contribution of potential covariates that can account for young-old differences in expression recognition. Next, we use fMRI to explore any age-related changes in functional response to expressions.

Within the second research area, behavioural methods are used to examine the relative contribution of conceptual information and stimulus-based cues to the perception and recognition of emotions. We then use fMRI to explore the contribution of these sources of information to the representations of emotions within different regions of the brain. For both studies within this research area we use Representational Similarity Analysis, a multivariate method of analysis that allows for the assessment of the ability of theoretical models to explain representations of emotions across multiple modalities.

In addition to the behavioural and fMRI studies within the second research area, a further study investigates individual differences in the role of conceptual and stimulus-based cues in the perception and recognition of expressions, by performing secondary analysis of the data gathered in the behavioural study. Substantial individual differences exist in the perception and recognition of facial expressions (Palermo et al., 2013), so the aim of this study was to explore whether variation in performance during behavioural tasks could be explained by variation in the role of conceptual or stimulus-based cues. As these cues are shown to play a role in the behavioural recognition of expressions, it is of interest to examine whether the role of a given cue is associated with better/worse performance at the tasks.

Chapters 2 and 3 cover the first research area, examining the effect of observer age on the processing of facial expressions. Chapters 4, 5, and 6 cover the second research area, examining the contribution of stimulus-based and conceptual information to behavioural and brain representations of emotion.

In chapter 2, differences in ability to recognise emotions from facial expressions between a group of younger and older adults are examined, and the relative contribution of several covariates to these age differences are explored.

In chapter 3, we use fMRI to examine the effects of age on the neural response to facial expressions. The research then aims to examine the relationship between brain and behaviour, by assessing the relationship between neural activation and accuracy during a recognition test.

In chapter 4, the relative contribution of conceptual and stimulus-based information to the perception and recognition of emotions during behavioural tasks area examined. This chapter explains the construction of three computational models, and the methods involved in Representational Similarity Analysis.

In chapter 5, we conduct secondary analysis on the data from the previous chapter, and explore the contribution of conceptual and stimulus-based cues to *performance* during two tasks. The aim of this chapter is to examine whether individual differences in performance can be explained by the contribution of any particular cue.

In chapter 6, fMRI is used to examine the relative contribution of conceptual and stimulus-based cues to neural representations of emotions, within several regions of the brain. The three models (as constructed in Chapter 4) are used in conjunction with Representational Similarity Analysis to explore which source of information can best explain the representational structure of emotions within these regions.

Chapter 7 provides a discussion of the results, and attempts to bring the two research areas together.

2 Behavioural age differences in the recognition of facial expressions

2.1 Introduction

The primary aim of our experiment was to examine which of these main accounts can best explain the young-old differences observed in emotion categorisation. To do so, we tested younger and older adults' ability to categorise the six basic facial expressions using labels, as often used within previous research (Ekman, 1992). We then assessed participants' short term memory, fluid intelligence, visual acuity, contrast sensitivity and face identity processing ability. We include a task requiring short term memory and a task requiring the use of fluid intelligence to dissociate these two processes from the more general term 'working memory', allowing us to examine the relative contribution of these two processes on the age differences in emotion recognition. Using performance on these tasks as covariates, we assessed the relative importance of these processes in the accurate labelling of each emotional facial expression.

A secondary aim of our experiment was to assess not only accuracy at labelling emotions, but to explore any age differences in the categorisation of emotions. A few studies into ageing and emotion recognition have presented full categorisation matrices (Henry et al., 2008; Isaacowitz et al., 2007; Mill, Allik, Realo, & Valk, 2009; Suzuki et al., 2007), reporting the number of instances that each presented facial expression was categorised using each of the emotional labels. Mill et al (2009) reported a strong correlation between the confusion matrices for younger and older participants, suggesting that the pattern of categorisation does not change across age. Other research however, reports that younger adults will erroneously label facial expressions of disgust as 'angry' more frequently than older adults (Suzuki et al., 2007). Research has yet to examine age differences in the exact patterns of labelling and mislabelling for all emotions, during these multiple-choice emotion recognition tasks. Here, we performed cell-by-cell comparisons of the full categorisation matrices between younger and older adults to further assess the young-old differences in the confusions made between facial expressions of emotion. For this we made no formal predictions other than that we expected older adults to perform more poorly than younger adults at correctly categorising angry, sad, and fearful facial expressions.

2.2 Methods

2.2.1 Participants

Two groups of participants were recruited; younger and older adults. The younger adults were recruited via the Brunel university participant pool and were granted course credits for participating.

The older adults were recruited from a range of sources, including a Brunel University database of older adults, a local sports group, a community newsletter, and advertisements in the local library and church. Ethical approval to conduct the research was granted by the College of Health and Life Sciences Research Ethics Committee at Brunel University London. Participant information is presented in Table 2.1.

Table 2.1: Participant information

Group	**Group size**	**Males: Females**	**Mean age**	**Standard Deviation**	**Range**
Young	50	10:40	20.52	3.10	18-27
Old	45	16:29	75.00	8.97	60-93

2.2.2 Design

A mixed design was used. We gave 2 independent groups of participants (young and old) an expression categorisation task, with 6 expressions. In addition to this, performance on tasks measuring visual acuity, contrast sensitivity, face identity processing, working memory, and fluid intelligence were used as covariates. We used independent samples t-tests to assess group differences in labelling accuracy, ANCOVA to assess whether the covariates can account for the group differences, multiple linear regression to assess the relative contribution of these covariates, and finally a series of Wilcoxon rank sum tests to assess group differences in the pattern of confusions. Participants viewed all stimuli at a distance of approximately 150cm under binocular viewing conditions. All visual stimuli were presented on an Iiyama monitor (Height = 10.3°, Width = 12.9°), and responses were made using keys on a standard QWERTY keyboard.

2.2.3 Expression categorisation task

Faces from the Radboud face database (Langner et al., 2010) were used for this task. For this task, we selected the front-facing images of all 67 models in the database, with each displaying the six basic emotions (angry, disgusted, fearful, happy, sad, surprised). Each model was trained to produce the facial expressions using the Facial Action Coding System (FACS; Ekman, Friesen, & Hager, 2002). Images were cropped to a square containing the whole face (but excluding the top part of the head – see Figure 2.1), and were 12cm x 12cm on the monitor (4.6° of vision).

Ten random examples of each expression were presented to participants in a random order, with six numbered emotion labels presented underneath Participants used a standard keyboard to indicate their response by pressing the numbered key corresponding to the emotion they perceived. A full categorisation matrix was collected for each participant, which recorded the number of instances that each of the presented expressions were labelled (or mislabelled) with each of the emotion categories.

Each stimulus was preceded by a fixation cross for 500ms. Then, the stimulus was presented until the participant responded, after which there was a blank screen for 200ms.

Figure 2.1: An example of a trial in the expression categorisation test.

2.2.4 Visual Acuity and Contrast Sensitivity task

Visual acuity and contrast sensitivity were measured using the Freiburg Visual Acuity Test (FrACT; Bach, 1996). In these tests, participants were presented with a Landolt-C (an incomplete circle) in one of eight orientations and were required to indicate the position of the gap in the circle with use of a button press. Thresholds were estimated via a best PEST (best Parameter Estimation by Sequential Testing) procedure.

For visual acuity, threshold was estimated by manipulating the size of the Landolt-C, and for contrast sensitivity, threshold was estimated by manipulating the spatial frequency of the Landolt-C in comparison to the background. Participants completed 18 trials for each threshold estimation at a viewing distance of 2m. Acuity was measured as decimal acuity (where 1.00 is considered normal

‘20/20 vision’) and contrast sensitivity was measured as a Weber percentage. Full task details are available at https://michaelbach.de/fract/)

2.2.5 Glasgow Face Matching Test

We used the short version of the Glasgow Face Matching Test (GFMT; Burton et al., 2010) as a measure of face identity processing. To our knowledge, the GFMT has not been used within ageing research. The Benton Face Recognition Test (A. L. Benton, Sivan, Hamsher, Varney, & Spreen, 1994) has been more widely used (e.g. Bucks, Garner, Tarrant, Bradley, & Mogg, 2008; Orgeta & Phillips, 2008), but the validity of this test has been questioned with prosopagnosics performing similarly to healthy controls (Duchaine & Nakayama, 2004). As the GFMT is a relatively challenging task with “large interindividual variation” (Burton et al., 2010, p. 290), we use it here as a sensitive measure of face identity processing that may highlight age differences that have not previously been observed.

In this test, participants were presented with 40 pairs of faces and must make same/different judgements. Of the 40 pairs of faces, 20 are matching and 20 are nonmatching. The pairs of faces comprise of two full face images; one taken with a still camera, the other taken from the frame of a video. Full stimuli can be found at http://www.facevar.com/glasgow-face-matching-test. Performance on this test has been shown to correlate with performance on face memory and object matching tasks (Burton et al., 2010). Stimuli were presented in a random order, and participants had no time limit to respond although they were encouraged to use their initial judgement. We used a signal detection approach (*d’*; Stanislaw & Todorov, 1999), rather than accuracy, as this provides a more sensitive measure of identity processing and is not subject to response biases.

2.2.6 WAIS-IV Digit Span

Short term memory was measured using the WAIS-IV Digit Span (Wechsler, 2008). Participants listened to sequences of digits, and were required to recall them forwards, backwards, or in ascending order across 3 subtests. Sequences ranged in length, from 2 digits to 9, and the raw score for this test was calculated as the sum of correctly recalled sequences across the 3 subtests. Two sequences of each length were presented, and each subtest stopped if the participant incorrectly recalled both sequences in the pair.

2.2.7 WAIS-IV Matrix Reasoning

We used the WAIS-IV Matrix Reasoning test (Wechsler, 2008) to measure fluid intelligence. For this test participants were presented with a sequence of incomplete matrices, containing images of coloured shapes. Participants were required to select which of 5 options best completed the matrix. The raw score was calculated as the sum of correct responses, and the test stopped when the participant provided 3 consecutive incorrect responses.

2.3 Results

2.3.1 Age differences in expression labelling accuracy

Labelling accuracy was calculated for each participant, as the percentage of correctly labelled facial expressions for each emotion. We conducted 6 independent t-tests to compare the accuracy for each emotion between the groups, correcting for multiple comparisons with the Bonferroni adjustment. Consistent with our predictions, older adults performed more poorly at labelling angry and sad faces. Unexpectedly, older adults did not differ from younger adults in the recognition of fearful facial expressions, and performed more poorly than younger adults in the recognition of surprise. Group distributions for each emotion are presented in Figure 2.2; results of the t-tests, descriptive statistics, and effect sizes are presented in Table 2.2.

Table 2.2: Means, standard deviations, t-statistics, p-values, and effect sizes (Cohen's d) for accuracies at correctly labelling each emotion between the two groups.

	Young		**Old**				
	Mean	**S.D.**	**Mean**	**S.D.**	**t**	**p**	**d**
Angry	78.40	17.54	65.71	18.37	3.709	<.001*	0.85
Disgusted	87.40	13.52	81.90	18.51	1.451	.150	0.31
Fearful	60.20	26.76	50.24	26.00	1.937	.056	0.52
Happy	96.80	5.13	95.48	7.72	1.475	.144	0.22
Sad	91.00	12.33	71.90	23.19	5.422	<.001*	1.35
Surprised	91.80	10.63	83.10	14.73	3.607	.001*	0.72

** indicates that the p-value falls below the Bonferroni adjusted alpha level of 0.008 (.05/6).*

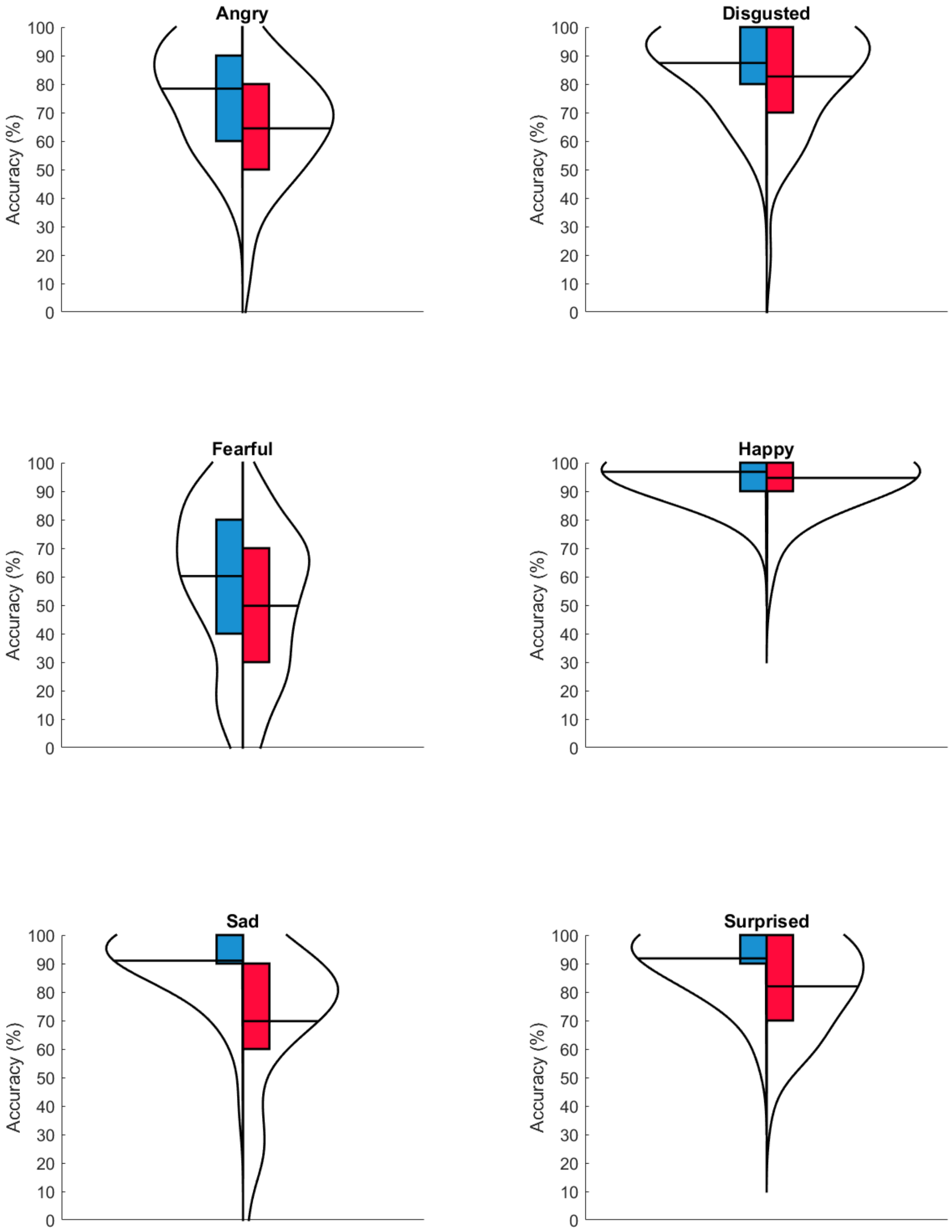

Figure 2.2: Split box plots showing the accuracy scores for younger (blue) and older (red) adults, for each emotion. Horizontal black bars show the mean, coloured boxes show the interquartile range, and violins show the shape of the distributions.

2.3.2 Age differences in control task performance

We then calculated age differences in the performance at each of the control tasks. To do so, we again conducted 6 independent t-tests between the raw scores for the WAIS subtests, GFMT d’, and the visual acuity and contrast sensitivity measures. Older adults performed significantly poorer than the younger adults on all tests. Group distributions for each control task are presented in Figure 2.3; results of the t-tests, descriptive statistics, and effect sizes are presented in Table 2.3. It is worth noting that the higher mean (and therefore negative t-statistic and effect size) for the Weber % reflects poorer contrast sensitivity for older adults.

All participants scored within 2.5 standard deviations from their group mean.

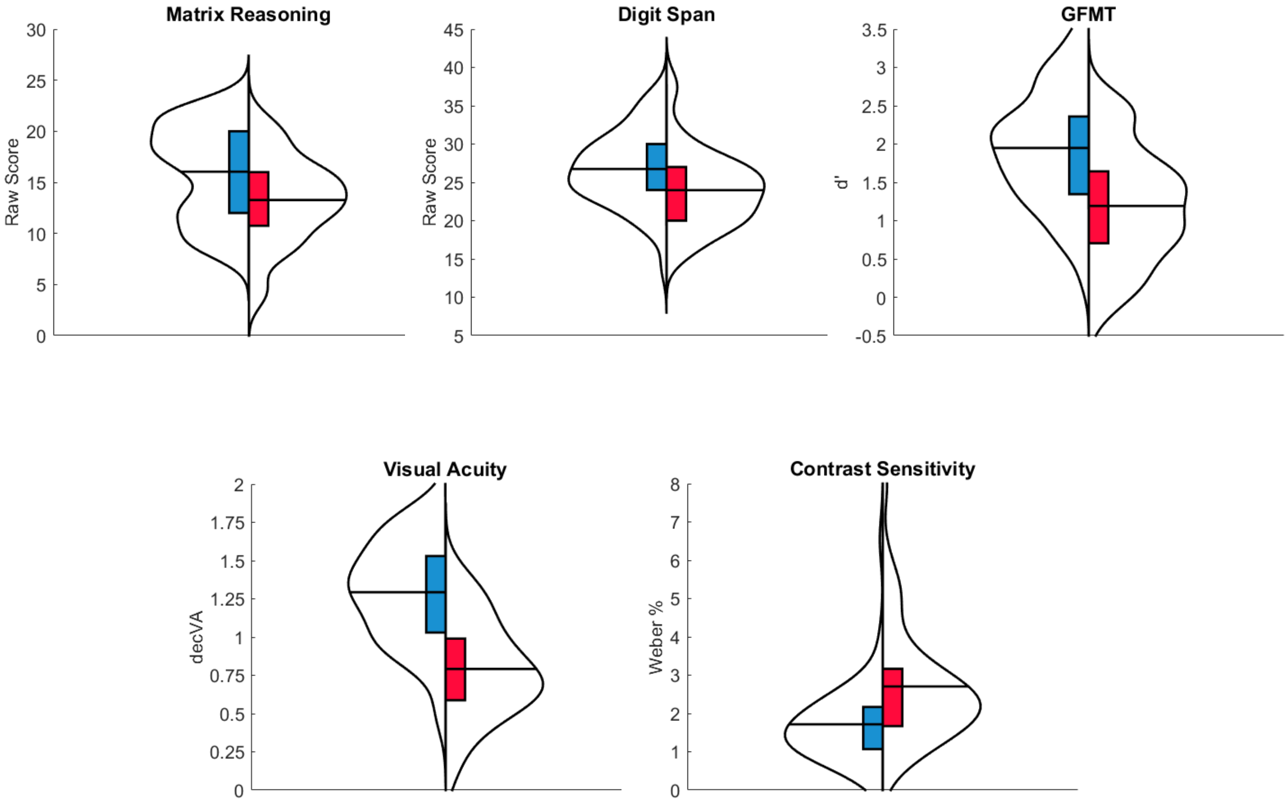

Figure 2.3: Split box plots showing the accuracy scores for younger (blue) and older (red) adults, for each of the five control measures. Horizontal black bars show the mean, coloured boxes show the interquartile range, and violins show the shape of the distributions.

Table 2.3: Means, standard deviations, t-statistics, p-values, and effect sizes (Cohen's d) for performance on the 5 control tasks between the two groups.

Measure	**Young**		**Old**		**t**	**p**	**d**
	Mean	**S.D.**	**Mean**	**S.D.**			
Matrix Reasoning (raw)	16.04	4.63	13.267	4.213	3.042	.003*	1.07
Digit Span (raw)	26.74	4.77	23.978	4.883	2.788	.006*	1.03
Glasgow Face Matching Test d'	1.95	0.75	1.292	0.744	4.929	<.001*	0.71
Visual Acuity (decVA)	1.29	0.33	0.792	0.313	7.637	<.001*	0.72
Contrast Sensitivity (Weber %)	1.72	0.97	2.705	1.486	-3.882	<.001*	-0.76

** indicates that the p-value falls below the standard alpha level of 0.05.*

2.3.3 Age differences in the recognition of anger and surprise can be explained by the control tasks.

After finding age differences in the recognition of anger, sadness, and surprise, we then tested to see whether these differences could be explained by the covariates. Three one-way ANCOVAs were performed, using emotion labelling accuracy as the dependent variable and group as the independent, while using the 5 control measures as covariates.

After correcting for multiple comparisons with the Bonferroni adjustment (alpha = .016) age differences fell to non-significant for the correct recognition of anger ($F(1,88) = 0.374$, $p = .543$, $\eta_p^2 = .004$) and surprise ($F(1,88) = 5.382$, $p = .023$, $\eta_p^2 = .058$) when accounting for the control measures, but remained significant for the recognition of sadness ($F(1,88) = 6.889$, $p = .010$, $\eta_p^2 = .073$). This suggests that age-differences in the recognition of anger and surprise can be accounted for by differences in the 5 control measures, whereas age differences in the recognition of sadness cannot. The R^2 values for each ANCOVA model show that age group and the 5 covariates can explain most variance in the recognition of sadness ($R^2 = .283$), followed by anger ($R^2 = .257$), then surprise ($R^2 = .137$).

To assess the relative contribution of each covariate to the recognition of anger and surprise, partial eta squared (η_p^2) was calculated for each covariate in the ANCOVA model. This is a measure of the proportion of variance accounted for by each covariate, so is used as a measure of the relative contribution of each covariate on recognition accuracy. These effect sizes, and the associated F and p-values, are presented in Table 2.4 for the recognition of anger and surprise. As such, we can see that performance on the GFMT was the largest contributor to the recognition of anger, whereas performance on the Matrix Reasoning test was the biggest contributor to the recognition of surprise. Analysis for the contribution of each covariate to the group differences in the recognition of the other emotions can be found in Appendix A (Table A1).

Table 2.4: F ratios, p-values, and effect sizes for each covariate within the ANCOVA model for the recognition of anger and surprise.

Covariate	**Anger**			**Surprise**		
	F	**p**	**η_p^2**	**F**	**p**	**η_p^2**
Matrix Reasoning	.693	.407	.008	1.067	.305	.012
Digit Span	2.320	.131	.026	.094	.759	.001
GFMT	5.032	.027	.054	.394	.532	.004
Visual Acuity	1.416	.237	.016	.045	.832	.001
Contrast Sensitivity	.043	.836	<.001	.079	.780	.001

2.3.4 Comparison of Confusion Matrices

The secondary aim of our experiment was to compare how younger and older participants confuse facial expressions. To do so, we first generated the mean categorisation matrix for each age group, presented in Figure 2.4. Each matrix shows the 6 presented facial expression categories on the y-axis, and the selected emotional label on the x-axis. Each cell in the matrices represents the mean number of instances that the expression on the y-axis was labelled with the emotional label on the x-axis, across all participants in each group.

Firstly, we performed a replication of the analysis used by Mill et al. (2009), who calculated the relationship between the confusion matrices from younger and older adults using all cells in averaged matrices from each group. The researchers reported a strong correlation (r = .97), suggesting that younger and older adults make similar patterns of confusions. After Mill et al. (2009), we performed a correlation between all cells within the confusion matrices for each group, and found a relationship of a similar strength (r(36) = .990, p<.001). Repeating this analysis for on-diagonal cells only (correct responses) shows a strong relationship (r(6) = 0.907, p = .013), although the small number of on-diagonal cells may have artificially inflated the coefficient. Interestingly, repeating the analysis using only the off-diagonal cells (the pattern of incorrect emotion categorisations) similarly shows a strong relationship (r(30) = 0.867, p<.001), suggesting that the relationship between the matrices is not driven by the (high) numbers of correct responses, but rather the patterns of confusions made between pairs of emotions.

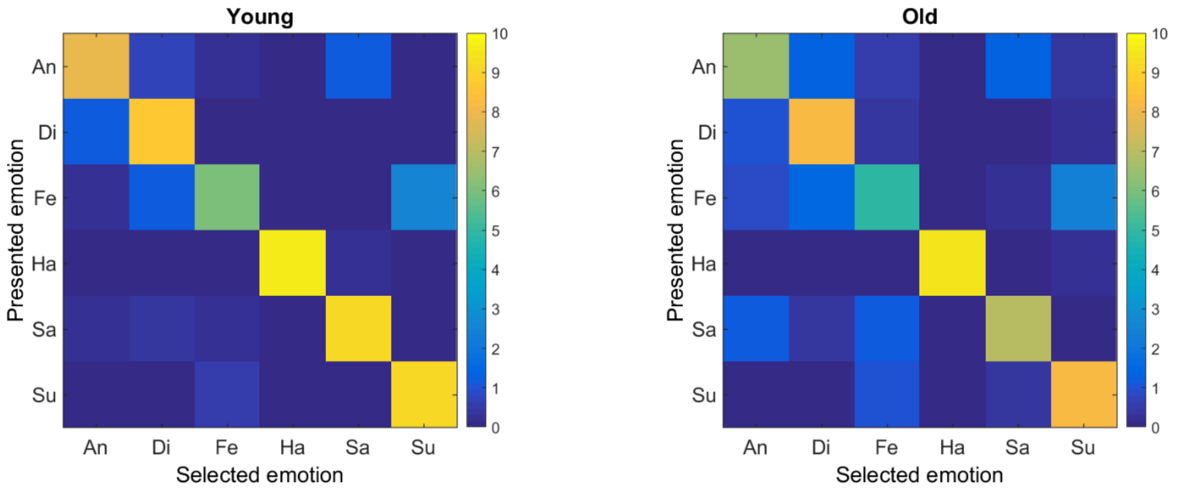

Figure 2.4: Mean categorisation matrices for younger and older participants. Each matrix shows the mean number of instances that each presented emotion along the y-axis was categorised using each emotion label along the x-axis. The value of the cells in each matrix have been presented here using a colourbar to aid in visualisation.

To assess the young-old differences in the exact pattern of categorisation of facial expressions, we then computed 36 Wilcoxon rank-sum tests between the corresponding cells in each matrix, and corrected for multiple comparisons using the False Discovery Rate correction (FDR; Benjamini & Hochberg, 1995). We opted to correct using this FDR correction as opposed to the more stringent Bonferroni adjustment, as the Bonferroni adjustment assumes independence between all comparisons. The results of this comparison are presented in Figure 2.5. Cells with significant young-old differences are indicated with asterisks, where the p-value of the Wilcoxon rank sum-test falls below the FDR corrected alpha level of $1.328*10^{-2}$.

The value of the associated Z-statistic for each cell has been scaled with a colourbar, such that blue cells indicate that the presented facial expression on the y-axis was categorised with the emotional label on the x-axis more by younger adults than older adults, and red cells indicate the opposite. The blue cells with significant differences along the diagonal are consistent with our initial analysis that younger adults correctly labelled angry, sad, and surprised facial expressions more than older adults.

In addition to this, we find significant age differences in a number of off-diagonal cells, suggesting that younger and older adults differ in their patterns of confusions between emotions. Older adults mislabel facial expressions of anger as fear, fear as anger, happiness as surprise, and sadness as anger and fear, more than younger adults. Younger adults, on the other hand, mislabel facial expressions of happiness as sad more than older adults.

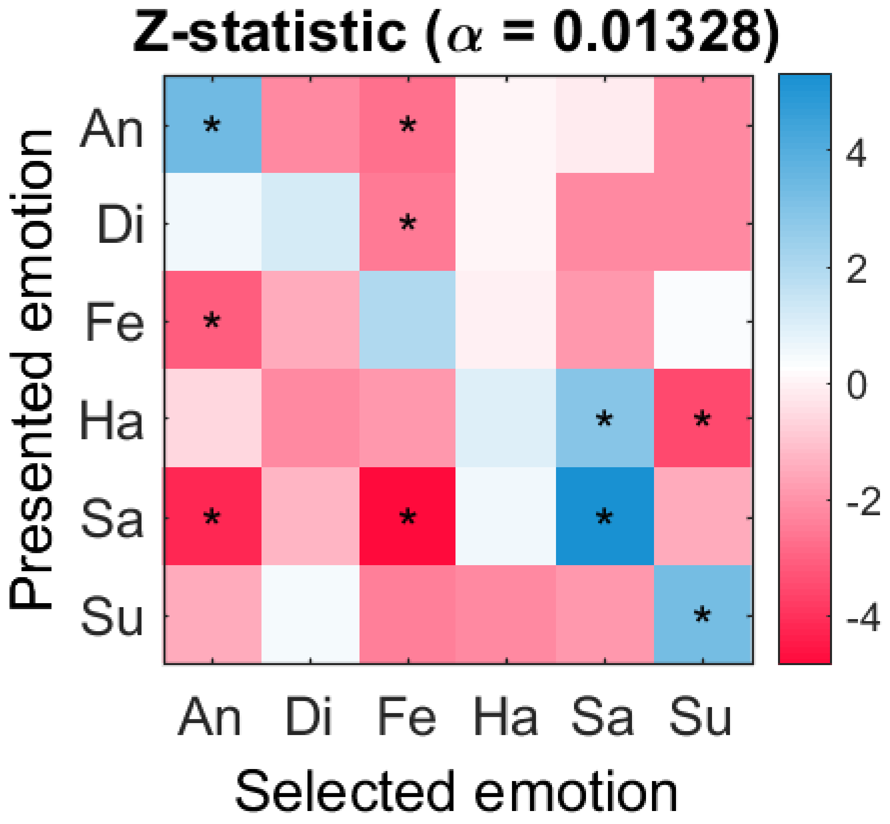

Figure 2.5: Young-old differences in facial expression categorisation. Each cell shows the Z-statistic associated with the Wilcoxon rank sum test between younger and older adults' categorisations. Asterisks indicate significant young-old differences (Blue cells: Younger>Older; Red cells: Older>Younger).

2.4 Discussion

Consistent with our hypotheses, we found significant age differences in the accurate labelling of anger and sadness. Unexpectedly, we found no differences in the recognition of fear, but we did for surprise. Our finding that older adults experience poorer recognition of anger and sadness in facial expressions is commonly reported in previous research (Calder et al., 2003; Horning et al., 2012;

Isaacowitz et al., 2007; Ruffman et al., 2008; Sullivan et al., 2007). The age differences in the recognition of surprise are reported less frequently (Ruffman et al., 2008). We found no age related improvement in the recognition of disgust as has been reported in some previous work, although this improvement is not reported as frequently across research (Ruffman et al., 2008). In addition to this, we found no differences in happy recognition due to ceiling effects, which is commonly reported (Isaacowitz et al., 2007; Ruffman et al., 2008).

Here we have also demonstrated that our measures of fluid intelligence, short term memory, face processing, visual acuity, and contrast sensitivity significantly account for the age differences only in the accurate labelling of angry and surprised faces, but not sad faces. The calculation of the effect sizes for each covariate within the ANCOVA models advances previous research by assessing the relative contribution of these control measures to the age differences in the accurate labelling of angry and surprised facial expressions. After doing so, we found that our measure of face identity processing (GFMT) accounted for the most variance in the recognition of anger, whereas our measure of fluid intelligence (the Matrix Reasoning test) accounted for the most variance in the recognition of surprise.

This is not entirely consistent with previous research that suggests the age-related decline in facial expression recognition is independent from any changes in general face processing (Orgeta & Phillips, 2008; Sullivan & Ruffman, 2004). This inconsistency may arise as we have analysed the effect on the recognition of each emotion separately, whereas this previous work has used concatenated scores as a measure of general emotion recognition accuracy. Alternatively, this result may be due to the signal detection approach that we adopted with the GFMT, which is arguably more sensitive than simple accuracy at quantifying face identity discrimination. We found significant age differences in the d’ scores, which is consistent with previous research suggesting an age-related decline in the ability to process face identity (Crook & Larrabee, 1992). Our results may highlight how age differences in facial expression recognition are not fully independent from the decline in face identity processing.

With regard to the influence of lower level visual processes, our results suggest that visual acuity is a more important contributor to labelling accuracy for angry faces than contrast sensitivity (after controlling for the other covariates). This suggests that face shape information may be a more important cue than surface information when labelling angry facial expressions. In the ANCOVA model for surprise recognition, differences in visual acuity and contrast sensitivity had a comparable influence. Future work could investigate any age-related changes in the relative usage of shape and surface information when categorising facial expressions. Sormaz, Young, and Andrews (2016) created sets of stimuli that varied only in shape (by warping the average surface texture to the original shapes) or only surface (by warping the original facial expressions to an average shape). In other words, shape cues were removed from one set of stimuli, while surface cues were removed from the other. Participants were then tested on their ability to recognise the emotions from these expressions. Applying this task within ageing research would allow for the examination of any age-related differences in the use of shape and surface information.

Previous research suggests that the age-related decline in 'working memory' is either independent from, or partially related to, the decline in emotion recognition from facial expressions (Horning et al., 2012; Orgeta & Phillips, 2008; Phillips & Allen, 2004; Ryan, Murray, & Ruffman, 2010). The present work furthers this by differentiating between processes of short-term memory and fluid intelligence, with use of the digit span and matrix reasoning tests. After controlling for all covariates, we found that the measure of short term memory shares more unique variance with the recognition of angry facial expressions than fluid intelligence, whereas the opposite is true for the recognition of surprise. On the other hand, we found that age differences in the recognition of sadness remained significant. Similarly, Murphy and Isaacowitz (2010) reported that sadness recognition accuracy was not associated with several cognitive, affective, and visual measures. Together, these results may suggest a specific age-related impairment in the recognition of this emotion.

The secondary aim of our experiment was to explore any age differences in the pattern of categorisation of facial expressions. While Mill et al. (2009) suggested that older adults categorise emotions similarly to younger adults, here we have highlighted age differences by performing a cell-by-cell comparison of the full categorisation matrices generated by each group. We found significant differences between the groups in some diagonal cells, reinforcing our previous finding of an age-related decline in the recognition of anger, sadness and surprise, even when all possible categorisations were accounted for. Interestingly, we found significant differences in several off-diagonal cells, suggesting that older adults mistake certain facial expressions for different emotions, more than younger adults. This could suggest that the facial expressions of these emotions become more perceptually similar across the lifespan.

While this was conducted with no formal hypotheses, it highlights how older adults differ from younger adults in the emotions they recognise from certain facial expressions. Interestingly, older adults differed from younger adults here in their erroneous usage of the labels 'anger' (in response to fearful and sad faces) and 'surprise' (in response to happy faces). We found that older adults were poorer at the accurate recognition of anger and surprise, so it would be expected that they use these emotion labels less frequently than younger adults. Our results here suggest that they differ from younger adults in their misuse of these labels, rather than simple avoidance of them. Similarly, this analysis compliments the result that older adults are poorer at the accurate recognition of sadness, by suggesting that they mislabel facial expressions of sadness as angry and fearful more than younger adults. It is also worth noting that several of the off-diagonal cells with significant age-differences lie between pairs of emotions that older adults typically find more challenging to identify in facial expressions. Our results suggest that older adults misperceive angry faces to be fearful, fearful faces to be angry, sad faces to be angry, and sad faces to be fearful, more than younger adults. Complimenting previous research that suggests an age-related decline in the accurate recognition of anger, sadness and fear in facial expressions, our results suggest that older adults make more confusions between pairs of these emotions than younger adults.

3 Age-related changes in neural response to facial expressions

3.1 Introduction

The recognition of emotions from facial expressions has been reported to decline with age, with older adults experiencing difficulty with the recognition of negative emotions. Specifically, the recognition of expressions of anger, sadness, and fear shows the most frequent young-old differences across research into this area (Ruffman et al., 2008). In Chapter 2, we tested a group of younger (mean age = 20.5y) and older (mean age = 75.0y) adults on their ability to recognise the 6 basic emotions, alongside a number of control tasks. We found that the young-old differences in the recognition of anger and surprise could be accounted for by measures of working memory, fluid intelligence, face processing, visual acuity, and contrast sensitivity, however these covariates could not account for the young-old differences in the recognition of sadness. In the current study, we focus on a neuropsychological account for age differences in expression recognition (Ruffman et al., 2008). This account explains the behavioural young-old differences in terms of the age-related structural changes that occur in regions of the brain that process specific expressions. As ageing is associated with poorer recognition of negative expressions (commonly anger, sadness and fear), it is expected that the regions involved in the processing of negative expressions undergo these age-related structural changes. By contrast, regions that are involved in the processing of other emotions (for example happiness) are expected the undergo fewer age-related changes.

Previous research has highlighted several regions that are subject to age differences in activation in response to facial expressions (see Chapter 1). This research commonly examines differences in activation between 2 distinct age groups, often excluding middle-aged adults (an exception to this is Williams et al. (2006) who used 4 age groups). Many of these studies have had sample sizes that may be considered small, ranging from as little as 8 participants in each group to 24. Given the problematic nature of conducting an adequately powered group study using fMRI (Thirion et al., 2007), it could be argued that a correlation-based approach may be better suited to study effects of age. Furthermore, as there is research to suggest that the recognition of certain expressions may begin to decline during middle-age (Calder et al., 2003; Horning et al., 2012; Williams et al., 2006), using a wider spectrum of ages may capture effects that have previously been overlooked. A common result of previous research is that the activation in the amygdala and areas of the prefrontal cortex is reduced in older adults, although there is a large network of regions that are responsible for the processing of different expressions. Using a correlation-based analysis may therefore reveal an age-related attenuation in these regions that group-studies have not.

In addition to examining any age-related changes in neural response to expressions, it is of interest to examine whether neural response is associated with the behavioural recognition of the emotion. While the neuropsychological account (Ruffman et al., 2008) does not necessarily specify any relationship between the degree of activation and the behavioural recognition of an emotion, finding such an association would provide support for any explanation of age differences in behaviour in terms of age differences in functional response. Older adults show both poorer recognition accuracy and speed of processing than younger adults, so it may be of interest to examine the relationship between functional response to expressions and both accuracy and reaction time to recognise them behaviourally. Any relationship between these behavioural measures and neural responses would provide support for the neuropsychological account, and provide new evidence associating specific regions of the brain to the age-related decline in expression recognition.

In the present study we conduct secondary analysis of fMRI data, using participants aged 18-65. The data was collected as part of a larger project investigating emotion processing in schizophrenia (Kumari et al., 2011), although was not included in the publication. Participants viewed facial expressions of anger, fear and happiness, in addition to a neutral expression, while undergoing MRI. This allows us to examine any effects of age on emotion-specific activation. In addition to this, participants took part in a behavioural facial expression recognition test, allowing us to examine whether any age-related decline in neural activation is associated with emotion recognition ability. Firstly, we identified regions that show greater response to each expression category in comparison to neutral faces. Next, we identified the brain regions in which the magnitude of this activation varied with age. Taking the view that the age-related decline in the recognition of negative emotions is related to reduced activation, we expect to find an age-related reduction in activation in response to angry and fearful faces. Finally, we assessed the relationship between the activation in these regions and performance at the emotion recognition test. If any age-related changes in activation are associated with the behavioural recognition of the emotion, a relationship between activation and behaviour is expected.

3.2 Methods

3.2.1 Participants

Data from 30 participants (21 males) were used. Participants were aged 20-65y (mean age = 33.9, S.D. = 11.65). All participants fell within the normal range across a range of neuropsychological tests, were not on any medication, and had no history of drug use.

3.2.2 Expression recognition task

Participants were presented with 128 faces (Ekman & Friesen, 1976) displaying neutral, happy, angry, or fearful expressions. Each face was presented for 3 seconds, and faces were presented in a pseudo-random order to avoid repetition of any emotion category. After the face disappeared, participants were presented with the question “What emotion did you see?” and were required to choose from one of 4 emotion labels (Neutral, Happy, Anger, and Fear). Participants responded using the mouse. Full task details can be found in Premkumar et al. (2008).

3.2.3 fMRI task and protocol

Participants were presented with angry, fearful, happy, and neutral faces (from Ekman & Friesen, 1976), each in separate blocks lasting 30s. Each block contained 8 faces, presented for 3.75s each. After each block of faces, participants were presented with an oval frame (matched for the luminance of the face blocks) lasting 15 seconds. Blocks for each facial expression category were presented 4 times each. During the face blocks, participants performed a gender discrimination task (to keep attention), where they indicated if each face was male or female using a button box. Full details on the fMRI paradigm can be found in Kumari et al. (2011).

3.2.4 fMRI Image Acquisition

MRI data was collected with a 1.5T GE Signa System. 240 T2*-weighted images were collected for each participant, using an Echo Planar Imaging (EPI) sequence with 16 near-axial slices aligned parallel to the intercommisural plane (TR = 3000ms, TE = 40ms, flip angle = 90°, voxel size = 3.1mm x 3.1mm x 7mm, matrix size = 64 x 64, interslice gap = 0.7mm). In addition to these function images, a high-resolution 3D inversion recovery prepared spoiled gradient recalled acquisition in the steady state volume data set was acquired (TR = 12.2ms, TE = 5.3ms, inversion time = 300ms, voxel size = 0.94mm x 0.94mm x 1.5mm).

3.2.5 Image preprocessing and beta estimation

For each participant, all functional images were realigned (registered to the mean of the whole session using 2nd degree B-spline interpolation) and resliced (using 4th degree B-spline interpolation). Each participant’s structural image was co-registered to their mean functional image, then functional images were normalised to MNI space (voxel size = 3mm x 3mm x 3mm) using the deformation field output from warping the structural to an MNI template. Functional images were smoothed with an 8x8x8mm FWHM Gaussian kernel, using the SPM12 toolbox in MATLAB 2016b. Each expression condition was modelled with a box-car, convolved with a standard haemodynamic response function, for each 30 second block. The 6 realignment parameters were included in this GLM.

3.2.6 Analysis

At the first level of analysis we contrasted the betas for each expression (Angry, Fearful, Happy) against the beta for the Neutral condition, for each participant. Using random effects analysis at the second level, we first investigated the effect of each expression (compared to neutral) across the group. Next, we used age as a second-level covariate to identify the regions in which the magnitude of activation (for each expression in comparison to neutral) was correlated with age. We tested for both positive and negative correlations with age. After identifying these age-sensitive regions, we then tested the correlations between the activation in response to an expression within the peak voxel (the voxel showing the greatest relationship with age in each region) and three behavioural measures: recognition accuracy and reaction time (during the behavioural task), and reaction time in the gender decision task participants performed in the scanner. Doing so allowed us to examine whether the activation in these regions was only associated with age, or whether it was also associated with differences in any of these behavioural measures.

3.3 Results

3.3.1 Behavioural Emotion Recognition Task (Offline)

The mean and standard deviation were calculated for reaction time and recognition accuracy for each expression. A Pearson’s correlation was also conducted to assess the relationship between accuracy at recognising each emotion and age. These results are presented in Figure 3.1 below.

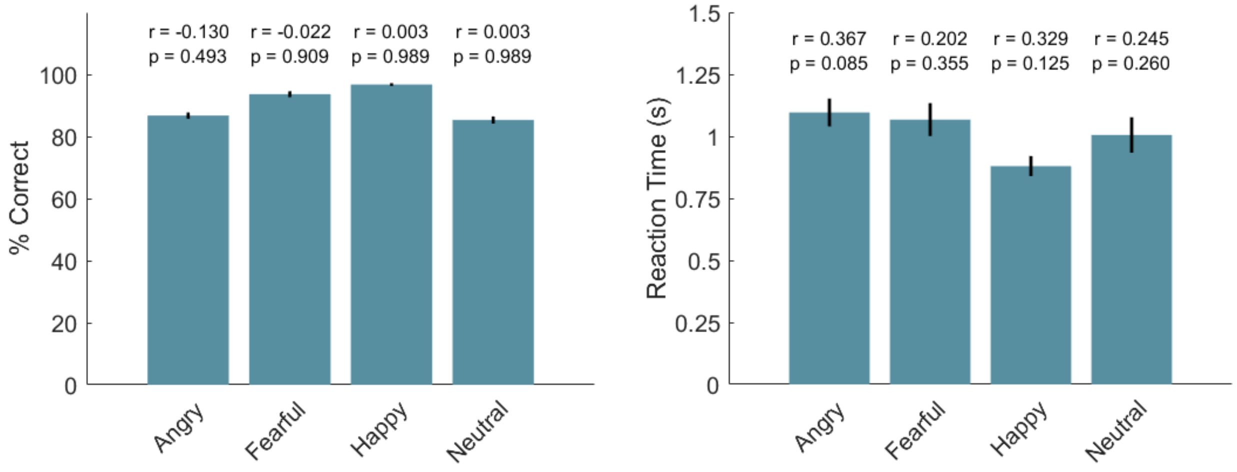

Figure 3.1: Accuracy (left) and reaction time (right) during the behavioural emotion recognition task. Error bars show 1 standard error. The results of the Pearson's correlation with participant age is presented above each bar.

3.3.2 Gender Discrimination Task (Online)

The mean and standard deviation for the accuracy and reaction time during the gender discrimination task was also calculated. Figure 3.2 shows these, and the results of the Pearson's correlation between each measure and age. Only reaction time to respond to angry faces was correlated with age (r(30) = .479, p = .007).

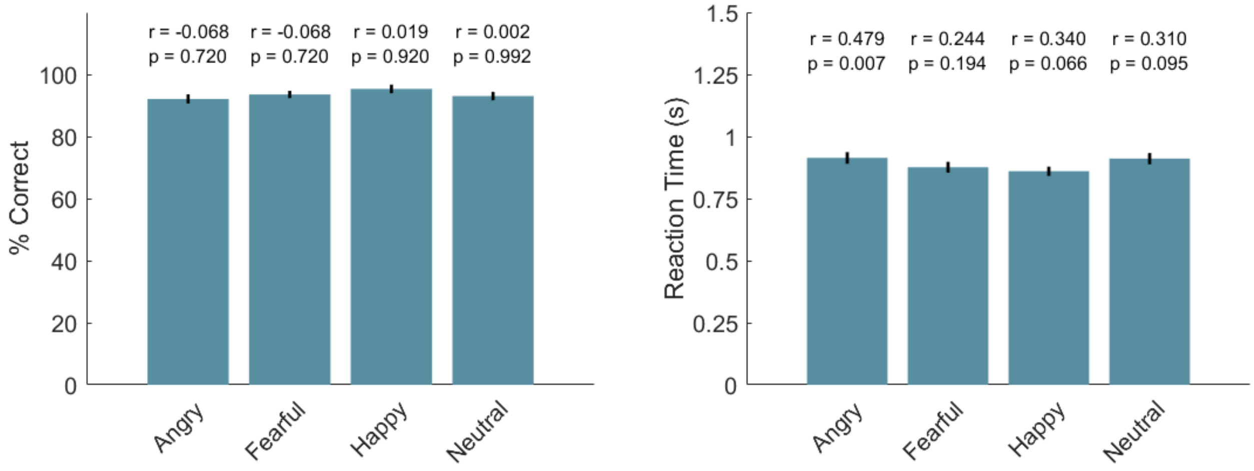

Figure 3.2: Accuracy (left) and reaction time (right) during the gender categorisation task, split by emotion category. Error bars show 1 standard error. The results of the Pearson's correlation with participant age is presented above each bar.

3.3.3 Effects of emotion across participants

A one-sample t-test was conducted comparing the magnitude of activation for each expression (in comparison to neutral) to 0. Using a threshold of p<.001 (uncorrected) and a cluster threshold of 10 voxels, significant activation was only found for fearful faces in comparison to neutral in the right parahippocampal gyrus. Results are reported in Table 3.3.

Table 3.3: Results of the random effects analysis for the effect of each emotion compared to neutral.

Contrast	**Hemisphere**	**Region**	**MNI Coordinates**			**Peak T**
			X	*Y*	*Z*	
Angry > Neutral	n/a					
Fearful > Neutral	R	Parahippocampal gyrus	9	-34	-10	4.16
Happy > Neutral	n/a					

3.3.4 The relationship between age and activation

Next, participant ages were entered as a covariate into the second level analysis to explore the regions in which the magnitude of activation in response to each expression was correlated with age. Following Kumari et al. (2003), we first identified clusters showing effects of age using a relatively liberal threshold (p<.001 uncorrected, cluster threshold = 10 voxels), then tested the significance using a threshold of p<.05 (FWE corrected) within a 5mm spherical ROI centred on the peak voxel within each cluster. Activation in several regions was negatively correlated with age for each expression. No regions showed a positive correlation with age (i.e. we found no regions in which increasing age is associated with greater activation to each expression).

Results are reported in Table 3.4.

Table 3.4: Regions in which activation is negatively correlated with age, for each expression.

Contrast	**Hemi-sphere**	**Region**	**MNI Coordinates**			**Peak T**	**p**	
			X	*Y*	*Z*		**Cluster**	**Peak**
Angry > Neutral	L	Postcentral gyrus	-42	-25	53	4.60	.003	.001
	L	Anterior cingulate	-9	26	17	4.54	.003	.001
	L	Precuneus	-9	-49	65	4.15	.003	.002
	R	Postcentral gyrus	36	-25	56	4.04	.003	.003
Fearful > Neutral	L	Superior parietal lobule	-21	-58	56	5.25	.002	<.001
			-21	-73	50	4.75	.003	<.001
	L	Ventral Dorsal Caudate	-3	-7	-13	5.17	.002	<.001
	L	Putamen	-24	2	-10	3.91	.004	.004
	R	Superior parietal lobule	21	-67	47	3.88	.002	.004
Happy > Neutral	R	Medial precentral gyrus	12	-22	53	5.58	.002	<.001
	R	Lateral precentral gyrus	30	-22	56	4.69	.002	.001
	L	Lingual gyrus	-27	-70	8	4.59	.003	.001
	L	Middle cingulate	-15	-7	44	4.52	.002	.001
Happy > Neutral	R	Middle frontal gyrus	30	32	26	4.51	.003	.001
	L	Precentral gyrus	-30	-22	53	4.23	.003	.002
	L	Superior parietal lobule	-24	-52	56	4.22	.004	.002
	L	Middle temporal gyrus	-48	-40	2	4.11	.002	.002
	R	Middle cingulate	18	8	35	4.03	.003	.003
	L	Angular gyrus	-42	-55	32	4.01	.004	.003
	R	Medial postcentral gyrus	6	-37	62	3.84	.004	.004

3.3.5 Overlap between age-sensitive regions for each expression contrast

To investigate whether there was any overlap in regions showing an age-sensitive response to each of the three emotions, we overlaid the results for the three emotions onto the average anatomical image across participants (Figure 3.3).

There was an overlap between the voxels showing significant age-related declines in the response to happy and fearful faces in the left superior parietal lobule (Figure 3.3, left). There were also overlaps between the voxels showing significant age-related reductions in the response to angry and happy expressions, in regions in the bilateral postcentral gyri (Figure 3.3, middle and right). There were no voxels showing significant age-related reductions in the response to both angry and fearful expressions, nor any showing an age-related reduction in activation in response to all three expressions.

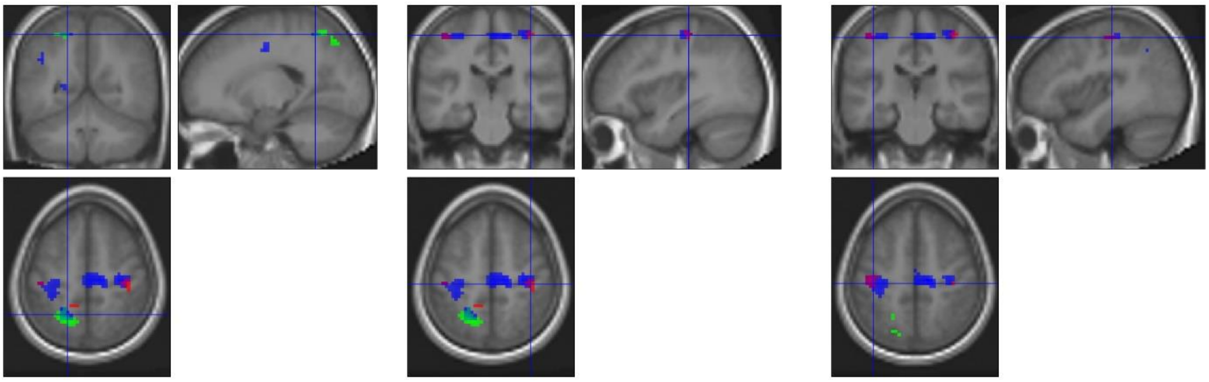

Figure 3.3: Regions in which age is negatively associated with response the 3 emotions (red = angry, green = fearful, blue = happy). Crosshairs are centred on overlapping regions showing an age-related reduction in response to both happy and fearful faces (Left), and both angry and happy faces (Middle, Right)

3.3.6 Correlation between activation and behavioural expression recognition

For each region showing significant age effects (regions in which the activation in response to an expression was negatively correlated with age), we performed a Pearson's correlation between the activation (within the peak voxel) and three behavioural measures (accuracy at the recognition of the emotion, reaction time to recognise the emotion, and reaction time to classify the gender of the face in the scanner). All correlations were performed within-emotion (e.g. the activation in response to happy faces was correlated with the reaction time to recognise happy faces). It should be noted that reaction times within the offline recognition task were missing for seven participants.

The only correlation to reach significance was between the activation in response to happy faces in the left middle cingulate (MNI coordinates = [-15, -7, 44]) and the reaction time to classify the gender of happy faces (r(30) = 0.370, p = .044). However, as this has not been corrected for multiple comparisons, we take this as no clear evidence that the reduction in activation across age is associated with behaviour. Full results are presented in Appendix B (Table B1).

3.4 Discussion

The main aim of this research was to examine whether the age-related attenuation in neural response to emotions from facial expressions was associated with the behavioural recognition of the emotion. Firstly, we found that a reduction in selectivity for emotional faces in several regions of the brain was associated with increasing age, across all 3 expression categories. We found a reduction in selectivity for angry faces in the bilateral postcentral gyri, the left anterior cingulate, and the left precuneus. We found a reduction in selectivity for fearful faces in the superior temporal lobule, left ventral dorsal caudate, and left putamen. We found the most regions showing effects of age in selectivity of happy faces, in the bilateral precentral gyri and middle cingulate cortices. Additionally, we found a reduction in lateralised regions including the left superior parietal lobule, lingual, middle temporal, and angular gyri, and in the right middle frontal and medial postcentral gyri. This was somewhat unexpected as typically the recognition of happy faces is maintained across age (Ruffman et al., 2008). Of note is that the activation in the superior parietal lobule and bilateral postcentral gyri showed an age-related reduction in activation across the different expressions. We found no regions in which ageing was associated with an increase in activation.

Interestingly, one study found cross-modal representations of face, body, and whole-person expressions of emotion in the left postcentral gyrus (Cao, Xu, Yang, Li, & Liu, 2018), comparable to the cross-modal representations of emotion found in the MPFC (Peelen et al., 2010; Skerry & Saxe, 2014). Additionally, another study reported involvement of the postcentral gyrus in taking a third-person perspective of emotion-inducing situations (Ruby & Decety, 2004), suggesting that this region may represent abstract emotion concepts and may be involved in theory of mind. As we found reduced selectivity for emotional faces in the bilateral postcentral gyri across age, perhaps the age-related decline in emotion processing may be associated with a reduction in theory of mind.

Of note is that we found reduced selectivity for fearful faces across age in the left dorsal caudate and putamen, part of the basal ganglia. Evidence from patients with Parkinson’s disease (a neurodegenerative disorder affecting the basal ganglia among other regions) suggests the involvement of the basal ganglia in the processing of emotions from both faces (Dujardin et al.,

2004) and voices (Pell & Leonard, 2003). Perhaps, the age related decline in the recognition of fearful faces may be some result of reduced processing in this region.

In relation to the main aims of this research, we found no strong evidence that activity within these regions was related to performance (accuracy or reaction time to recognise the emotion, or reaction time to classify the gender of the face). Together, this suggests that the reduction in activity across the lifespan is age-related, and is not a reflection of behavioural differences in the recognition of the expressions.

Some of these results are consistent with those in previous studies. For example, Iidaka et al. (2002) reported reduced activation in response to positive facial expressions, in the lingual and angular gyri. This is comparable to some results of the present study, in which there was an age-related reduction in the neural response to happy faces in these regions. Williams et al. (2006) reported young-old differences in the response to happy faces in a frontal region (the medial prefrontal cortex). In the present study, we found an age-related decline in activation in response to happy faces in some frontal areas (the middle frontal gyrus and middle cingulate).

There are, however, several results that are not entirely consistent with previous research. A common result reported by previous research is young-old differences in amygdala activation, with a reduced response to negative (Iidaka et al., 2002), angry (Fischer et al., 2005), happy (Keightley et al., 2007; Williams et al., 2006) and fearful (Williams et al., 2006) faces in older adults. Similarly, previous research often reports that older adults have reduced activation in some other areas of the limbic system in response to facial expressions and during facial expression discrimination tasks (Fischer et al., 2005; Gunning-Dixon et al., 2003; Iidaka et al., 2002). In the present study, we found no age-related decline in activation in any limbic areas in response to any of the facial expression categories. In contrast, we found that the activation in several occipital and parietal regions was negatively correlated with age. These differences could reflect our use of correlational analysis, in comparison to the group-based analysis used throughout previous research. Furthermore, the lack of any age effects in the amygdala may be due to our cluster threshold (Keightley et al., 2007).

The neuropsychological account of age differences in expression recognition (Ruffman et al., 2008) explains the behaviourally observed young-old differences in terms of age-related changes in structure and function of regions involved in the processing of specific facial expressions. Two results of the current study may not necessarily be consistent with this position. The first is that there were numerous regions in which the response to happy faces declined with increasing age. As the recognition of happy faces is relatively spared during ageing, it would be expected that the neural response to happy faces is not associated with ageing.

The second is that no regions (in which a reduction in activation was associated with increasing age) showed a relationship between activation and any of the behavioural measures associated with the recognition of the emotion. As this suggests that the reduction in activation does not reflect any differences in behaviour, it brings to question the link between the behaviourally observed age-differences and the age-related changes in neural response as proposed by the model.

It may be difficult to draw conclusions from this lack of a relationship with behaviour however, as the behavioural emotion recognition task may not have been sensitive enough to capture any relationship with neural activity. For example, ceiling effects were observed for the recognition of happy and fearful faces (with mean recognition accuracies of 96% and 93% respectively) so it is difficult, therefore, to examine the relationship between these measures and neural activity. Perhaps the use of a more challenging emotion recognition task may produce scores with sufficient variance to be able to examine the relationship with neural activity.

A potential reason for the differences between the results of our study and the results of previous research is the age range. Previous research often uses two distinct groups, with the minimum age of the older group starting at approximately 60. The recognition of certain expressions is suggested to begin to decline during middle-age (Calder et al., 2003; Horning et al., 2012; Williams et al., 2006), so perhaps the results of our study capture neural basis of the changes in emotion recognition that occur during middle age. It may be the case that some common results of previous research (for example, the reduction in amygdala response) may begin to occur during older adulthood. Future research could investigate the age at which these effects begin using an age range with older adults that we used.

4 The influence of conceptual and stimulus-based cues on the perception and recognition of facial expressions

4.1 Introduction

Previous research has shown that tasks that require the perception and the categorisation of facial expressions of emotion involve the use and integration of both stimulus-based cues and conceptual information. There is, however, little understanding of the relative importance and usage of different types of information to the different tasks.

Palermo et al. (2013) have shown different patterns of associations of individual differences in perceptual and categorical tasks, which suggest that the processes used in both tasks are not completely overlapping. To assess the relative usage of stimulus-based and conceptual cues on both the perception and categorisation of facial expressions, we take a Representational Similarity Analysis (RSA) approach. RSA is a powerful technique that allows for the comparison of the structure or geometry of representations across different modalities, methods, or groups, that are ordinarily incomparable (e.g. the brain, theoretical models, and behaviour; Kriegeskorte, Mur, & Bandettini, 2008). In RSA, the similarities (or dissimilarities) between the responses to all pairs of stimuli or conditions in one modality are computed (for example, pairwise measures for the similarity of facial expressions, measured using a behavioural task), and are used to construct a Representational Dissimilarity Matrix (RDM). Separate RDMs can be created to measure the similarities of stimuli within other modalities, and can then be compared across modalities, typically by correlating the RDMs or using them in regression models. RSA has been previously been used to investigate the role of concepts in the perception of facial expressions (Brooks & Freeman, 2018), the similarity of emotion representations across sensory modalities (Kuhn, Wydell, Lavan, McGettigan, & Garrido, 2017) and the integration of high- and low-level representations in judgements of personality traits from faces (Stolier, Hehman, & Freeman, 2018; Stolier, Hehman, Freeman, Keller, & Walker, 2018).

In our case, we aimed to use RSA to explore the types of information that participants use in perceptual and categorical facial expression tasks. Therefore, participants completed two tasks: a Perceptual Task in which they discriminated between facial expressions relying mostly on perceptual processes (no labelling was involved), and a Categorisation Task in which they categorised facial expressions using one of 6 emotion labels. From these tasks, we computed a perceptual and a categorical RDM for each participant. We then investigated whether model RDMs based on shape, surface, and conceptual information could explain the behavioural RDMs. Using multiple linear regression, we expected to see that each model can independently predict behaviour as measured by categorisation patterns and perceptual discriminability, and explored the different extents to which each source of information is used.

RDMs that contain the representational structure of facial expression percepts have been computed using a number of methods, often requiring participants to make subjective judgements or involving the presentation of emotion labels (Brooks & Freeman, 2018; Said, Moore, Engell, et al., 2010; Sormaz, Watson, et al., 2016). It is possible that these methods may recruit some top-down processes, so we aimed to design a task to reduce this top-down influence.

As shape, surface, and conceptual cues have all been shown to play a role in the perception and recognition of emotions, we expect all three of these cues to explain behaviour in the perceptual and categorisation tasks. Given that the presence of emotion labels may activate emotion concepts, we expect that conceptual cues may play more of a role in the categorical task than in the perceptual task.

4.2 Methods

4.2.1 Participants

50 participants (40 women) were recruited using the Brunel University Participant Pool, and by word of mouth. All participants were aged 18 or over (*M* = 19.02; *S.D.* = 1.70; range from 18 to 27) and reported normal or corrected-to-normal vision. Ethical approval to conduct the research was granted by the College of Health and Life Sciences Research Ethics Committee at Brunel University London.

Design

This study used a within-subjects design, so all participants completed both the Perceptual and the Categorical Tasks. The Perceptual Task was conducted first, so the participants were only exposed to the emotion labels during the Categorical task.

4.2.2 Perceptual Task

Materials

We selected pictures of facial expressions of emotion from the Radboud Faces Database (Langner et al., 2010). Three male identities and three female identities were chosen based on the ratings of genuineness and intensity for the six basic emotions (using validation data from Langner et al., 2010). First, we calculated the mean and standard deviations for the ratings of genuineness and intensity across the six basic emotions for each identity in the database. Next, identities were ranked according to these ratings allowing us to select only those identities with above average means and below average standard deviations (so that the genuineness and intensity ratings had less variability across the six emotions for the individual). From this selection we then chose the highest equal number of Caucasian male and female identities, leaving us with three males and three females. In total, there were 36 different pictures (6 identities x 6 expressions).

For each identity, we created morphed continua between each pair of six emotions. Each face was marked with 112 fiducial points (using the positions in the FantaMorph software; www.fantamorph.com) to allow for linear interpolation between every pair of expressions, within identity (Figure 4.1). Although Fantamorph was used to position the points, MatLab was used to create the continuum, which contained 100 discrete steps. Images were cropped to a square containing the whole face.

Figure 4.1: Seven examples from the happy-disgusted continuum. The stimuli in the task could be taken from any point along the continuum.

Procedure

During each trial, participants simultaneously viewed 3 faces aligned horizontally (Height/Width = 8.0°, Width of 3 images = 28.4°, with an average viewing distance of 60cm), each displaying one of two expressions. Beneath each face were numbers (1-3), and participants were required indicate which one displayed a different expression to the other two, by pressing the corresponding key (1-3) on a standard QWERTY keyboard. The faces were presented for a maximum of 5 seconds, or until the participant made a response. There was an ISI of 300ms. All faces were of different identities, and the position of the target was random.

To measure the perceptual similarity of pairs of expressions, we calculated discrimination thresholds using a psychophysical method. Psychophysical methods have been used in previous research to calculate sensitivity at which emotions can be detected in warped neutral-expressive pairs (Calvo, Avero, Fernández-Martín, & Recio, 2016; Marneweck, Loftus, & Hammond, 2013; Suzuki, Hoshino, & Shigemasu, 2006). Each trial of the Perceptual Task was used in the threshold estimation for one of 15 possible pairs of emotions. Each of the 3 face images was the result of linear interpolation between two original expressive images. A staircase procedure (Cornsweet, 1962) was used to adjust the weighting of the expressions in each image by 10% of the remaining distance in each step. This meant that the fiducial points of one expression were moved towards the corresponding points of the other expression (by 10% of the distance) for correct responses, and were moved away from the points of the other expression for incorrect responses (Figure 4.2).

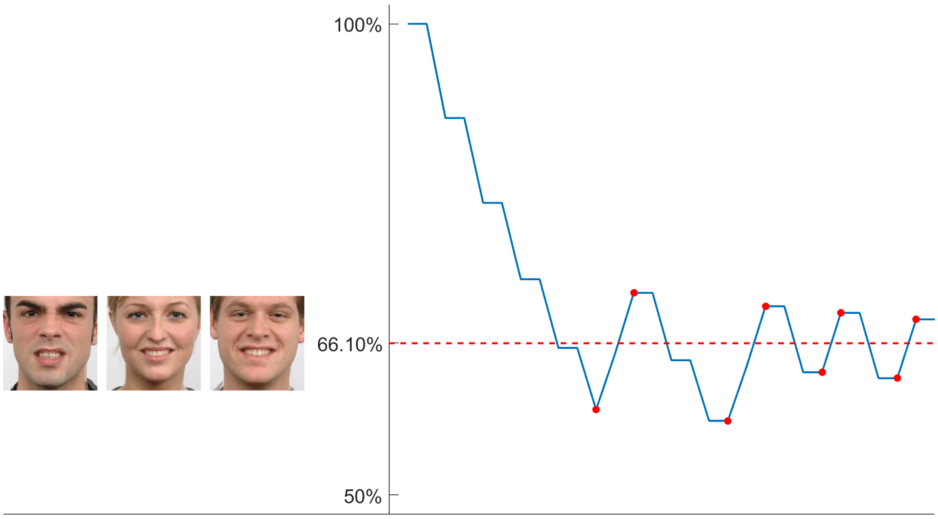

Figure 4.2: An example of the staircase adjustment of the weighting for a subject's happy-disgust discrimination threshold. Red markers indicate reversals in performance. The dashed red line indicates the threshold, which was calculated as the mean weighting at the last 7 reversals. The three faces show an example trial at threshold weight.

A 1-up-2-down design was used such that the participants were required to consecutively respond correctly 2 times for the weight to be adjusted downwards. The threshold estimation for each emotion pair started at 100% (the original images), and no exaggerations were shown during the task (e.g. if a participant responded incorrectly on the first trial of one threshold estimation, weighting was capped at 100%). The threshold estimation for each pair of emotions was terminated after 8 reversals in performance, and the discrimination threshold for a given pair of emotions was taken as the mean weighting at the last 7 reversal points. A perceptual matrix for each participant was constructed from the discrimination thresholds for each pair of emotions.

Trials for each emotion pair were presented in a random order, before the weighting was adjusted and all (remaining) emotion pairs were presented again in a random order.

4.2.3 Categorical task

Materials

We selected pictures of facial expressions of emotion from the Radboud Faces Database (Langner et al., 2010). Ratings of genuineness (using validation data from Langner et al., 2010) were used to select the top 40 most genuine examples of each emotion. In total, there were 240 images (40 x 6 emotions). Images were cropped to a square containing the whole face.

Procedure

During each trial participants were presented with a single picture of a facial expression in the centre of the screen (Height/Width = 9.6°, with an average viewing distance of 60cm). To avoid ceiling effects and ensure that the task was sufficiently challenging, each stimulus was presented for 200ms. This ensured that participants did not study the image in too much detail but were still able to make an informed decision. Brief presentation times have been used in validated facial expression recognition tests to reduce ceiling effects (Ekman & Friesen, 1974; Matsumoto et al., 2000).

After the image, participants were presented with 6 emotional labels with numbers 1-6 and were required to label the facial expression using the corresponding number keys on a keyboard. We recorded the number of correct responses to each emotion, as well as the number of instances each emotion was mislabelled with another.

The categorical RDM was constructed from the raw confusion matrix generated by each participant. Although this RDM does not measure ‘categorical similarity’ of emotions, each subject’s pattern of categorisation encodes the similarity of emotions as reflected by the behavioural confusions between a facial expression and an emotion label. Raw confusion matrices have previously been used with RSA (Skerry & Saxe, 2015 (Supplemental Information)).

As the confusion matrix is not necessarily symmetrical along the diagonal, mirroring cells in the upper and lower triangles were averaged, to produce a categorical matrix for each participant (e.g. the sad-anger cell in the categorical matrix contains the average number of instances a participant mislabelled a sad face as angry, and an angry face as sad).

4.2.4 Model Construction

We constructed three models of the types of information that could explain the participants' pattern of categorisations in the Categorical Task and perceptual discrimination sensitivity in the Perceptual Task. A matrix was constructed for each model, where each cell of the matrix represented the discrimination between the corresponding pair of emotions, using a different source of information for each model. Two models discriminated between pairs of expressions using stimulus-based cues (Shape and Surface information), whereas another model discriminated between the emotion concepts (Conceptual).

Shape

Similarity of face shape was measured by performing Procrustes analysis between the fiducial points of the faces used in the perceptual task. This analysis allows for the comparison of any two shapes, and has previously been used to calculate the similarity of facial expression shapes (Kuhn et al., 2017; Sormaz, Watson, et al., 2016). Procrustean analysis computes the average squared distance between each pair of corresponding fiducial points, after correcting for size and position in 2D space by allowing shape translation, rotation, and scaling without morphing or non-linear distortion. The distance measure is then scaled such that the value of the output lies between 0 and 1. This analysis was performed between every within-identity pair of facial expressions as used in the perceptual task, to construct a shape dissimilarity matrix for every identity. To construct the shape model used in this experiment, we averaged these identity-level matrices. The resulting matrix was subtracted from 1 to keep the direction consistent with the other matrices: as such, higher values indicate greater similarity between the shapes of the corresponding facial expressions.

Surface

To measure surface similarity between the pictures used in the perceptual task, we computed the Fischer's Z-transformed Pearson's correlation coefficient between the pixel intensities for within-identity pairs of facial expressions. A similar procedure has been previously used in previous research to measure the similarity of face textures (Kuhn et al., 2017; Sormaz, Watson, et al., 2016). First, we found the average face shape across all facial expressions, by averaging the locations of the corresponding fiducial points. Then, we warped all face stimuli to this average face shape using Psychomorph (Tiddeman, Stirrat, & Perrett, 2005) to remove shape cues and converted all images to greyscale. We then calculated the correlation coefficient of the pixel intensities, for pixels falling within a mask that excluded all non-face pixels, and transformed them using Fischer's Z-transformation. A matrix was constructed for each identity, then averaged across identities to create the surface model.

Conceptual

The conceptual model was computed based on data form Skerry and Saxe (2015), which was generously provided by the authors. In that study, participants on Amazon's MTurk rated 200 verbal stimuli describing an emotional event that happened to a character on the extent to which the character was experiencing the six basic emotions, on a scale from 1 to 10. In each story the character experienced one of 20 'fine-grained' emotions (e.g. a story about a character experiencing the emotion loneliness was about them finding it difficult to make friends after moving to a new city). Other examples of these fine-grained emotions include 'disappointment', 'nostalgia', and 'embarrassment', although these labels were never shown to participants. 10 stories were written for each of the 20 'fine-grained' emotions. Full details of stimuli and procedure can be found in Skerry and Saxe (2015). A total of 1556 ratings for each of the six basic emotions were provided for the 200 short stories. From this data, we calculated the mean ratings for the six basic emotions for each of the 20 categories (e.g. we found the mean ratings for 'anger', 'disgust', etc. across stories in which a character was feeling 'nostalgic' etc.).

To generate the matrix for conceptual similarity, we calculated the Fischer's Z-transformed pairwise Pearson correlation coefficients between the ratings for the six basic emotions across the 20 subtle emotions. Pairs of the six basic emotions with higher transformed coefficients therefore had similar subtle emotions attributed to them than pairs with lower correlations. As such, cells with higher values suggest a greater conceptual overlap between the corresponding emotions than cells with lower values.

4.2.5 Data Analysis

For each task, we first assessed the relationship between the behaviour and each of the three models using Spearman’s correlations. The correlation was performed between the behavioural matrices and each of the 3 models separately, for each subject. The array of coefficients for each model was then tested against 0 using a one-sided Wilcoxon signed rank test.

To assess the relative contribution of each model in explaining the behavioural tasks, we used multiple linear regression. The three models were entered into a multiple linear regression model (with a constant of ones) to explain each behavioural task, for each participant. The behavioural measures and the models were z-scored to calculate the standardised beta weights, allowing us to examine the relative contribution of each model. The arrays of standardised beta weights were tested against 0 using a one-sample t-test. All analyses were conducted using only the lower triangle (15 off-diagonal cells) of each matrix.

4.3 Results

4.3.1 Behavioural Matrices

For each participant, we constructed a confusion matrix from their choice of labels in the categorisation task, and a perceptual similarity matrix from the pairwise discrimination thresholds in the perceptual task. Figure 4.3 shows the categorical matrix and the perceptual matrix, averaged across all participants for visualisation.

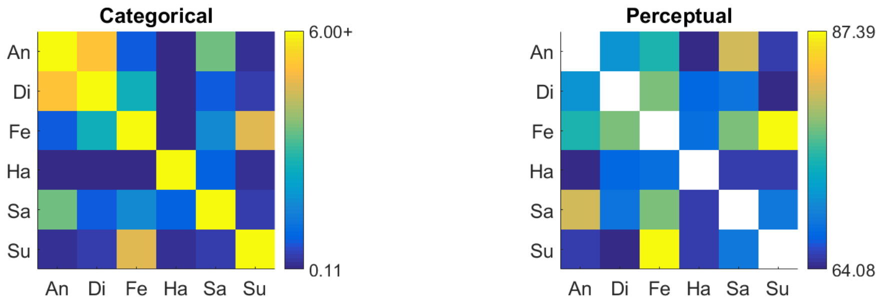

Figure 4.3: The mean categorical matrix (left), which displays the mean number of instances pairs of emotions were confused with each other. The mean perceptual matrix (right), which displays the perceptual discrimination thresholds for each pair of expressions in the perceptual task. The colourbars are scaled to the minimum and maximum values in the off-diagonal triangles.

4.3.2 Inter-subject reliability

To test how consistent were the Perceptual and Categorical matrices across participants, we computed inter-subject reliability for each type of matrix by correlating (Spearman's correlation coefficient) each participant's matrix with the average matrix for all remaining participants. Inter-subject reliability is presented in Figure 4.4, and the behavioural matrices showed good inter-subject reliability, with mean correlation of .661 for the Perceptual matrices and .765 for the Categorical Matrices.

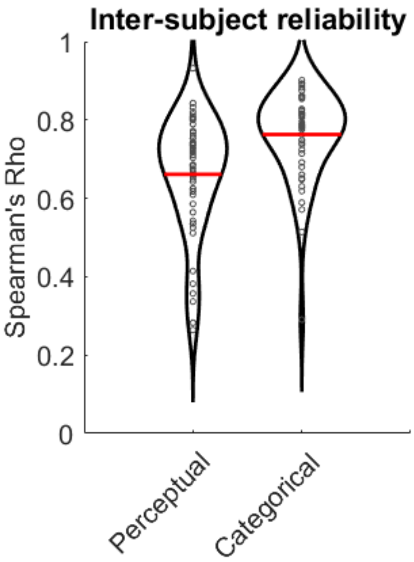

Figure 4.4: Inter-subject reliability. For each participant's perceptual and categorical matrices, we computed the correlation with the average of all other participants' matrices. Red bars represent the mean correlation coefficient.

4.3.3 Models

Figure 4.5 shows the matrices for the 3 models used in the analysis. We then investigated the correlations between the different models. Pairwise Spearman's correlations showed no significant correlation between Conceptual and Shape (rho(15) = .043, p = .883), a small non-significant correlation between Conceptual and Surface (rho(15) = .354, p = .196), and a large and significant correlation between Shape and Surface (rho(15) = .707, p = .004).

To check that the models were not colinear, we calculated the variance inflation factor (VIF) between the models. The VIF for the Shape and Surface models was 1.80, for the Shape and Conceptual models was 1.00, and for the Surface and Conceptual models was 1.11. None of these values exceeds the recommended threshold of 5 (Montgomery, Peck, & Vining, 2012).

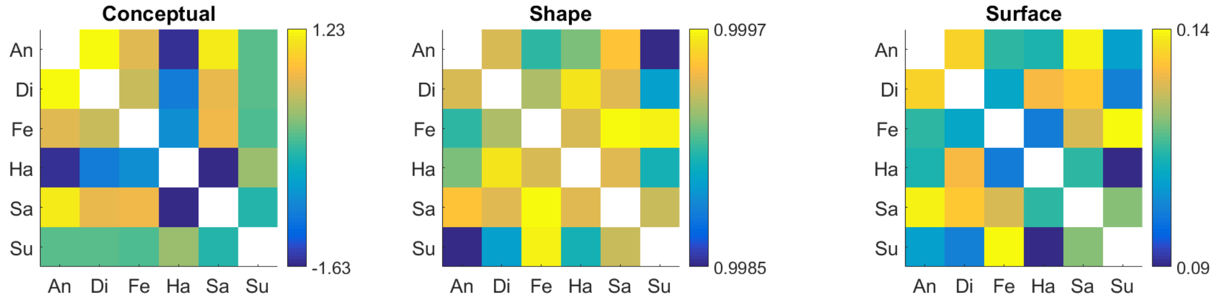

Figure 4.5: Conceptual (Fischer Z-transformed correlation coefficients; left), Shape (1-Procrustes distance; centre), and Surface (Fischer Z-transformed correlation coefficients; right) models.

4.3.4 Explaining perceived similarities in Perceptual Task

To investigate the role of the conceptual, shape, and surface cues on the Perceptual Task, we first computed the Spearman's correlation coefficient between each participant's perceptual matrix, and each of the three models to evaluate their individual contribution. All arrays of correlation coefficients were significantly higher than zero (Conceptual: mean rho = .361, Z = 1258.5, p < .001; Shape: mean rho = .373, Z = 1273, p < .001; Surface: mean rho = .430, Z = 1275, p < .001), after correcting for multiple comparisons with the Bonferroni adjustment (a = .0167). These results show that judgments in the Perceptual Task could be explained by each of the models that we used here.

Figure 4.6 shows the correlation coefficients, and the estimated noise ceiling, which was computed in a similar manner to Nili et al. (2014). The upper bound of the noise ceiling shows the average Spearman's correlation coefficient between each participant's perceptual matrix and the average of all participants' perceptual matrices, after rank transforming all matrices. The lower bound of the noise ceiling is the average Spearman's correlation coefficient between each participant's perceptual matrix and the average of all other participants' perceptual matrices, after rank transforming all matrices. The proximity of the upper and lower bounds of the noise ceiling suggest that participants were behaving very similarly in the perceptual task. These results show that, while the correlations were significantly above zero for each model, none of the correlations reached the noise ceiling, so no individual model could explain most of the variance in participants' perceptual dissimilarities.

Pairwise comparisons (using Wilcoxon rank-sum tests) revealed no significant differences between the distributions of correlation coefficients (Conceptual-Shape: Z = -0.141, p = 0.888; Shape-Surface: Z = 1.565, p = 0.118; Conceptual-Shape: Z = 1.534, p = 0.125).

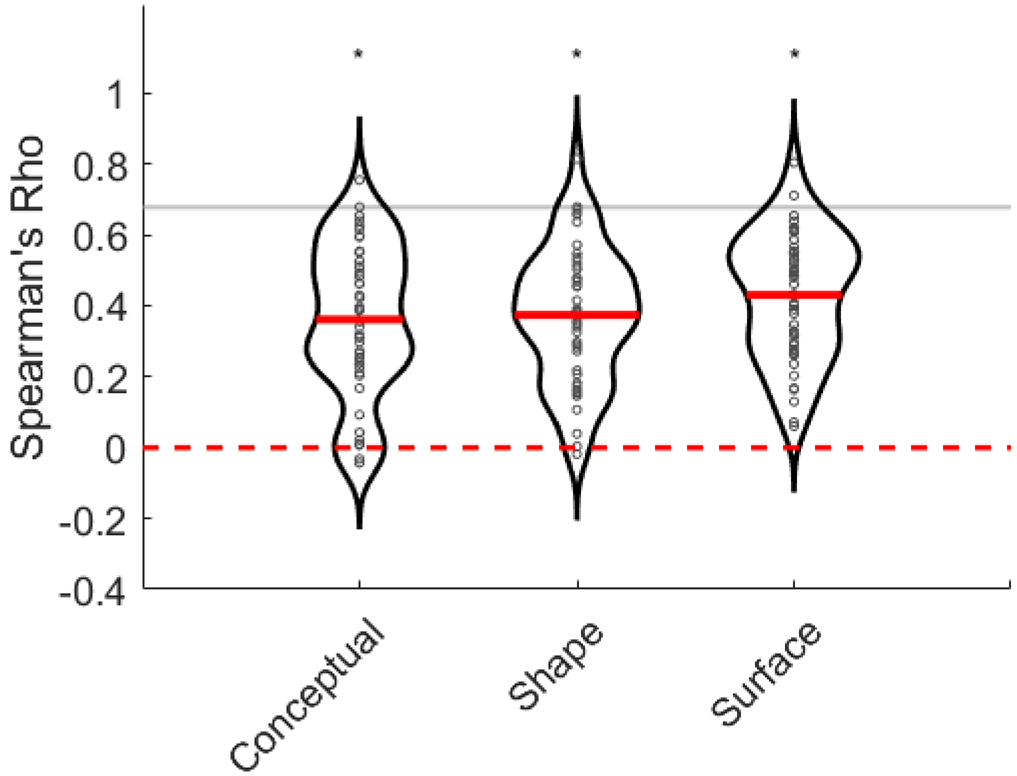

Figure 4.6: Distributions of Spearman's correlation coefficients between each participant's perceptual matrix and each of the models. Red bars represent the mean correlation coefficient. The grey bar represents the upper and lower bounds of the noise ceiling.

We then used multiple linear regression to estimate the individual contribution of each model for the similarities in the Perceptual judgments. The beta weights for each model were significantly higher than zero (Conceptual: *t*(49) = 11.72, *p* < .001; Shape: t(49) = 8.72, p < .001; Surface: t(49) = 3.40, p = .001), after correcting for multiple comparisons with the Bonferroni adjustment (a = .0167). The mean R^2 value across subjects was 0.386 (S.D. = 0.158), so approximately 38.6% of the variance was explained by all three models. Pairwise comparisons revealed greater contribution of conceptual than surface (t(49) = 2.96, p = .005, d = 0.74), no significant difference between the contributions of shape and surface (t(49) = 2.23, p = .030, d = 0.60), and no significant difference between the contributions of conceptual and shape (t(49) = 0.67, p = .504, d = 0.10), after correcting for multiple comparisons with Bonferroni adjustment (a = .0167). Distributions of standardised beta-weights are presented in Figure 4.7.

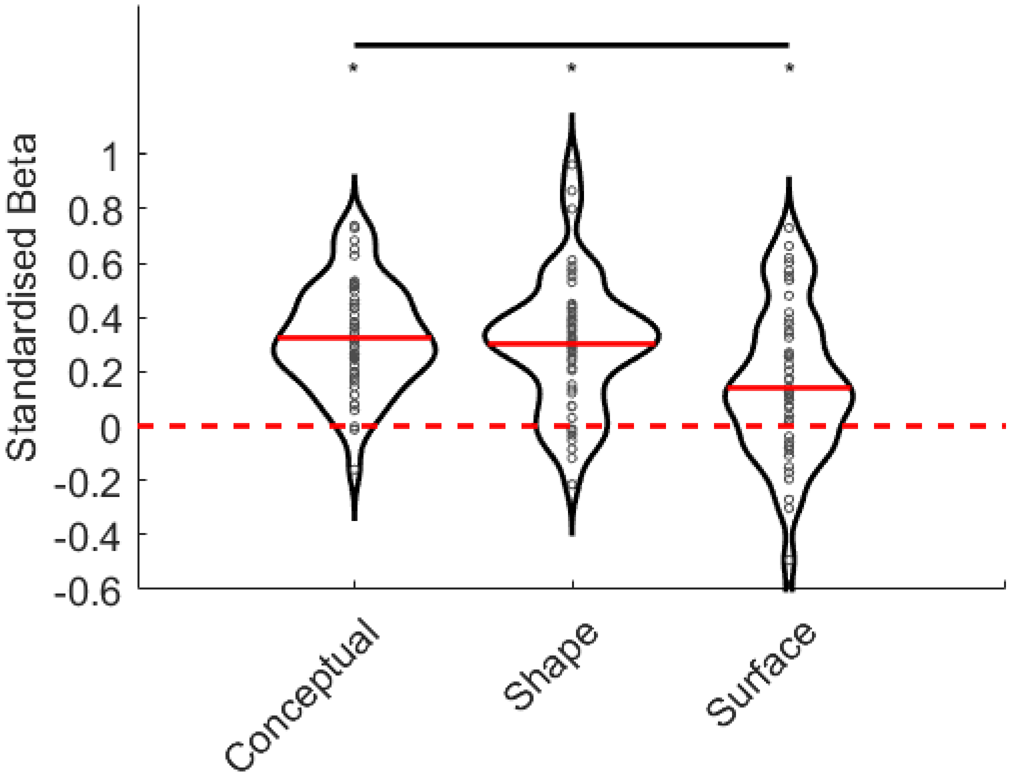

Figure 4.7: Distributions of standardised beta weights for each model as a predictor of each participant's perceptual matrix. Red bars represent the mean standardised beta-weight and the dashed red line represents the test value of 0.

4.3.5 Explaining judgments in Categorical Task

To investigate the role of the conceptual, shape, and surface cues on the Categorical Task, we first computed the Spearman's correlation coefficient between each participant's categorical matrix, and each of the three models to evaluate their individual contribution. All arrays of correlation coefficients were significantly higher than zero (Conceptual: mean rho = .508, Z = 1275, p < .001; Shape: mean rho = .379, Z = 1274, p < .001; Surface: mean rho = .557, Z = 1275, p < .001), after correcting for multiple comparisons with the Bonferroni adjustment (alpha = .0167). These results show that judgments in the Categorical Task could be explained by each of the models that we used here. Figure 4.8 shows the correlation coefficients, and the estimated noise ceiling. The upper and lower bounds were computed in the same way as for the Perceptual Task. These results show that, while the correlations were significantly above zero for each model, none of the correlations reached the noise ceiling, and so none of the models could explain well the confusion matrices in the Categorical Task.

Pairwise comparisons (using Wilcoxon rank-sum tests) revealed higher correlation coefficients for the conceptual model than the shape model (Z = 4.009, p < .001), higher coefficients for the surface model than the shape model (Z = 5.636, p < .001, but no difference between the coefficients for the conceptual and surface models (Z = 1.610, p = .107).

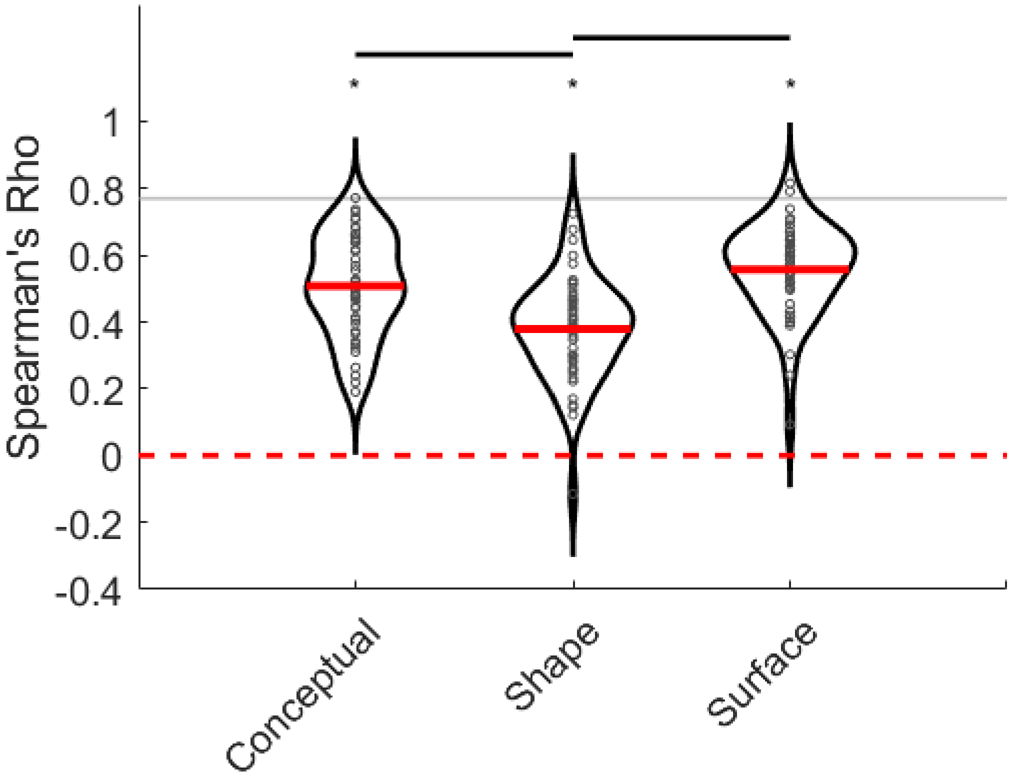

Figure 4.8: Distributions of Spearman's correlation coefficients between each participant's categorical matrix and each of the models. Red bars represent the mean correlation coefficient. The grey bar represents the upper and lower bounds of the noise ceiling.

We used multiple linear regression to estimate the unique contribution of each model, in order to predict each participant's Categorical matrix. All arrays of standardised betas were significantly higher than 0 (Conceptual: t(49) = 18.23, p < .001; Shape: t(49) = 7.54, p < .001; Surface: t(49) = 12.18, p < .001), after correcting for multiple comparisons with the Bonferroni adjustment (a = .0167). The mean R^2 value across subjects was 0.418 (S.D. = 0.125), so approximately 41.8% of the variance was explained by all three models.

Pairwise comparisons revealed a greater contribution of conceptual than shape (t(49) = 10.50, p < .001, d = 1.66), greater contribution surface than shape (t(49) = 4.50, p < .001, d = 1.17), but no significant differences between the contributions of conceptual and surface cues (t(49) = 0.838, p = .406, d = 0.21) after correcting for multiple comparisons with the Bonferroni adjustment (alpha = .0167). Distributions of standardised beta-weights are presented in Figure 4.9.

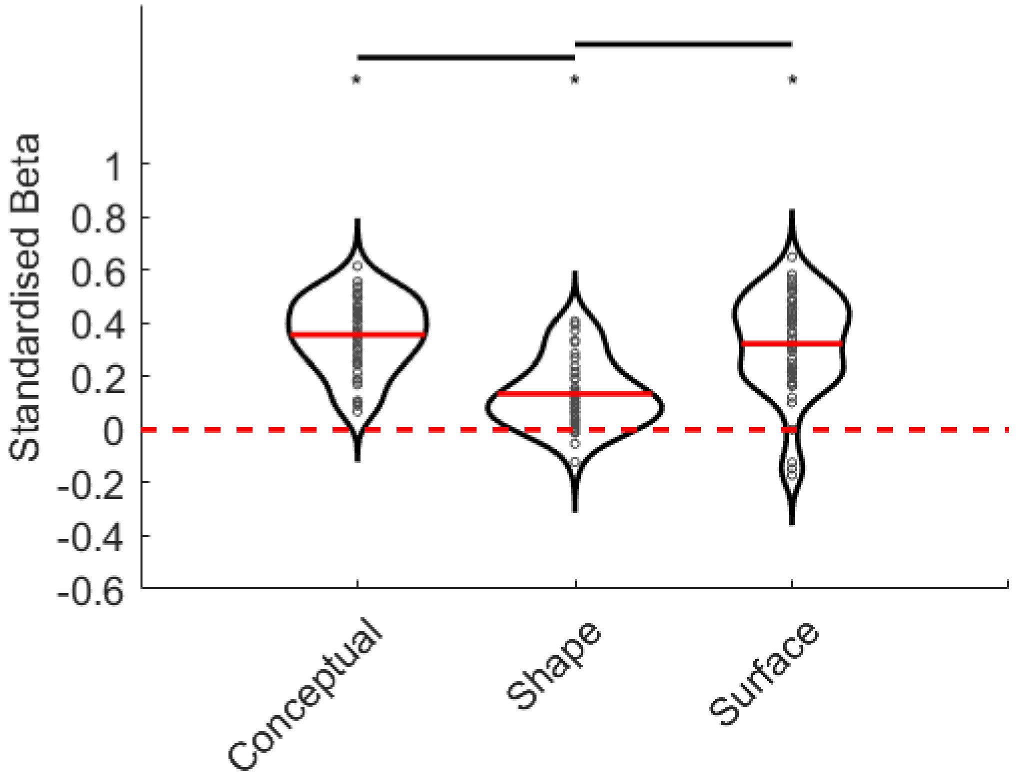

Figure 4.9: Distributions of standardised beta weights for each model as a predictor of each participant's categorical matrix. Red bars represent the mean standardised beta-weight and the dashed red line represents the test value of 0.

4.3.6 Differences between categorical and perceptual regression coefficients

To investigate whether the association of each cue with the behavioural tasks differed between each task, we compared the percentage of variance that was accounted for by each predictor between the two tasks, following analysis from Mur et al. (2013). In that study, the researchers compared the proportion of variance of behavioural and brain RDMs that was accounted for by several object category models. For each regression model for each subject, we estimated the percentage of variance accounted for by each predictor, by calculating the squared standardised beta weight as a percentage of the sum of squared standardised betas for all predictors. Doing so provided us with a normalised measure of the variance that each predictor accounted for. These percentages were then compared between the two tasks across subjects, using a paired samples t-test for each predictor. There was no difference between the percentage of variance that the conceptual model accounted for between the Perceptual and Categorical Tasks (t(49) = 1.730, p = .090). The shape model accounted for more variance within the Perceptual task than the Categorical task (t(49) = 6.710, p < .001), whereas the surface mode accounted for more variance within the Categorical task than the Perceptual (t(49) = 2.975, p = .005). The percentages of variance accounted for by each predictor for each task are presented in Figure 4.10.

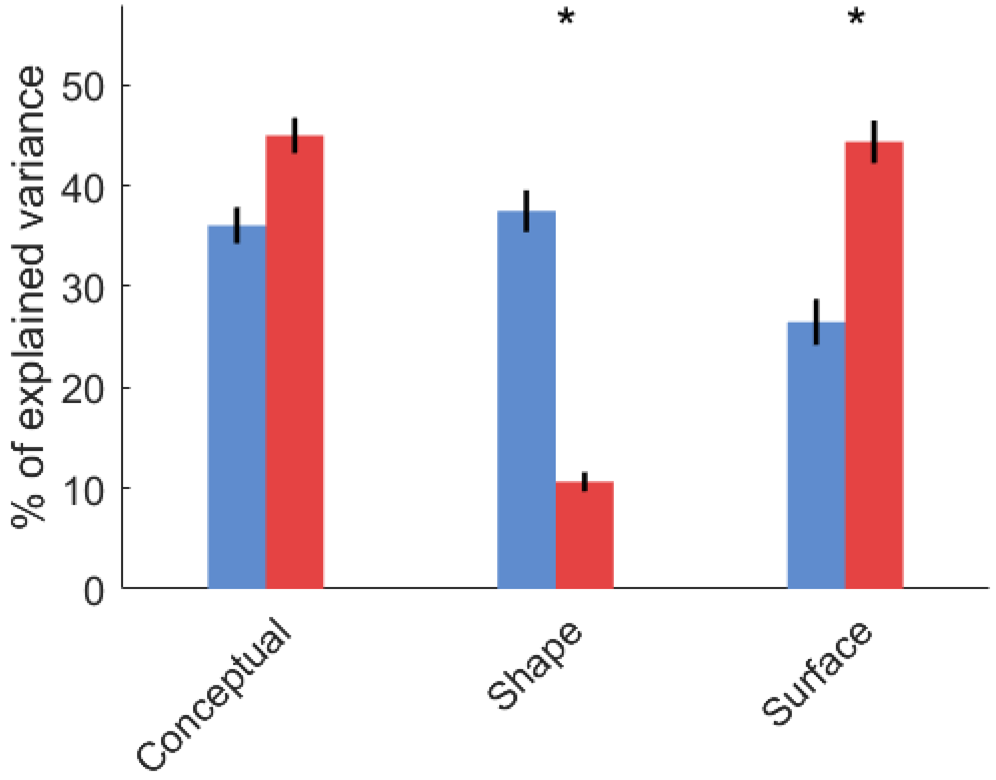

Figure 4.10: The mean percentages of variance explained by each of the three predictors. Blue bars show the percentage of variance explained in the Perceptual Task, red bars show the percentage of variance explained in the Categorical Task. Error bars show one standard error around the mean.

4.4 Discussion

In this study, we aimed to explore the relative usage of conceptual, shape, and surface cues in perception and categorisation tasks of emotions from facial expressions. First, as predicted, we found that all three cues seem to be used in both the perceptual and categorical tasks that we employed. This is consistent with previous research that suggests people make use of conceptual and stimulus-based information during these tasks (Brooks & Freeman, 2018; Sormaz, Watson, et al., 2016; Sormaz, Young, et al., 2016), but we furthered the research by using multiple linear regression to show that each cue plays a role even when controlling for the other cues. This is particularly interesting when considering the relative usage of shape and surface information, which inherently vary together (Bruce & Young, 1998).

Second, we found that conceptual information is used approximately equally between our tasks. This was not entirely consistent with our predictions that conceptual information would explain the behaviour in the categorical task better than the perceptual. Previous research has reported that conceptual information is used in both the perception and explicit labelling of emotions from facial expressions (Brooks & Freeman, 2018; Widen et al., 2011), so this result is consistent with the literature. It is clear that labelling of emotions requires access to emotion concepts to choose the correct label, which has been previously reported (Widen et al., 2011). Here we extend this and provide evidence that concepts seem to be as readily available when performing a perceptual discrimination task that required no explicit labelling of emotions. Our measure of the perceptual similarity of facial expressions was designed in an attempt to tap into perceptual discrimination processes, and reduce the top-down influence during the task. Despite this, we still found that conceptual information could explain perceptual discrimination well above chance, even when controlling for the similarity of stimulus-based cues, supporting the conclusions of previous research (Brooks & Freeman, 2018). The result that conceptual information can explain patterns of perceptual discrimination better than surface information is surprising, as we expected that processes involved in perceptual discrimination would rely more on stimulus-based cues than emotion concepts.

Third, we found a dissociation between the role of shape and surface cues, in that shape cues could explain more variance of the perceived similarities in the Perceptual Task than the confusions in the Categorical Task, and surface cues could explain more variance in the Categorical than Perceptual

Task. Taking the view that perceptual processes occur before the labelling of emotions (Palermo et al., 2013), this suggests that initial perceptual processes place greater weight on shape information, while surface information is required more so in the categorisation of emotions.

While the results provide a basis for the relative use of conceptual and stimulus-based cues in these two tasks, there may be some limitations to consider. One is that there were frequently a lot of tied ranks in the participants' categorical matrices. As healthy adults often perform at ceiling for labelling tasks (especially with certain emotions), the off-diagonal cells often contained a number of 0's. For example, as happy is particularly easy to recognise, there were very few instances of participants mislabelling a happy face as sad, or other negative emotions. We attempted to overcome this using two methods. The first was to average the mirroring off-diagonal cells (so that each cell contained the number of instances a participant mislabelled (e.g.) happy as sad, and sad as happy). The second was to use a short stimulus presentation time, to make the task sufficiently challenging. To overcome these tied ranks, it would be best to use a higher number of trials.

Another limitation is that from the perspective of psychophysical research, the number of trials in the perceptual task may not have been enough to accurately measure the 'true' discrimination threshold. Our threshold estimation terminated after 8 reversals in the staircase, whereas some vision researchers consider even 20 reversals to be short (García-Pérez, 1998). In any case, we still found that those thresholds were highly reliable across participants.

An important conceptual issue to consider is that these results do not necessarily show us that participants were 'using' any of the cues. As we used a correlation approach, the results show us that there is simply a relationship between the measures. To assess whether participants make use of the cues during the tasks, one could take the approach of Sormaz, Young and Andrews (2016) who systematically removed each of the two stimulus-based cues from sets of stimuli. While it may be more challenging to remove conceptual cues, one could take the semantic satiation approach used in previous research (Gendron et al., 2012; Lindquist et al., 2006) to disrupt access to the concepts.

Together, these results provide information about the influence of different cues in the perception and recognition of facial expressions, in our sample of healthy younger adults. Such a paradigm may be of interest to use in clinical research to study group differences in the extent to which the cues can explain behaviour during the tasks. For example, older adults experience difficulty with the recognition of emotions from facial expressions (Ruffman et al., 2008), and have reduced visual acuity and contrast sensitivity relative to younger adults (Rubin et al., 1994). It may therefore be the case that older adults rely more on conceptual information and less on stimulus-based cues than younger adults. In relation to the conceptual issue discussed in the previous paragraph, this research would not necessarily show that one group is ‘using’ any cue more than another, but it would allow to the assessment of any group differences in the extent to which each cue can explain the behaviour during the tasks. This potential for research is discussed further in the Chapter 7.

An inspection of the distributions of standardised beta weights in the two regressions we performed reveals a considerable range of the use of different sources of information. Previous research suggests that there are large individual differences in both perceptual and labelling tasks (Palermo et al., 2018, 2013). One question that remains, is whether performance at perceptual and labelling tasks is associated with greater use of conceptual or stimulus-based cues. It is of interest to examine whether individuals who perform better at these tasks make greater use of a certain type of information than those who are poorer at the tasks. Alexithymia, a sub-clinical trait characterised by difficulty identifying emotional states of the self, is associated with poorer performance at emotion recognition tests (Cook, Brewer, Shah, & Bird, 2013). Furthermore, Lewis, Lefevre, and Young (2016) suggest that the ability to recognise emotions from facial expressions is dependent in part on a modality-independent emotion processing factor. Perhaps, the ability to recognise emotions from facial expressions is therefore associated with greater access to emotion concepts, so it would be expected that individuals who perform better at the labelling task may make greater use of conceptual cues than individuals who are poorer at the task. Further analysis of the current dataset is conducted in the next chapter in an attempt to answer this question.

Our conceptual model used data from separate research (Skerry & Saxe, 2015), to create a measure of general conceptual similarity of two emotions. While this measure did account for perceptual discrimination and categorisation errors, it may be of interest to measure the similarity of emotion concepts within each subject. Having a subject-specific conceptual measure would allow for the analysis of the subject-specific relationship between emotion concepts and behaviour in both tasks. This is discussed in more detail in Chapter 7.

In conclusion, these results show that shape, surface, and conceptual sources of information can explain patterns of perceptual discrimination and emotion categorisation. Each source of information is still used above chance, even when accounting for the other sources. Shape cues account for more variance in a task designed to use perceptual processes, whereas surface cues account for more variance in the categorical task. Conceptual information accounts for a similar amount of variance in both tasks. The results highlight the role of conceptual information, even when one does not need to assign any emotion labels to a face.

5 Individual differences in the role of conceptual and stimulus-based cues on the perception and recognition of facial expressions

5.1 Introduction

There are substantial individual differences in the ability to recognise facial expressions of emotion, within the non-clinical population (Palermo et al., 2018, 2013). Variation in performance was reported across a battery of tasks measuring the perception and recognition of facial expressions, in a large sample of participants with no psychiatric disorders (Wilhelm, Hildebrandt, Manske, Schacht, & Sommer, 2014).

Palermo et al. (2013) designed two tests to assess individual differences in the perception and recognition of emotions. The first was a perceptual matching task to test participants' ability to discriminate between facial expressions using perceptual processes, without having to assign an emotion label. In this task, participants chose which one of three presented faces displayed a different expression to the other two. The second task was a labelling task, where participants chose which one of six emotion labels best suited the emotion displayed by a face. There was a large range in performance at both tasks (suggesting individual differences in perceptual matching and labelling), and there was a moderate correlation between the two tasks (suggesting that the processes used in both tasks are partially overlapping). In addition to these two tasks, participants completed a vocal emotion labelling task. Performance at this task was correlated with the facial expression labelling task, but not with the perceptual matching task. This suggests that the emotion labelling task recruits a multimodal process used to assign emotion labels to a stimulus (regardless of the stimulus modality) that the perceptual task does not.

In the Chapter 4, we investigated the use of conceptual, shape, and surface information in a perceptual task and a labelling task. We used multiple linear regression to assess the relative contribution of these 3 cues on patterns of categorisation and perceptual discrimination. While we found that the distributions of standardised beta weights were significantly higher than 0 in all cases (indicating that all sources of information can explain the patterns of behaviour during the tasks to some extent), there was variation within these weights, suggesting that there are individual differences in the relative use of these sources of information.

Taken together with the results from Palermo et al. (2013), a question that remains is whether the performance at each task is associated with particular sources of information. For example, it may be the case that individuals who are better at labelling emotions make greater use of high-level conceptual cues, or perhaps that individuals who are better at discriminating between expressions make greater use of stimulus-based cues.

The second question that this chapter aims to answer is whether there are any individual differences in patterns of categorisation and perceptual discrimination. While the results of Palermo et al. (2018, 2013) suggest that performance at these two tasks is related to each other, we aim to extend these findings by investigating whether the patterns of confusions that people make can also vary from individual to individual. When a participant completes a labelling task, there is a wealth of information contained in the exact patterns of categorisation. For example, there are certain pairs of emotions that are frequently confused (e.g. angry faces are often mislabelled as disgust; Young et al., 1997). Taking the average accuracy across the stimuli overlooks both the accuracy at labelling individual emotions, and specific patterns of mislabelling of facial expressions. We have yet to assess whether differences in perceptual processes can account for individual differences in the exact pattern of categorisation an individual may make. To test whether individual differences in perceptual discrimination can account for differences in the pattern of categorisation, we will investigate idiosyncratic relationship between each subject's perceptual and categorical representations of emotions. Here, we expect to find a relationship between the representational structure across the two modalities and expect the within-subject relationships to be higher than the between-subject relationships.

In the current chapter we investigate these two research questions using the data and results from the previous chapter (Chapter 4). First, we investigate whether greater performance at the two tasks is associated with a greater role of conceptual, shape, or surface information. If a given cue plays a greater role in explaining task performance for those who are better at either task, we would expect to see a positive correlation between the measure of performance and the regression coefficient for the cue. Second, we investigate whether there is any idiosyncratic relationship between an individual's pattern of perceptual discrimination and their pattern of categorisation. If there is, we expect the within-subject relationship between the two tasks to be greater than the between-subject relationship.

5.2 Methods

For this experiment, we used the data and the results of the regressions from Chapter 4. Please refer for Chapter 4 for full experimental methods and results.

5.3 Results

5.3.1 Individual differences in role of top-down and bottom-up cues

First, we calculated a measure of performance at each task, for each individual. The measure of performance for the perceptual task was taken as the average discrimination threshold for the 15 expression pairs. As such, a lower average discrimination threshold represents greater discrimination sensitivity and so is taken as a general measure of performance at the Perceptual Task (those with lower average thresholds perform better at the task than those with higher average thresholds). The measure of performance for the categorical task was taken as the average of the correct categorisations. The distributions of these measures are presented in Figure 5.1.

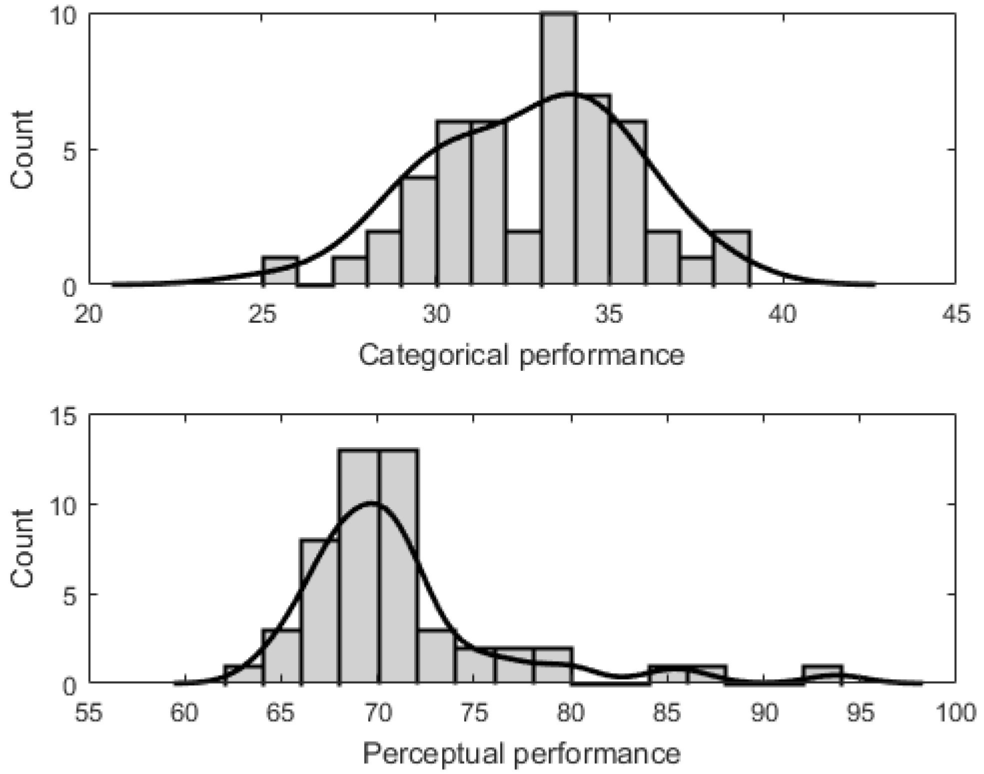

Figure 5.1: Distributions of the measures of performance at each task.

To investigate whether these measures of performance at each task were associated with the roles of conceptual, shape, and surface cues, we conducted a Pearson correlation between each measure of performance and the standardised betas from the regressions in Chapter 4 (presented in Figures 4.7 and 4.9). For example, to test the association between performance at the Perceptual Task and the role of conceptual cues, we performed a correlation between participants' average discrimination thresholds in the Perceptual Task and the standardised beta weights for the Conceptual model in the regression for the Perceptual Task. The results of these correlations are reported in Table 5.1. None of the six correlations reached significance, suggesting that performance at each task is not associated with the usage of any of the three cues.

Table 5.1: Results of the correlations between performance and relative role of three cues.

Cue	**Task**			
	Categorical		**Perceptual**	
	r	*p*	*r*	*p*
Conceptual	-.112	.397	.003	.984
Shape	-.135	.350	.045	.757
Surface	.061	.672	.059	.682

5.3.2 Relationship between patterns of perceptual discrimination and patterns of categorisation

Before investigating whether there is any idiosyncratic relationship between a participant's patterns of perception and patterns of categorisation, we first established whether there was a relationship between these measures across participants. Using only the 15 off-diagonal cells within each matrix, we calculated the Spearman's correlation coefficient between each participant's perceptual and categorical matrices (Mean Rho = 0.462, S.D. = 0.219). A one-sided Wilcoxon signed rank test showed that this array of coefficients was significantly higher than 0 (Z = 1.664, p < .001).

5.3.3 Investigating the idiosyncratic relationship between categorical and perceptual

As a confirmatory measure, we replicated the correlation between averaged performances at each task as conducted by Palermo et al. (2013).

It is worth noting that this is not exactly comparable as they used the average accuracy at a 3AFC task, whereas here we take average perceptual threshold as a general measure of perceptual discrimination ability. Consistent with this previous research, we found a significant relationship between the two measures (rho(50) = -.491, p < .001), suggesting that performance on one task is related to performance on the other (note that the correlation is negative because lower thresholds of discrimination indicate greater sensitivity). Figure 5.2 shows a scatter plot for this correlation. The correlation reported by Palermo et al. (2013) was of a similar strength (rho = .47, p < .001).

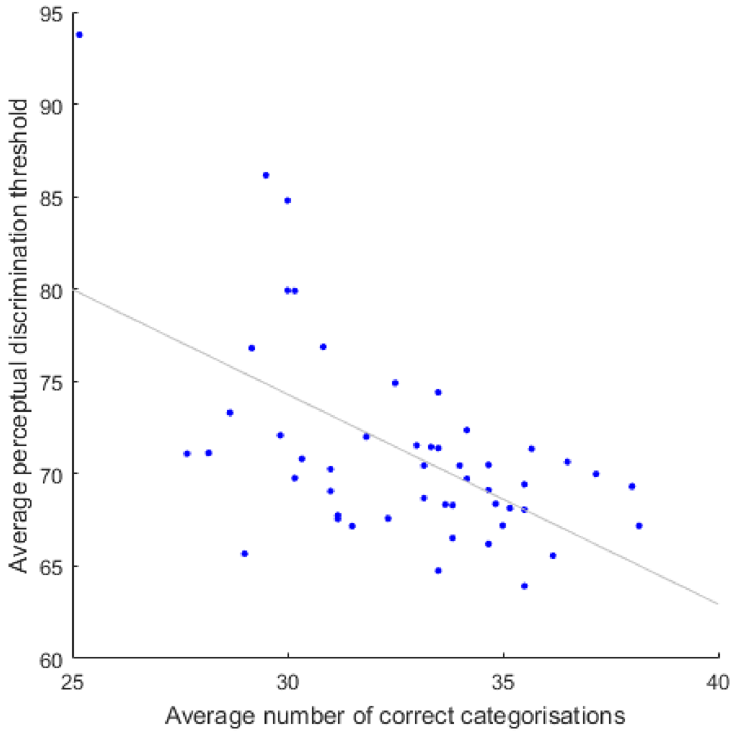

Figure 5.2: A scatter plot of the performance at the perceptual task against the categorical tasks.

To examine whether individual differences in perceptual discrimination can account for individual differences in emotion categorisation errors, we first computed a subject similarity matrix (Figure 5.3) where each cell represents the Spearman's correlation coefficient between all perceptual matrices (y-axis) and categorical matrices (x-axis). The diagonal cells represent the within-subject correlations (mean rho = 0.462, S.D = 0.219) and the off-diagonal cells represent the between-subject correlations (mean rho = 0.453, S.D. = 0.211).

Following the analysis as used by Charest, Kievit, Schmitz, Deca and Kriegeskorte (2014) to examine the idiosyncratic relationship between neural RDMs, we then subtracted the average between subject correlation (off diagonal cells) from the average within subject correlation (diagonal cells). Under the null hypothesis that there is no idiosyncratic relationship between the categorical and perceptual matrices the subject labels are exchangeable. To examine how the observed within-between subject difference compares to this null hypothesis, we randomised the subject labels for the categorical dimension (x-axis) of the subject similarity matrix 10,000 times. After each random permutation, we re-calculated the difference between the average within and the average between subject correlations to simulate a distribution representative of the null hypothesis that the subject labels are exchangeable. If the observed within-between subject difference lies within the top 5% of this distribution, then we can reject the null hypothesis that there is no idiosyncratic relationship between a participant's perceptual and categorical matrices. After following this analysis, we found 26.8% of the within-between subject differences from the distribution with randomised subject labels fell above the observed difference (0.009), so we fail to reject the null hypothesis suggesting that there is no idiosyncratic relationship between each participant's perceptual and categorical matrices.

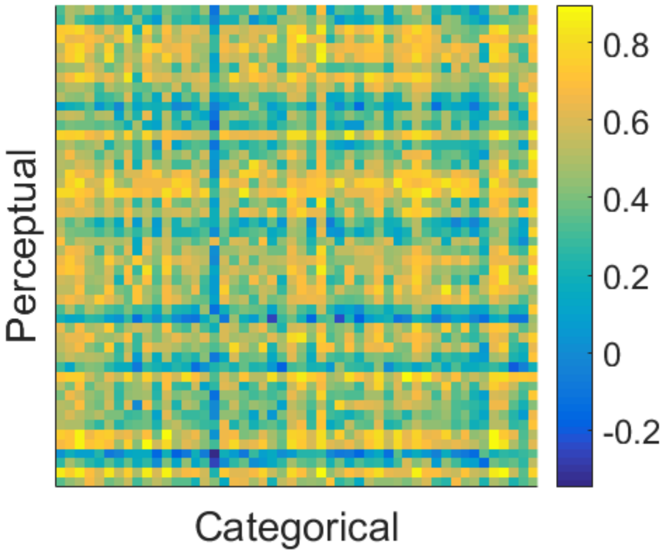

Figure 5.3: The subject similarity matrix. Each cell represents the Spearman's correlation coefficient between each of the 50 perceptual matrices (y-axis) and the 50 categorical matrices (x-axis). Coefficients have been visualised with a colour bar. Diagonal cells represent within-subject correlations, and off-diagonal cells represent between-subject correlations.

5.4 Discussion

The aim of this chapter was to examine two aspects of individual differences in the perception and recognition of facial expressions.

Firstly, we examined whether the ability to perceptually discriminate between facial expressions, and the ability to correctly label facial expressions, was associated with the relative contribution of conceptual, shape, or surface information. These results suggest that there is no association between the role of these cues and performance, suggesting that individual differences in perception and categorisation are independent from the use of any particular cue.

Secondly, we examined whether there was any idiosyncratic relationship between the patterns of perceptual discrimination and categorisation. While we found that there was a relationship between these patterns of behaviour in each task, we found no greater relationship within-subject than between-subjects, suggesting that similar patterns of categorisation errors and pairwise perceptual discrimination thresholds were observed across subjects. This is supported by the proximity of the upper and lower bound of the noise ceilings in the previous chapter (Chapter 4).

These results are consistent with literature suggesting large variation in perceptual discrimination and emotion categorisation (Palermo et al., 2018, 2013). Here we add to the literature by showing that any variation in performance within a non-clinical population is not due to any variation in the use of conceptual or stimulus-based cues.

The categorical matrices were constructed from the raw confusion matrices during a categorisation test, so contain a number of tied ranks (see Chapter 4 for exact methods, and a discussion of the issue of tied ranks in relation to that study). It could be suggested therefore that this method may not sensitive enough to capture individual differences in categorisation patterns. However, the proximity of the upper and lower bounds of the noise ceiling for the correlations with the perceptual matrices suggests that the pattern of perceptual discrimination was similar across subjects (see Chapter 4 for the calculation and visualisation of the noise ceilings). This in turn could suggest that there is no observable individual component to the relationship between patterns of perceptual discrimination and emotion categorisation.

To conclude, we found variation in our performance measures for perceptual discrimination and emotion categorisation, but these measures of performance were not associated with differences in the relative contribution of stimulus-based and conceptual cues when performing the tasks. We also found that, while there is a relationship between patterns of perceptual discrimination and emotion categorisation, there is no observable individual component to this relationship.

6 The influence of conceptual and stimulus-based cues on neural representations of facial expressions

6.1 Introduction

There are several regions of the brain in which the representations of emotions from facial expressions can be decoded. Research using multivariate pattern analysis has shown that patterns of activation in response to facial expressions can be decoded in the FFA, OFA, and STS (Harry et al., 2013; Said, Moore, Engell, et al., 2010; Wegrzyn et al., 2015; Zhang et al., 2016). Moreover, patterns of activation in response to emotional stimuli can be decoded in the MPFC (Peelen et al., 2010; Skerry & Saxe, 2014, 2015).

There is, however, little research investigating which sources of information can best explain how these regions discriminate between expressions. Sormaz, Watson, et al. (2016) showed that representational similarity of expressions in the OFA and STS can predict the perceptual similarity of expressions, which can also be explained by the similarities of face shapes and surface textures. On the other hand, more anterior regions of the MPFC seem to process more abstract or conceptual information about emotions (Peelen et al., 2010; Skerry & Saxe, 2014). Critically, conceptual information is not only represented in the frontal cortex, in that Brooks et al. (2019) reported that the representational structure of facial expressions in the right FFA can be explained by differences in emotion concepts, even when controlling for differences in several stimulus-based properties. In Chapter 4, we investigated the relative influence of shape, surface, and conceptual information on behavioural representations of emotions. In the current chapter, we aim to investigate the relative influence of these properties on brain representations of emotions, in regions of the brain involved in the processing of facial expressions.

Brooks et al. (2019) used three measures of visual similarity as control variables in multiple linear regression RSA (similarity of face silhouettes, similarity of pixel intensity maps, and similarity of ‘higher-level visual features’ as output from the HMAX model of object recognition). While these measures are reported to explain representations in the early visual cortex and FFA (Kriegeskorte et al., 2008), we chose to use shape and surface similarities as controls given the importance of these cues in the perception of facial expressions (Bruce & Young, 1998; Kuhn et al., 2017; Sormaz, Young, et al., 2016). Furthermore, the similarity of face shapes and surface textures can explain perceptual similarity of expression pairs (Sormaz, Watson, et al., 2016).

In addition to these stimulus-based cues, we also included conceptual similarity (Brooks et al., 2019; Skerry & Saxe, 2014). Doing so will test whether the representational structure of emotions can still be explained by similarities of emotion concepts, even when controlling for stimulus-based properties that are specific to facial expressions, and vice-versa.

To investigate the relative influence of these three cues, we have followed the approach of multiple previous studies (including Chapter 4) and used RSA (Kriegeskorte et al., 2008). In Chapter 4, we measured the perceptual similarity and mean categorisation errors between each pair of the 6 basic emotions. We then constructed three models based on the similarity of face shapes, surface textures, and emotion concepts, and used RSA to assess the relationship between the models and behaviour. Here, we measured the dissimilarity of neural representations of emotions and used the same three models to explain the representational distances in the brain.

We have chosen to examine the three core face regions (the FFA, OFA, and STS), as each of these regions are reported to represent facial expressions (Harry et al., 2013; Said, Moore, Engell, et al., 2010; Wegrzyn et al., 2015; Zhang et al., 2016), and the representational structure may be linked to differences in shape and surface properties (Sormaz, Watson, et al., 2016). Should the perception of facial expressions act in a completely feed-forward manner, then we would expect that shape and surface cues best explain the representational structure within these regions and concepts do not. If, however, emotion concepts are accessible earlier on in the perceptual process, then we would expect that concepts also explain the representational structure of emotions in these regions. We have also examined the representational structure of emotions from facial expressions in the MPFC. As representations of emotions in this region are likely modality independent (Peelen et al., 2010; Skerry & Saxe, 2014), we expect that shape and surface properties of the stimuli do not explain the representational structure of emotions in this region, whereas the similarities of emotion concepts do.

In addition to examining the relative influence of these 3 models on representations, we also examined the relationship between the neural representations and two models derived from the two behavioural tasks in Chapter 4. Previous research suggests that the perceptual similarity of expression pairs is associated with the representational similarity within the core face regions (Said, Moore, Engell, et al., 2010; Sormaz, Watson, et al., 2016). This research, however, used subjective judgements on a 7-point scale to measure the perceptual similarity of expression pairs. We argue that the psychophysical method that we used in Chapter 4 was a measure of perceptual similarity that was less reliant on top-down processes and emotion concepts. It is of interest therefore, to examine whether the representational structure of expressions within these regions can still be explained by perceptual similarity using this measure. Furthermore, we will examine whether the representational structure can be explained by categorisation errors, as this will allow us to explore which of the two tasks is best associated with the representational structure of expressions within each region.

6.2 Methods

6.2.1 Preregistration

Methods and analysis plan were pre-registered on 08/11/18 and are available on the Open Science Framework (https://osf.io/34fm7/)

6.2.2 Participants

Thirty participants (19 females, mean age: 26.10 years, S.D: 6.45, range: 18-46) were recruited via posters, advertisements on the university participant pool, and word of mouth. All participants had normal or corrected-to-normal vision, no history stroke, neurological, or diagnosed emotion processing disorders. Ethical approval to conduct the research was granted by the College of Health and Life Sciences Research Ethics Committee at Brunel University London.

6.2.3 Multiple choice task

Stimuli

Facial expressions of anger, disgust, fear, happiness, sadness and surprise were selected from the Radboud face database (Langner et al., 2010). We used the validation data from Langner et al. (2010) to rank the front facing images for each emotion by genuineness of expression, then selected the top 5 pictures for each emotion. Images were cropped to a square containing the whole face but removing the neck and the top of the head (Figure 6.1).

Figure 6.1: An example trial of the multiple-choice task

Procedure

Before participants entered the scanner, they completed a brief multiple-choice style expression categorisation test. Participants viewed each face for 5000ms in the centre of a laptop screen, with 6 labels (state the labels) presented underneath. Each label had a corresponding number (1-6), and participants were required to indicate which of the labels best described the emotion in the presented face. The purpose of this task was to encourage participants to discriminate between the faces in terms of the 6 basic emotions.

6.2.4 MRI data acquisition

MRI data was collected with a 3T TIM Trio MRI scanner (Siemens, Erlangen) using a 32-channel head array coil at the Combined Universities Brain Imaging Centre (CUBIC). Functional images were acquired for the experimental and localiser runs with an echo planar imaging sequence using multiband imaging, with 46 axial slices aligned with the ventral surface of the temporal and occipital lobes, covering the whole brain excluding the cerebellum in most participants (TR = 2000ms, TE = 34ms, Flip angle = 76°, voxel size = 2.5mm x 2.5mm x 2.5mm). For participants with larger brains, the upper most part of the parietal lobe was excluded. A high-resolution T1-weighted MPRAGE anatomical scan was also acquired for each participant (TR = 1830ms, TE = 3.03ms, Flip angle = 11°, Voxel size = 1mm x 1mm x 1mm).

Runs were divided into experimental runs and functional localiser runs. Participants completed 10 experimental runs, 2 theory of mind area localiser runs, and 1 face area localiser run. Experimental runs were stopped after 8 and 9 runs for 2 participants due to discomfort, and one participant did not complete the theory of mind localiser.

6.2.5 Experimental fMRI task

Stimuli

We selected the top 11 most genuine examples of each of the six basic emotions (Anger, Disgust, Fear, Happiness, Sadness, and Surprise) from the Radboud face database, using the validation data from Langner et al. (2010). Participants had previously viewed 5 examples of each expression category in the behavioural task. During each run, participants viewed all 66 images.

Procedure

An event-related design was used for the experimental runs. The 66 pictures of facial expressions were presented once each in each experimental run. Pictures were presented sequentially for 1000ms each (height = 12.5°, width = 16.7°, at a viewing distance of 80cm). After each presentation, a blank fixation screen was presented at a jittered duration of between 1000ms and 3000ms. Participants performed a 1-back task, by pressing a button whenever there was a consecutive repetition of any facial expression – the repetition was always of a different identity (i.e. it was a different picture), encouraging participants to attend to the expression rather than just the image.

During each run, the 66 faces were presented in a pseudo-random order: initially the order of 60 (10 examples of 6 expressions) was randomised until there were no consecutive repetitions of the same facial expression. Each of the 6 remaining images of facial expressions were inserted into this sequence after the position of a random example of the same expression, to provide a repetition of each expression for the 1-back task.

This randomisation procedure was conducted independently for each run and each participant. A blank fixation screen was presented for the first 4 seconds of each run.

6.2.6 Functional localisers

To localise the face responsive regions, participants viewed 16 second blocks of expressive faces, neutral faces, and scrambled faces from the Radboud face database (Langner et al., 2010), with additional 16 second blocks of rest (no stimuli). Blocks of expressive faces comprised a randomly selected mix of angry and fearful faces from the front facing angry and fearful faces of the database. Each face was also scrambled using MatLab, by overlaying the image with a 20x20 grid and randomly rearranging the position of the 'tiles'. During each block, 16 faces (or scrambled faces) were selected at random. In each block, each stimulus was presented for 900ms (ISI = 100ms). Blocks of stimuli were presented in a pseudo-random order. Each block occurred 4 times, and there were never consecutive repetitions of the same block.

To localise the middle MPFC, we used stimuli from Dodell-Feder, Koster-Hale, Bedny and Saxe (2011) Participants were presented with short textual scenarios that require inferences about either the mental state of an individual (belief condition) or physical state of a scene (photo condition). Full stimuli are available at http://saxelab.mit.edu/superloc.php. Participants completed a true/false task in response to a statement presented beneath the text, by pressing a button with their left hand for true and right hand for false. The text and true/false statement appeared on screen for 18 seconds, followed by a blank screen for 12 seconds. It is worth noting that we used timings that differed from those used in the original paper.

6.2.7 Image preprocessing and general linear model

For each participant, all functional images were realigned (registered to the mean of the whole session using 2nd degree B-spline interpolation) and resliced (using 4th degree B-spline interpolation). Each participant's structural image was segmented and co-registered to their mean functional image, then functional images were normalised to MNI space (voxel size = 2mm x 2mm x 2mm) using the deformation field output from warping the structural to the MNI template. Functional images for the localiser tasks were smoothed with a gaussian kernel at FWHM = 8mm. All preprocessing was performed in the SPM12 toolbox in MATLAB 2016b. Runs were excluded if the participant moved more than 2.5mm in any direction, or rotated more than 1 degree along any axis.

To estimate betas for each event of the experimental runs (i.e. each of the 66 pictures of facial expressions), we used the LS-S approach (Mumford, Turner, Ashby, & Poldrack, 2012), where each event was fitted with a separate linear model containing a regressor for the event of interest and a separate regressor that models all other events, along with 6 regressors for the realignment parameters within each run. This approach aims to lead to more accurate estimates of activation than modelling each trial with a separate regressor within the same model (Mumford et al., 2012), and has previously been used to estimate patterns of activation in response to facial expressions (Wegrzyn et al., 2015). The GLMs were convolved with a standard haemodynamic response function and high-pass filtered at 128s. Due to technical issues, some stimuli were unexpectedly presented after the scanner had stopped for some participants (a total of 6 stimuli across all runs across all participants were presented after the scanner stopped). Betas for any event presented within 3 seconds of the scanner finishing were not estimated (18 stimuli across all participants).

6.2.8 Region of Interest definition

To define the face responsive regions and the MPFC, a group-constrained subject-specific approach was used (Fedorenko, Hsieh, Nieto-Castañón, Whitfield-Gabrieli, & Kanwisher, 2010; Julian, Fedorenko, Webster, & Kanwisher, 2012). This method allows us to define these regions without experimenter bias. Briefly, we used group masks for each region of interest from previous studies and then intersected each group mask with each participant's activation map to define individual ROIs.

Group level maps from previous research were used as masks for the middle-MPFC (Dufour et al., 2013), and 3 core face regions (Julian et al., 2012). For each participant, we performed standard univariate analysis for each of the two localiser tasks. To localise face responsive regions, we subtracted the response to scrambled faces from the response to expressive faces. To localise theory of mind responsive regions, we subtracted the response to the photo conditions from the response to the belief conditions in the Theory of Mind localiser task. Using a liberal threshold of $p<.05$ (uncorrected), we found the peak voxel for each participant within each mask and used a sphere with a 6mm radius, centred on these coordinates, as the ROI for each participant. If no peak voxels were significant below $p<.05$, we used the peak coordinates from second level random effects analysis to centre the sphere. The second-level analysis was conducted at the group-level, using a one-sample t-test for each contrast at $p<.001$ (uncorrected), within the same group level maps from previous research (Dufour et al., 2013; Julian et al., 2012) as used in the subject-specific approach.

6.2.9 Model construction

In Chapter 4, we constructed three models to explain behaviour during two tasks. For each model, a matrix was constructed where each cell in the matrix is a measurement of the similarity of each pair of six emotions (15 pairs). For the current experiment, we use these three models in addition to the behavioural tasks to explain neural representational similarity. The construction of these three theoretical models (and the two behavioural models) is summarised below, but more details are presented in Chapter 4. All models are presented in Figure 6.2.

Shape

First, all faces used in the experimental MRI task were marked with 112 fiducial points. Following Sormaz, Watson, and Andrews (2016), Procrustes analysis was performed between every pair of images and the resulting distance measure was averaged for each expression pair to create a 6x6 matrix. The resulting matrix was subtracted from 1 to keep the direction consistent with the other models; as such, higher values indicate greater similarity.

Surface

The Fischer's Z-transformed Pearson's correlation coefficient was calculated between the pixel-intensities for faces used in the experimental MRI task. Following Sormaz, Watson, and Andrews (2016), this analysis was conducted for every possible pair of faces, and averaged across the expression pairs to create a single 6x6 matrix. All faces were first warped to an average face shape to remove shape cues, then converted to greyscale. Non-face pixels were excluded from the analysis.

Conceptual

Data from Skerry and Saxe (2015) was used to construct a model for conceptual similarity of emotions. Participants were asked to rate stories describing an event that happened to a character on how much the character was experiencing each of the 6 basic emotions. To construct our model, we computed the Fischer Z-transformed Pearson's correlation coefficient between the ratings for each pair of emotions. As such, pairs of emotions with greater semantic overlap will result in higher coefficients than more semantically distinct pairs.

Perceptual Task

The perceptual similarity of every pair of facial expressions was measured using a psychophysical task to adjust the 'weight' of expressions in morphed faces. Participants performed a 3 Alternate Forced Choice task with two different expressions in each trial. Psychophysical discrimination thresholds were estimated using a staircase procedure, where correct responses adjusted the weight of the expressions down (so that the two different expressions in each trial were more similar), and incorrect responses adjusted the weight of the expressions up (so that the two different expressions were more distinct). This procedure was performed for every pair of emotions, to construct a matrix for each participant (from Chapter 4). To construct the Perceptual model used in the present chapter, we averaged the matrices across participants.

Categorical Task

In Chapter 4, participants categorised facial expressions during a multiple-choice style categorisation test. A confusion matrix was measured for each participant, recording the number of instances that each expression category was labelled (or mislabelled) with each emotion label. Mirroring cells were then averaged to measure the mean number of instances that one emotion was confused for another. To create the model used in the current experiment, these matrices were then averaged across participants.

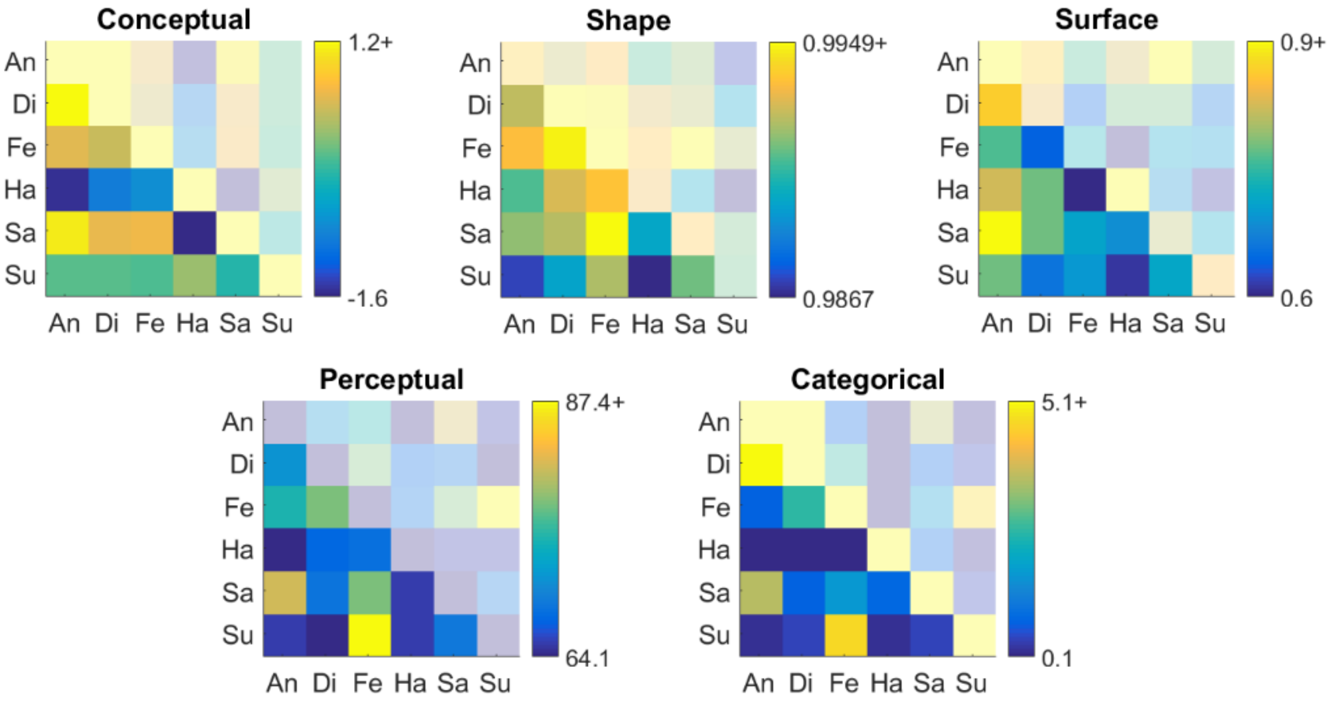

Figure 6.2: The three theoretical models (upper row) and two models derived from behaviour (bottom row).

6.2.10 Univariate Analysis (Experimental Task)

For exploratory purposes, we assessed any differences between the univariate responses to each of the facial expression categories within each of the ROIs. Betas for each emotion were averaged across all voxels within each ROI, then averaged across runs. To assess any differential response between them, paired t-tests were performed between every pair of betas across all participants, using FDR correction to account for multiple comparisons (Benjamini & Hochberg, 1995).

6.2.11 Representational Similarity Analysis

After betas were estimated for each event in each run, they were averaged for each emotion (creating six averaged response patterns per run), then these averaged response patterns within each region were vectorised and each pattern was z-scored (i.e. the pattern of activation for each condition across voxels was zscored to mean of zero and standard deviation of one — see Goesaert & Op de Beeck, 2013). A 6x6 Representational Dissimilarity Matrix was constructed by taking the squared Euclidean distances between each z-scored vector, for each region of interest. We chose this distance measure (squared Euclidean) as we used multiple linear regression with RSA, which requires a distance measure that sums linearly (Brooks et al., 2019; Carlin & Kriegeskorte, 2017).

Rows and columns of the RDMs were sorted by expression and identity consistently across runs, and corresponded to the order of the emotions in the model matrices (i.e. Angry, Disgusted, Fearful, Happy, Sad, then Surprised). For each participant, an average RDM was computed by averaging the RDMs from all runs. Models were reversed to keep the direction and size consistent with the neural RDMs. The relationship between each of the models and the neural RDMs was first examined using a Spearman’s correlation, for each participant. The array of correlation coefficients was then tested against 0 (i.e. no correlation) using a one-sided Wilcoxon signed rank test.

In addition, we ran multiple regression to examine the unique predictor value of each model and whether a combination of models could better explain the brain representational distances. For each participant, multiple linear regression was performed using the conceptual, shape, and surface models as predictors and the brain RDMs (separately for each region of interest) as the outcome (Figure 6.3). All predictors and the neural RDM were z-scored to calculate the standardised betas for each model. A constant of ones was also entered into each regression model. The distributions of standardised beta weights across participants were tested against 0 using a one-sample t-test, for each model, for each region of interest.

To assess the relationship between the neural RDMs and perceptual and categorical models, these were each entered as predictors in separate regression models. As with the previous regressions, the predictor and the neural RDM were z-scored and entered into the model with a constant of ones, and the array of standardised betas were tested against 0 using a one sample t-test.

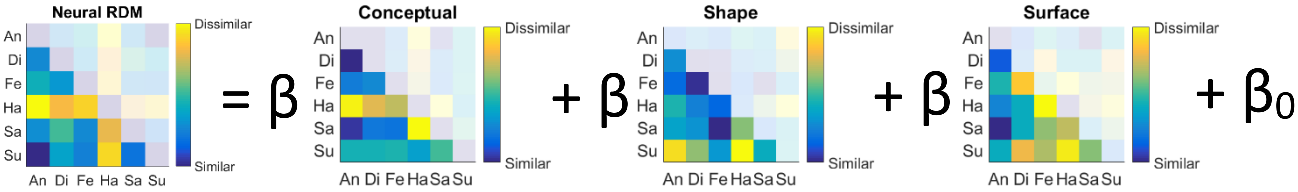

Figure 6.3: Illustration of the regression model performed per participant, to assess the relative contribution of conceptual, shape, and surface information.

6.3 Results

6.3.1 Data exclusion

One participant moved more than our threshold (2.5mm) during the face localiser and 5 of the experimental runs, so we opted to exclude this participant from any further analysis. One experimental run was also excluded from each of three additional participants due to movement. Finally, one participant was found to have a large structural abnormality, so was excluded from any further analysis, leaving 28 participants for the main analysis (with 10 experimental runs for 23 participants, 9 runs for 4 participants, and 8 runs for 1 participant).

6.3.2 Multiple choice task

We calculated the mean and standard deviation for the accuracy at correctly recognising each emotion during the behavioural multiple-choice task conducted outside the scanner. The results are presented in Table 6.1 below. Participants were most accurate at the recognition of happy faces (with an average accuracy of 98.00%), and were least accurate at the recognition of angry and fearful faces (with recognition accuracies of 61.33% and 66.00% respectively). As this task was conducted to familiarise participants with the six basic expressions, these results were not used in any further analysis.

Table 6.1: The mean, standard deviation, minimum and maximum accuracy scores for the recognition of each emotion.

Emotion	**Mean (%)**	**S.D.**	**Min**	**Max**
Angry	61.33	25.69	0	100
Disgusted	91.33	17.95	20	100
Fearful	66.00	34.10	0	100
Happy	98.00	6.10	80	100
Sad	92.00	14.48	40	100
Surprised	94.00	10.70	60	100

6.3.3 ROI definition

Using the approach described in the methods section, we used the localiser tasks to define the regions of interest for each participant. Table 6.2 shows the number of participants in which we found at least one voxel showing significant differential activation, and the mean coordinates in MNI space across these participants, for each region. For these participants, we placed a sphere (of 6mm radius) around the peak voxel for each contrast and extracted response patterns for each condition from these spheres. Each ROI at this radius comprised 123 voxels.

Table 6.2: Results from the group-constrained subject-specific approach to region of interest definition. Number of subjects in which at least one-voxel showing significant differential activation within each mask, and the average x, y, and z coordinates across these subjects are shown.

Region	**Number of subjects (/28)**	**Mean coordinates**		
		x	*y*	*z*
FFA	27	40.8	-48.2	-19.8
OFA	25	44.8	-74.9	-9.3
STS	24	52.5	-47.6	10.0
MPFC	27	3.6	56.4	14.2

As described in the methods section, we conducted second level analysis across all participants, and used the peak coordinates from this analysis to centre the sphere for the remaining participants for each ROI. Figure 6.4 shows the group level maps for this analysis, constrained using masks from previous research (Fedorenko et al., 2010; Julian et al., 2012).

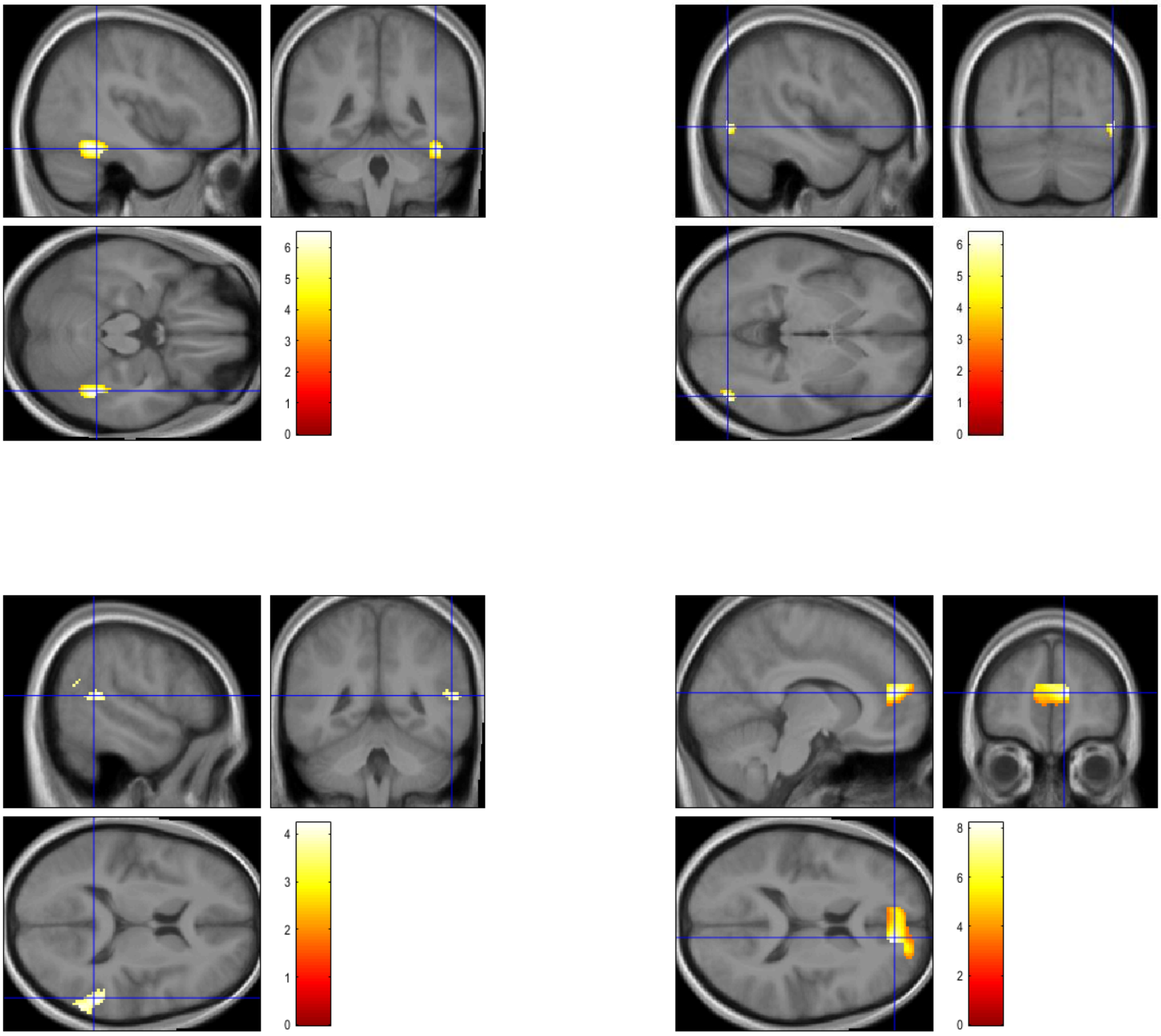

Figure 6.4: Group maps for the FFA (upper left), OFA (upper right), pSTS (lower left), and MPFC (lower right), presented on the average structural image of the 28 participants included in the main RSA. Maps have been masked by group maps from previous research (Fedorenko et al., 2010; Julian et al., 2012), thresholded at p < .001. Crosshairs are presented at the peak voxel for each map (MNI coordinates [x, y, z]: FFA = [42, -44, 20]; OFA = [46, -74, -4]; STS = [54, -46, 12]; MPFC = [10, 48, 14]).

6.3.4 Univariate analysis (Experimental Task)

To assess whether there was any differential univariate response to the facial expressions within each of the ROIs, the betas in response to each emotion were averaged across all voxels within each ROI, and then averaged across runs. Paired *t*-tests were then performed between every possible pairwise combination of these mean betas. FDR correction (Benjamini & Hochberg, 1995) was used to account for multiple comparisons. Results are presented in Figure 6.5. A similar pattern of results was observed across the three core face regions, where fearful expressions evoked the largest response, followed by surprised, then angry faces. Happy faces evoked the smallest response. Interestingly, the response to all facial expressions was negative in the MPFC.

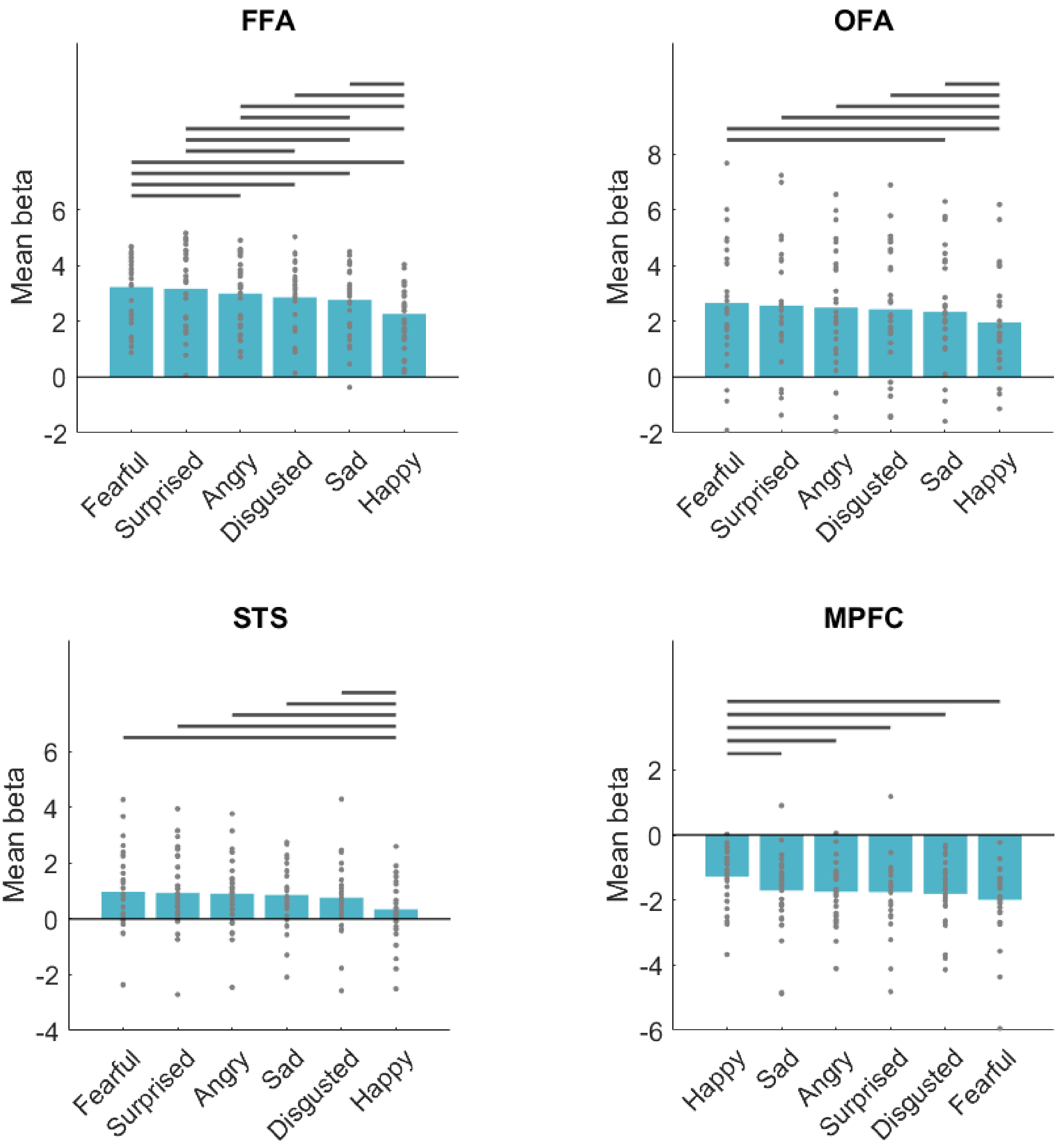

Figure 6.5: Univariate response to each expression category within each ROI. Horizontal black bars indicate the p-value for the pairwise comparison falls beneath the FDR corrected alpha level (FFA alpha = .021; OFA alpha = .005; STS alpha = .007; MPFC alpha = .013)

6.3.5 Correlation between models

Before conducting the RSA, we first assessed the relationship between the models by calculating the Spearman's correlation coefficient between the lower diagonal cells of each of the three model RDMs (Shape, Surface, and Conceptual). No correlation was found between any of the models

(Shape-Surface: rho(15) = -0.068, p = .812; Shape-Conceptual: rho(15) = 0.311, p = .259; Surface-Conceptual: rho(15) = 0.311, p = .259).

6.3.6 Relationship between models and RDMs

We first explored the relationship between each model and the representational structure within each region. To do so, we calculated the Spearman's correlation coefficient between the lower diagonal cells of each model RDM and the corresponding cells in the brain RDM for each region and each participant. Brain RDMs are presented in Figure 6.6.

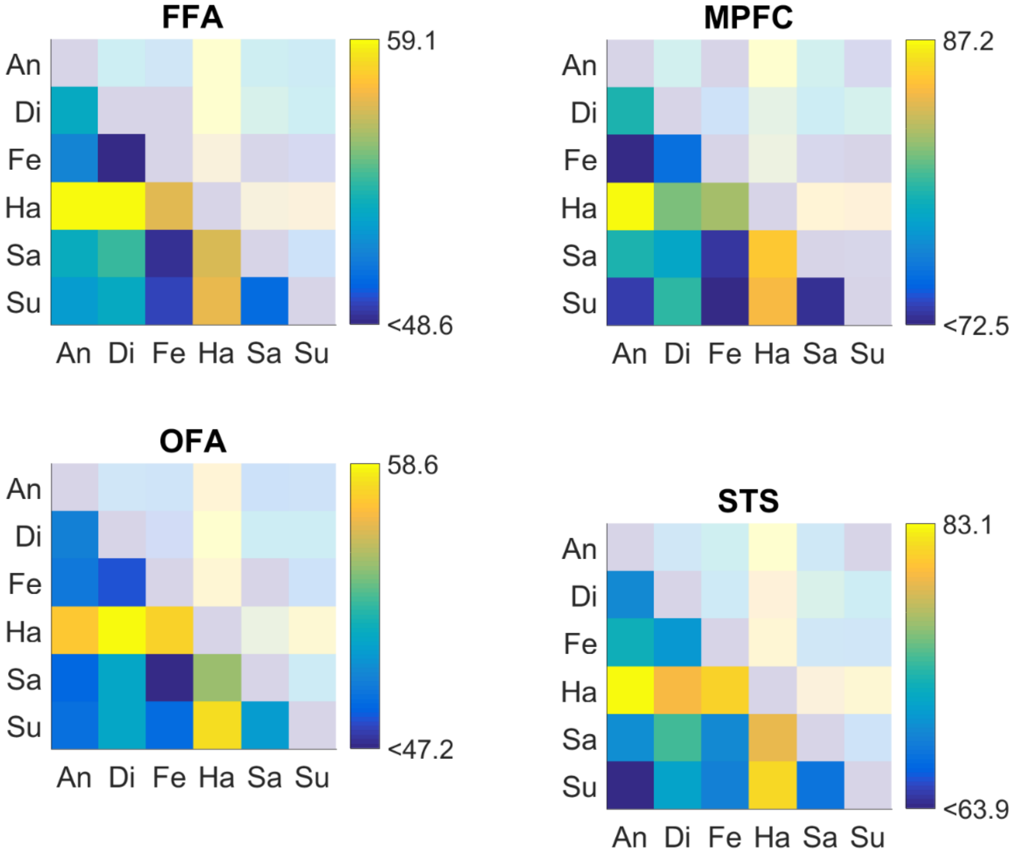

Figure 6.6: Brain RDMs for each ROI. Cells of each matrix used in the analyses are highlighted.

The array of correlation coefficients (i.e. coefficients across all participants) was then tested against 0 using a one-sided Wilcoxon signed rank test. FDR correction was used to correct for multiple comparisons within each ROI. The mean correlation coefficients, standard deviations, associated z-statistic from the Wilcoxon signed rank test, alpha levels, and p-values are reported in Appendix C (Table C1).

Conceptual, Categorical, and Perceptual similarities were related to the representational distances in all four ROIs. The structure of the Shape Model was only associated with the representational structure in the FFA and MPFC, whereas the Surface model was not associated with the representational structure in any region. Figure 6.7 shows the correlation coefficients, and the estimated noise ceiling, which was calculated following Nili et al. (2014). The upper bound of the noise ceiling for each region shows the average Spearman’s correlation coefficient between each participants’ RDM (for that region) and the average of all participants’ RDMs (for the same region), after rank transforming all matrices. The lower bound of the noise ceiling is the average Spearman’s correlation coefficient between each participant’s RDM and the average of all *other* participants’ RDMs, after rank transforming all matrices. The lower-bound of the noise-ceilings ranged from 0.243 in the MPFC to 0.340 in the FFA. The only model to reach the noise ceiling in any region was the Perceptual Model in the MPFC, suggesting this model performs as well as any model can, given the noise in the data (Nili et al., 2014).

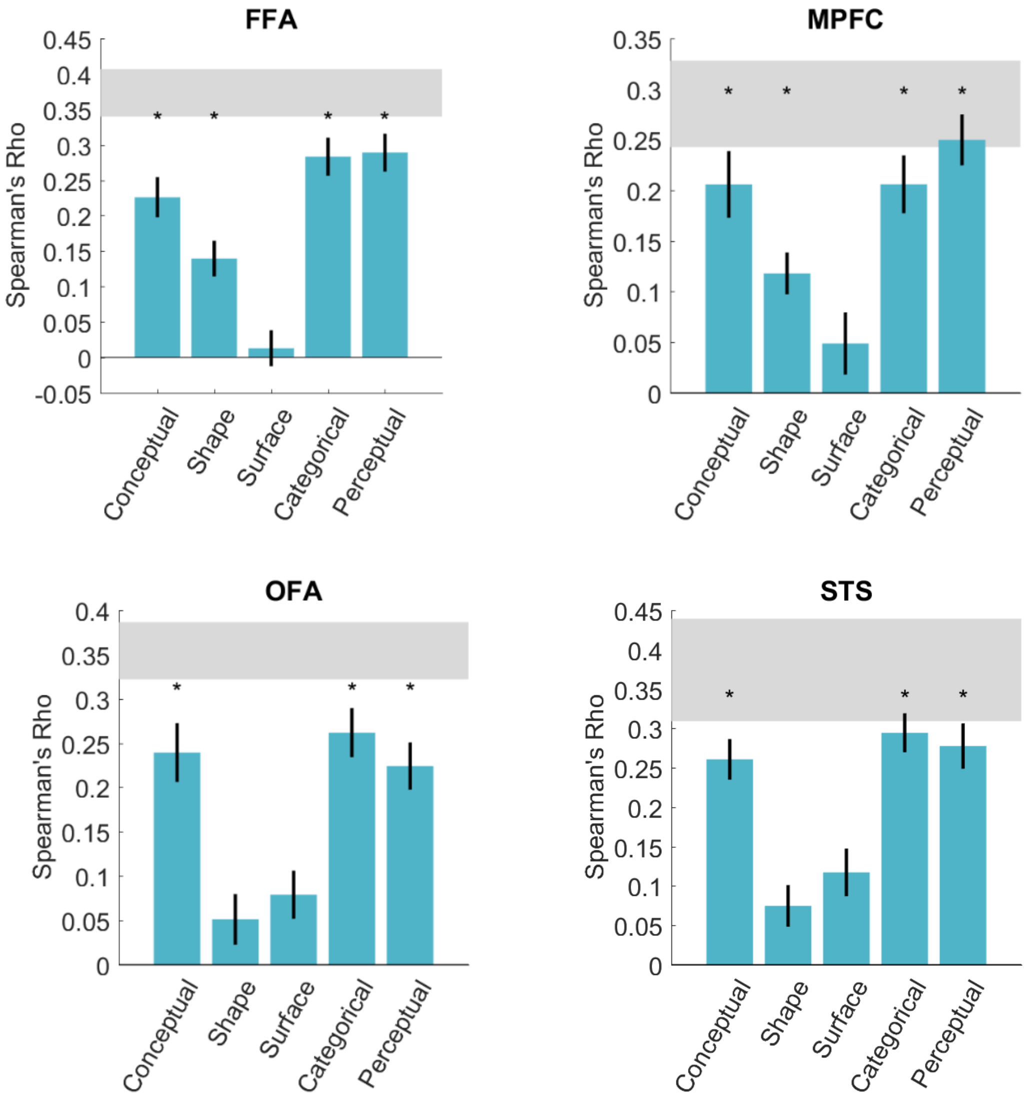

Figure 6.7: The mean correlation coefficient between each model and the RDM for each region, across participants. Error bars represent one standard error. Asterisks show that the array of coefficients is significantly larger than 0. Grey bars show the upper and lower bounds of the noise ceiling.

6.3.7 Multiple Linear Regression Representational Similarity Analysis

To assess the relative contribution of the three models (conceptual, shape, and surface) to the representational structure of emotions in each of the 4 regions, we used multiple linear regression with each of the models as predictors and each subject's RDM as the dependent variable. Models and RDMs were z-scored to calculate the standardised beta value for each predictor. Standardised betas were then compared against 0 using a one-sample t-test, and compared to each other using a paired sample t-test. Alpha levels were adjusted using FDR correction separately for each test (see Appendix C (Tables C2 and C3) for the adjusted alpha levels).

The mean standardised beta and standard error for each predictor are presented in Figure 6.8. Results of the one-sample T-tests are presented in Appendix C (Table C2), and results of the pairwise comparisons are presented in Appendix C (Table C3). Conceptual similarity significantly explained some of the variance of the representational structures in all four regions after controlling for the similarities of face shapes and surface textures. Interestingly, after controlling for conceptual similarities, shape and surface similarities did not share any variance with representational similarity in any region. The three models together explained most variance in the OFA (mean R^2 = 0. 377), followed by the STS (mean R^2 = 0. 350), FFA (mean R^2 = 0.309), then MPFC (mean R^2 = 0.322).

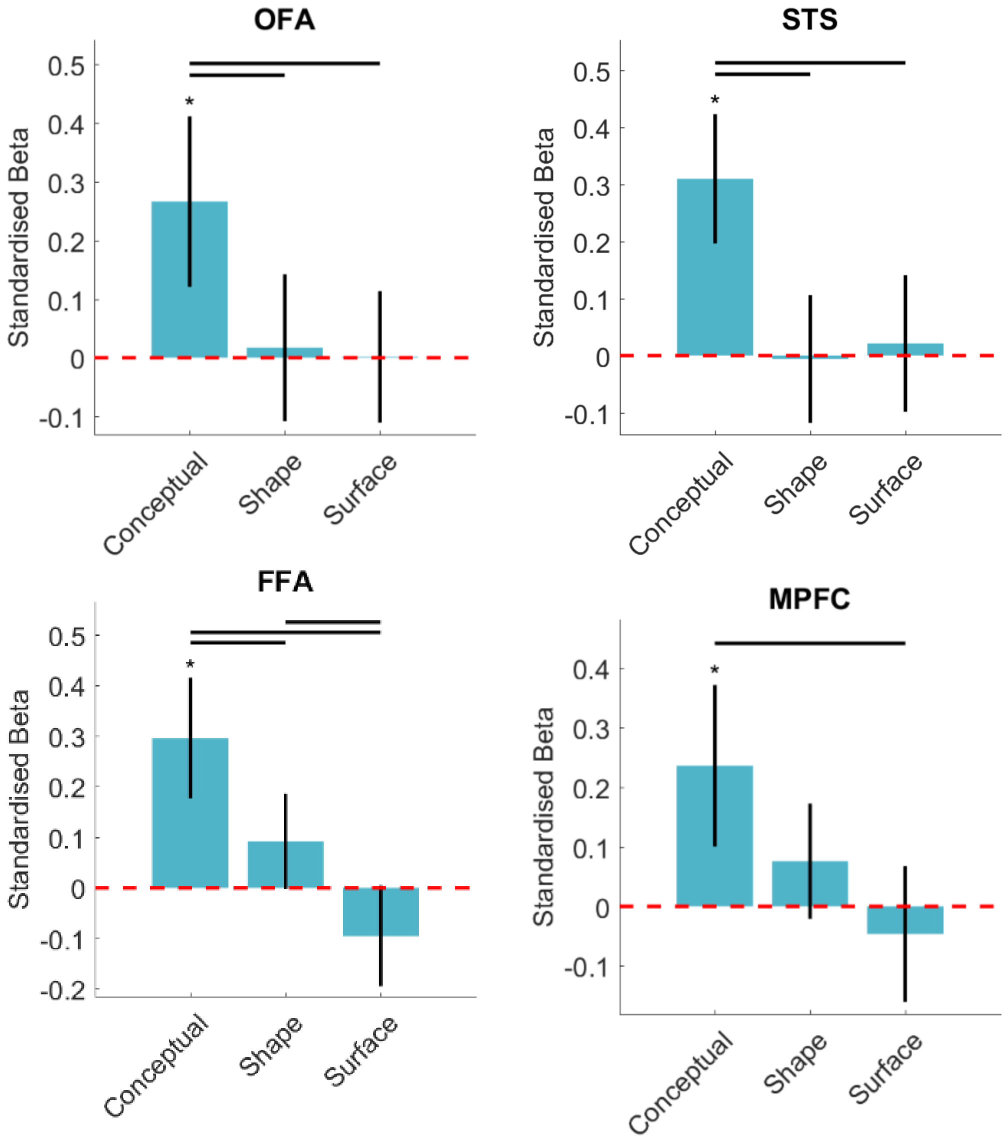

Figure 6.8: The mean standardised betas for each of the 3 models, for each region. Error bars show standard error. Asterisks indicate that the regression coefficients are significantly larger than 0, and horizontal bars indicate significant differences between the regression coefficients.

6.3.8 Perceptual and categorical models

We then assessed whether the representational structure within each region is best associated with the Categorical or Perceptual tasks (derived from the results of Chapter 4). For this analysis, we conducted a separate regression for each of the two tasks, using the model as a predictor of the neural RDM for each ROI. This analysis was conducted separately from the previous regressions as it would not be appropriate to include the theoretical models (Shape, Surface, and Conceptual) in the regression model when assessing the fit of the task-based models (Perceptual and Categorical). As with the previous regressions, the neural RDMs and predictors were z-scored, and the array of resulting standardised beta weights were compared against 0 using a one-sample t-test. Both models were able to predict the representational structure in all regions above chance. The mean standardised beta, mean R squared value, and the results of the t-test for the categorical and perceptual models are presented in Table 6.3 below.

Table 6.3: The mean standardised beta across participants, the standard deviation, and the results of the t-test for the perceptual and categorical models as predictors of the representational structure in each region.

Region	**Predictor**	**Mean standardised beta**	**S.D.**	**Mean R^2**	**T-test**
FFA	Perceptual	0.295	0.253	0.149	t(27) = 6.166, p < .001
	Categorical	0.228	0.282	0.129	t(27) = 4.283, p < .001
OFA	Perceptual	0.246	0.268	0.130	t(27) = 4.853, p < .001
	Categorical	0.214	0.267	0.115	t(27) = 4.242, p < .001
STS	Perceptual	0.247	0.315	0.156	t(27) = 4.149, p < .001
	Categorical	0.227	0.224	0.100	t(27) = 5.371, p < .001
MPFC	Perceptual	0.232	0.275	0.127	t(27) = 4.450, p < .001
	Categorical	0.163	0.275	0.099	t(27) = 3.143, p = .004

We compared the overall fit of the two models, by performing a paired sample t-test between the arrays of R^2 values output from the regressions. The Perceptual Model explained more variance than the Categorical Model in the STS (t(27) = 2.851, p = .008), but no difference was found in the FFA (t(27) = 0.809, p = .425), OFA (t(27) = 0.805, p = .428), or MPFC (t(27) = 1.290, p = .208).

6.4 Discussion

In this study, we aimed to explore the relative role of conceptual and stimulus-based cues in the neural mechanisms underpinning facial expression perception. The results highlight the particular role of conceptual information, as the conceptual model showed the highest correlations with the representational distances within three face-responsive regions and an MPFC region involved in the processing of theory of mind. Such results add to previous research into the role of these three cues in neural representations of facial expressions (Brooks et al., 2019; Sormaz, Watson, et al., 2016), by showing that representational distances in all regions we examined (the FFA, OFA, STS, and MPFC) are only explained by the similarities of emotion concepts (and not the similarities of shape and surface cues), after controlling for the variance shared by the other cues.

We found a similar pattern of results in all four regions that we examined, where the representational structure was explained by similarities of emotion concepts but was not explained by similarities of either of the stimulus-based properties. This pattern of results in the OFA highlights the accessibility of emotion concepts in the early perception of facial expressions.

The result that the two stimulus-based cues did not explain the representational structure was unexpected as this area is reportedly involved in early stages of the visual processing of faces and facial expressions. It may be the case that the representational distances of facial expressions within the OFA could have better been explained by similarities of other low-level image properties. For example, Weibert et al. (2018) found that the correlations between GIST descriptors (spatial frequency distributions after passing each image through a series of Gabor filters; Oliva & Torralba, 2001) could explain the representational similarity of facial expressions in the three core face regions. Similarly, Brooks et al. (2019) used three measures of visual similarity as controls in the RSA regression model (the similarity of face silhouettes, similarity of pixel intensity maps, and similarity of ‘higher-level visual features’ as output from the HMAX model of object recognition). While the regression coefficients of these models were not reported, their measure of conceptual similarity did not explain representational distances within the OFA after controlling for these measures. Perhaps these low-level measures of image similarities can better explain the representational structure of expressions within the OFA than shape and surface similarities.

For the MPFC these results were in line with our predictions as previous research has shown that representations of emotions within this area are modality independent (Peelen et al., 2010; Skerry & Saxe, 2014), and so are not structured around any property of the stimulus but rather conceptual knowledge of emotions.

Previous research has shown that multivariate patterns of activation elicited by emotional stimuli in the MPFC are cross-modal (e.g. the pattern of activation elicited by an angry face is similar to that elicited by an angry voice; Peelen et al., 2010). The results of the current research have furthered this by demonstrating that the similarity of patterns of activation in response to facial expressions is explained by the similarity of emotions concepts, and is not explained by the similarity of properties of the stimuli.

To our knowledge, research has yet to assess whether shape and surface properties of facial expressions can explain representations in core face areas. Despite this, the result that these properties did not explain variance in the OFA and STS (as they did in the FFA) was surprising. Several studies have suggested that the representational structure within these regions is explained by the perceptual similarity structure of pairs of facial expressions, as measured behaviourally (Said, Moore, Engell, et al., 2010; Sormaz, Watson, et al., 2016). Research has also highlighted the important role of shape and surface properties to the perception of expressions (Sormaz, Watson, et al., 2016; Sormaz, Young, et al., 2016). Similarly, in Chapter 4, we showed that pairwise perceptual similarities were explained above chance by shape and surface properties, even when controlling for conceptual information. Given these two lines of evidence, we expected to find that shape and surface similarities would explain representational similarities in the OFA and STS, in addition to the FFA.

The second aim of this experiment was to explore which of the perceptual and categorical tasks (from Chapter 4) was better associated with the representational structure of emotions within each brain region. Representational distances within all four regions we examined were explained by both tasks above chance, and the Perceptual task explained more variance than the Categorical in the three core face regions, but not in the MPFC. This trend for the Perceptual task to better explain representations than the Categorical suggests that the representational structure within the three core face regions is better associated with the perceptual similarity of expressions than categorisation errors. Sormaz, Watson, (2016) found that perceptual similarity of expressions was associated with representational similarity in the OFA and STS, but not the FFA. The results of our study suggested that the representational structure in all three of these regions is explained by perceptual similarity. A potential reason for the difference of results in the FFA is our measure of perceptual similarity, which arguably uses fewer high-level decision-making processes than the subjective judgements used by Sormaz and colleagues.

In our study, we found that representations of facial expressions in the MPFC can be explained by conceptual knowledge of emotions, in addition to perceptual similarity of expressions and categorisation errors. These results suggest that, while the MPFC may represent modality independent emotion concepts, it also plays a role in perception and categorisation of facial expressions of emotion tasks. Future work could examine the exact role of the MPFC in earlier stages of the perception of facial expressions, perhaps with use of TMS to disrupt activity within this region.

While our results provide an understanding of the role of conceptual and stimulus-based properties in brain representations of emotion, there are some limitations to consider. Our model of conceptual similarity of emotions was derived from data from an independent study (Skerry & Saxe, 2015). Although this model predicted the representational structure of emotions better than the other models we used, a potential limitation is that this model is not specific to the individual. While previous research has measured conceptual similarity of emotions within-subject (Brooks et al., 2019; Brooks & Freeman, 2018), research has yet to test for an individual component to this relationship between conceptual and representational similarity. Constructing a conceptual model for each subject would allow us to examine whether an individual's own idiosyncratic conceptual knowledge of emotions predicts their representational structure, better than an averaged model. Similarly, the perceptual and categorical models were constructed using the data from Chapter 4, using a separate group of participants. Measuring perceptual similarity and confusion errors for each subject of the current study would allow us to examine any individual component to the relationship neural representations and behaviour.

In conclusion, these results highlight the important role of conceptual knowledge of emotions in the neural mechanisms underpinning facial expression perception. The conceptual model outperformed both the stimulus-based models in predicting the representational structure within all 3 of the core face regions, in addition to an area involved in theory of mind, adding to the literature showing that conceptual knowledge shapes visual perception of expressions.

7 General discussion

7.1 Summary of main results

This thesis has focussed on two main research areas. The first was to explore the contributing factors to the age-related decline in emotion recognition from facial expressions. The second was to explore the relative contribution of conceptual and stimulus-based cues to the perception, recognition, and neural representations of emotions. Chapters 2 and 3 covered the first research area, and Chapters 4, 5 and 6 covered the second.

In Chapter 2 we examined the contribution of several cognitive, visual, and behavioural measures to age differences in emotion recognition from facial expressions. We measured accuracy at recognition of the six basic emotions, alongside short-term memory, fluid intelligence, face identity processing, visual acuity, and contrast sensitivity, in younger and older adults. We found age differences in the recognition of anger, sadness, and surprise, and that the control measures could account for differences in the recognition of anger and surprise only. Our measure of face identity processing was the biggest contributor to age differences in the recognition of anger, whereas our measure of fluid intelligence was the biggest contributor to the age differences in the recognition of surprised facial expressions. In addition to this, we also found a number of age differences in the pattern of confusions made by participants when categorising each of the expressions.

In Chapter 3 we examined the age-related changes in neural response to facial expressions and the relationship between activation and behaviour. We conducted secondary analysis of a pre-existing dataset, in which participants viewed angry, fearful, happy, and neutral facial expressions while undergoing fMRI. We found several regions in which the response to each facial expression category declined with age, and overlaps between these maps in the superior parietal lobule and bilateral postcentral gyri. We also found no strong evidence for a relationship between activation in response to a given expression and several behavioural measures associated with the recognition of the emotion.

Chapter 4 examined the relative role of conceptual and stimulus-based cues to the perception and recognition of emotions from facial expressions. Participants completed two tasks to measure the perceptual similarity of pairs of facial expressions, and number of confusion errors made during a categorisation task. Three models were constructed that measured the similarity of emotion concepts, face shapes, and surface textures. We used RSA and found that all three of the cues were related to behaviour during both tasks, and that the conceptual information outperformed the two stimulus-based cues in explaining behaviour.

In Chapter 5 we used the data and results from the previous Chapter to examine (a) whether the strength of the relationship between each cue and behaviour is associated with the performance at each task, and (b) whether there is an individual component to the relationship between perception and categorisation. We found (a) that performance at each task was not associated with the greater role of any particular cue, and (b) there was no individual component to the relationship between perception and categorisation

Finally, in Chapter 6 we examined the relative role of conceptual and stimulus-based information in explaining neural representations of emotions in 4 regions of the brain. Participants viewed facial expressions of the six basic emotions while undergoing fMRI. We used RSA to examine the relative role of the three models constructed in Chapter 4 in explaining the representational structure of emotions in the three core face areas (the FFA, OFA, and STS), and an area involved in theory of mind (the MPFC). We found that similarity of emotion concepts best explains neural similarity, within all four regions examined. We also found that the similarity of patterns of activity within the four regions was associated with perceptual similarity and number of categorisation errors, using the results from Chapter 4.

The current chapter includes a more general discussion of our findings on the effects of age on emotion recognition (from Chapters 2 and 3), the relative contribution of conceptual and stimulus-based cues (from Chapters 4, 5, and 6), and the broader implications of both lines of studies for understanding the processing of facial expressions.

7.2 Ageing and the recognition of emotions from facial expressions

In Chapter 2, we showed that older adults were poorer at correctly labelling facial expressions of anger, sadness, and surprise than younger adults. Furthermore, differences in short-term memory, fluid intelligence, face identity processing, visual acuity, and contrast sensitivity accounted for age differences in the recognition of anger and surprise, but not sadness. The results of Chapter 3 showed several regions of the brain in which the response to angry, fearful, and happy facial expressions decreases with age. In addition to this, the results showed that activation was not related to several behavioural measures associated with the recognition of the emotion (recognition accuracy and reaction time during an expression categorisation task, and reaction time to classify the gender of faces presented during scanning). Together the results of the research provide an understanding of the neural basis behind the changes in the processing of facial expressions that occurs with age.

There are, however, some noteworthy inconsistencies between the results of the two studies. In Chapter 2, we found significant age differences in the recognition of facial expressions of anger (among others). In Chapter 3, however, we found no relationship between age and the recognition of anger. Similarly, we found no relationship between age and the recognition of fear, despite previous research suggesting that older adults typically have difficulty recognising this emotion (Ruffman et al., 2008). There are two possible sources for the discrepancies between the results of the two chapters. The first is that substantial ceiling effects were observed in the emotion recognition test used in Chapter 3, which may not have been sensitive enough to capture the effects of age that were observed in Chapter 2. The second reason is that the age range was larger in Chapter 2 than in Chapter 3. This issue is discussed in more detail later in this section.

In Chapter 2 we found no age differences in the correct recognition of happy facial expressions, however in Chapter 3 we found several regions showing an age-related reduction in response to happy faces. As there was no difference between younger and older adults in the recognition of happy faces in Chapter 2, and the recognition of happy faces did not decline with age in Chapter 3, we expected that there would be little difference in the neural processing of happy faces across age.

This does, however, raise the important conceptual issue of whether a reduction in activation actually reflects poorer performance. There are situations in which reduced activation reflects easier processing of stimuli, for example in fMRI-adaptation studies in which repeated instances of stimuli evoke comparatively smaller neural responses (e.g. Grill-Spector & Malach, 2001). However, the converging evidence that older adults are poorer at the recognition of emotions from facial expressions and have attenuated neural response to facial expressions is consistent with the hypothesis that reduced activation in older participants may reflect poorer performance at the recognition of the emotion. For this reason, in Chapter 3 we expected to find age-related reduction in activation for expressions that older adults typically find more challenging to recognise (i.e. anger and fear), and no relationship between age and activation in response to happy faces.

Contrary to expectations, we did not find strong evidence for a relationship between activation in response to an expression and several behavioural measures associated with the recognition of the emotion. This result suggests that any reduction in activation is not associated with the ease or difficulty of processing the stimuli and is instead associated with ageing or other age-related changes/factors. While there is evidence suggesting that older adults have reduced activation in response to facial expressions of emotion, the results of the present research question the relationship between this reduction in activation and the difficulty recognising the emotion, and instead suggest that the reduction in activation may reflect other factors associated with ageing.

The neuropsychological account suggests that the age-related decline in emotion recognition is a result of age-related changes in structure and function of regions associated with the processing of certain expressions. As we found no clear relationship between activation in response to an expression and the behavioural recognition of the emotion, the results suggest that age-differences in the recognition of the emotion may not simply be a result of reduced activation in response to an expression.

These studies have contributed to the literature on the effects of age on the processing of facial expressions. In Chapter 2, we showed how the pattern of confusions made during emotion categorisation differs between younger and older adults. Mill et al. (2009) had reported a strong correlation between the confusion matrices from younger and older adults, suggesting that younger and older adults make similar confusions. By performing a direct comparison between corresponding cells, we have shown that younger and older adults do differ in the exact pattern of confusions they make during categorisation tasks.

In Chapter 3, we showed that the age-related attenuation in neural response to facial expressions could occur independently from several behavioural measures associated with the recognition of the emotion. While previous research had reported that several regions showed a reduction in activation in response to facial expressions, the present results furthered this by examining this relationship with behaviour (and showing the relationship is not straightforward).

It is worth noting that we only examined the relationship between neural response and behaviour in regions that showed a decline in activity across age. Furthermore, previous research has found age differences in several regions that we did not. As such, it would not be appropriate to claim that there is no relationship between behaviour and neural response within regions that we did not examine. For example, several studies have highlighted age differences in amygdala response to facial expressions (Fischer et al., 2005; Iidaka et al., 2002; Keightley et al., 2007; Williams et al., 2006). As this region is commonly implicated in the processing of emotional stimuli, it may be possible that any age-related attenuation in response within this region is associated with behavioural age-differences in recognition.

By combining the results of the two studies, potential future research is highlighted. In Chapter 2, we showed that age differences in the recognition of anger and surprise were controlled for by several cognitive measures. In contrast, Chapter 3 showed that the age-related decline in emotion processing was not associated with the behavioural recognition of the emotion. Future work could perhaps examine whether age differences in the neural response to facial expressions can be explained by these cognitive measures.

These studies are, however, not without their limitations. While the results of Chapter 3 provided an insight into how the neural processing of expressions changes across the lifespan, the age range of participants should be considered. In Chapter 2, we tested two distinct age groups, where the older group ranged from age 60 to 93 years. In Chapter 3, the age of participants ranged from 20 to 65. While the recognition of emotion begins to decline around middle-age (Calder et al., 2003; Horning et al., 2012; Williams et al., 2006), it must be taken into consideration that the effects of age observed in the two chapters may not be exactly comparable. Similarly, this may account for the discrepancies between the results of Chapter 3 and previous research.

In the behavioural experiment, we examined age differences in the recognition of six emotions, whereas the data we used in the fMRI experiment only concerned the effect of age on neural response to facial expressions of anger, fear and happiness (compared to neutral). As such, it is not clear how the neural response to facial expressions of the remaining emotions (disgust, sadness and surprise) changes across age, nor the relationship between activation and behaviour. Future work could combine these studies and examine the relationship between the neural response to each of the six basic emotions and the behavioural recognition of the emotion, ensuring that the recognition task is sufficiently difficult to capture effects of age. Perhaps a larger age range with two distinct age groups could be used, employing a similar ANCOVA model to that used in Chapter 2, to examine whether age differences in the activation in response to an expression remain after controlling for the behavioural recognition of the emotion. Such research would further examine whether any age differences in neural response are controlled for by behavioural performance, or whether they are age specific.

7.3 Top-down and Bottom-up processing

In Chapter 4 we showed that the similarity of emotion concepts can explain both perceptual similarity of expressions and categorisation errors, even when controlling for shape and surface properties of the face stimuli. The results of Chapter 6 furthered this, by showing that the similarity of emotion concepts can explain the similarity of neural representations of emotions, after controlling for the same stimulus-based properties.

Considering both the behavioural and neuroimaging results together provides evidence that conceptual knowledge of emotions impacts perception, perhaps by shaping representations of emotions within regions involved in the perceptual processing of facial expressions of emotion.

Research by Brooks and Freeman (2018) used RSA to show that the similarity of emotion concepts predicts the perceptual similarity of facial expressions, claiming that knowledge of emotion concepts shapes the perception of expressions. Two aspects of the current research have furthered these results. The first is the methodological difference between the measurements of perceptual similarity. Arguably, our measure of perceptual similarity is less dependent on top-down processes, as emotion labels were not present in the task. The replication of the results, despite this change, further demonstrates the role of emotion concepts in the perception of facial expressions.

Secondly, we have shown not only that knowledge of emotion concepts influences perception, but also the explicit categorisation of facial expressions. This finding highlights the role of conceptual knowledge of emotions in a common emotion recognition task, and is comparable to the results of research showing that categorisations of gender and race is influenced by top-down expectations (Levin & Banaji, 2006; Macrae & Martin, 2007).

The follow up study from Brooks and colleagues investigated the role of conceptual information on brain representations of emotion, and found that conceptual similarity can explain representational similarity within the right fusiform gyrus, after controlling for the similarity of several low-level image properties (Brooks et al., 2019). Again, the current research furthered these results by showing that conceptual information can explain brain representations of emotion in other regions involved in the processing of facial expressions. It is worth noting that Brooks et al. (2019) used a searchlight with multiple linear regression RSA, and the only region that survived multiple comparisons was a region in the right fusiform gyrus. The difference between the results of the present research and the results of Brooks et al. (2019) in the number of regions in which conceptual information explains neural representations may arise from our *a priori* definition of regions of interest.

The results of the research are consistent with several recent theories of social perception suggesting that top-down beliefs and expectations interact with bottom-up processes to shape our visual perception of others. For example, Stolier, Hehman, and Freeman (2018) propose a model of face-trait judgements, that posits that the space in which these judgements are made (for example, where ‘friendly’ falls along dimensions of dominant and trustworthy) is shaped by top-down beliefs and stereotypes. Using the example of judgements of female faces, the authors suggest that gender stereotypes (e.g. that dominant females are viewed as less trustworthy) manipulates the space in which judgements of traits from faces are made.

Similarly, Freeman and Johnson (2016) propose a dynamic interactive model of social perception. This computational model treats the initial perception of others as an interaction between visual features and prior expectations (e.g. from stereotypes, attitudes, or goals). The model suggests that there are feed-forward and feed-back connections between facial feature space and social category representations (e.g. between the facial feature of a larger jaw and the social category of male), and between social category representations and stereotypes, attitudes and goals (e.g. between the social category 'male' and the stereotype 'aggressive'). As such, representations of social categories and facial features are influenced in part by higher-level social cognition, dynamically shaping the visual perception of others. The model proposes a network of brain regions involved in this split-second social perception, consisting of the fusiform gyrus, anterior temporal lobe, and orbitofrontal cortex. It is suggested that the anterior temporal lobe retrieves social-conceptual information (e.g. stereotypes), which is then used by the orbitofrontal cortex to implement top-down predictions that shape representations of faces in the fusiform gyrus. The results of the current research are consistent with these models of social perception, that put emphasis on prior knowledge and expectation in shaping the perception and categorisation of others.

The focus of this section thus far has been on the role of conceptual information, however we aimed to examine the relative influence of conceptual and stimulus-based cues. The results for the role of the stimulus-based cues, however, have not been quite as clear. In Chapter 4 we found that the similarities of both shape and surface cues can explain perceptual similarity and categorisation errors, where shape information played a particular role in explaining behaviour in the perceptual task and surface information best explained behaviour in the categorical task. However, the results of Chapter 6 are not entirely consistent with the behavioural results, as these cues did not share any unique variance with the representational distances in any region (after controlling for the similarity of emotion concepts). As we found that shape and surface information still play a role in explaining perceptual similarity after controlling for conceptual similarity, and there is research suggesting that perceptual similarity is explained by representational similarity within these regions (Said, Moore, Engell, et al., 2010; Sormaz, Watson, et al., 2016), it was unexpected that these cues did not explain neural representations in the brain regions that we examined.

In Haxby's original model of the neural systems involved in face perception, the OFA is proposed to be involved with the early perceptual processing of faces, the STS is involved with changeable aspects of the face (e.g. expressions), and the FFA is involved with the processing of face identity (Haxby et al., 2000). In addition to these core regions, an extended system comprising the intraparietal sulcus, amygdala and limbic system, and anterior temporal cortex, are suggested to be involved with further processing of faces. Several studies have proposed updates to this model, as the core regions and several regions of the extended system all represent facial expressions of emotion (Harry et al., 2013; Said, Moore, Engell, et al., 2010; Wegrzyn et al., 2015; Zhang et al., 2016). Given the results of Chapter 6, in which we found that the representational structure of facial expressions within the MPFC is explained by the similarity of emotion concepts, this region could be considered as an addition to the extended system in the model.

While these studies provided an understanding of the relative influence of conceptual and stimulus-based information on behaviour and brain representations of emotion, there are some limitations to consider. To explore the relative contribution of these sources of information in both studies we used RSA, which is inherently correlational. As such, we cannot be sure of any causal relationship between any particular cue and behaviour or neural representations. For example, it would not be appropriate to infer that a given pair of facial expressions are perceptually more similar *because* the corresponding emotion concepts are more similar.

This issue of causality raises a further conceptual issue, which is that we cannot be sure that participants are ‘using’ any of the three cues we examined. For example, in the regression model for the Perceptual Task in Chapter 4 the average beta for the conceptual model was larger than that of the surface model, but the claim that participants use conceptual information more than surface information would be unwarranted.

One further limitation to note is that the regression model for each of the four ROIs (in Chapter 6) produced low average R-squared values across participants, suggesting that there are additional sources of variance that can account for the representational structure within these regions. Of course, the three sources of information we chose to examine are not an exhaustive list of factors that can affect the processing of facial expressions. Several low-level image properties are reported to explain representations of emotions within the core face regions. Weibert et al. (2018) found that the correlations between the spatial frequencies of pairs of images (measured using GIST descriptors; Oliva & Torralba, 2001) explained the representational structure within the three core face regions. Similarly, Brooks et al. (2019) constructed RDMs that measured the similarity of the silhouettes, pixel-by-pixel intensities, and a measure output from a computational model of object recognition (HMAX; Serre, Oliva, & Poggio, 2007). While the exact influence of these models on the representational structure was not reported, they acted as control measures in the regression models. In addition to the cues examined within this research, the perception of facial expressions is well documented to be affected by multiple personality traits, hormones, and age, so it is likely that these factors may account for additional variance of the representational structures we observed. Should future work include individual-level measures (e.g. personality traits), more complex multilevel regression models should be used to account for this variance at the individual-level (in addition to variance between emotion-pairs).

This research showed that emotion concepts can influence the perception of facial expressions, perhaps by shaping neural representations within several regions responsible for the visual processing of faces. These studies therefore show that the perception of facial expressions is not a purely stimulus-driven process, and that some top-down mechanisms play a role. One question that remains is how these mechanisms are initiated. Bar et al. (2006) addressed this question in the domain of object recognition. The researchers tested a model of object recognition proposing that a partially analysed version of the input image is projected to the orbitofrontal cortex, which then activates representations in temporal recognition-related regions that are constrained by the low spatial frequencies of the initial image. Magnetoencephalography (MEG) was used to measure the time course of activation in the OFC and recognition-related regions of the temporal cortex (the fusiform gyrus), in response to briefly presented objects. Results showed that the activity in the OFC preceded activity in the fusiform gyrus by 50ms for objects that were consciously recognised, suggesting that the OFC is involved in facilitating top-down recognition of objects. It may therefore be possible that the OFC is involved in implementing top-down emotion concepts to 'fine-tune' representations of emotions in face processing regions. Indeed, the model of social perception proposed by Freeman and Johnson (2016) suggests that the OFC shapes facial feature representations in the fusiform gyrus, by implementing top-down social knowledge. Support for this possibility comes from evidence suggesting the OFC is involved in predicting the affective value of stimuli. A region within the OFC was found to be activated in response to both objects with positive valence, and objects with greater associative strength with other objects (Shenhav, Barrett, & Bar, 2013). Future work could therefore investigate the potential role of the orbitofrontal cortex in implementing top-down knowledge of emotion concepts in shaping representations in face processing regions. Perhaps the approach of Bar et al (2006) could be used to investigate the time course of activation in the orbitofrontal cortex and the face processing regions.

Another question that future research could address is whether there are individual differences in the role of emotion concepts. In the current research we constructed a model of conceptual similarity of emotions by using data from Skerry and Saxe (2015). While this model performed well in predicting behaviour and neural representations of emotions, a potential limitation of this approach is that using an averaged model overlooks cultural and individual differences in the similarities of emotion concepts. In Chapter 5 we sought to investigate whether there is an individual component to the relationship between perceptual similarity of expressions and categorisation errors. While these two measures were correlated (pairs of facial expressions that were more perceptually similar were more likely to be confused), there was no greater relationship within-subject than there was between-subject. As we used a model of conceptual similarity that was not subject-specific, we were not able to test whether there is an individual component to the relationship between conceptual similarity of emotions and behaviour during the perceptual and categorical tasks. Brooks and colleagues measured the similarity of emotion concepts for each participant and reported that their measure of conceptual similarity can predict both perceptual similarity (Brooks & Freeman, 2018), and neural representational similarity (Brooks et al., 2019), although they did not examine whether there is an individual component to this relationship. Doing so would allow us to test whether an individual's perceptual similarity of expressions, categorisation errors, and neural representational similarity, is best explained by their own conceptual similarity of emotion pairs, or by an averaged model.

7.4 General discussion

As this thesis has addressed two main problems, this Chapter has primarily focussed on discussing these problems independently. The aim of this section is to bring the two together. First, the common results shared across the two areas will be highlighted. Next, the broader context and future questions surrounding the possible integration of the two areas will be discussed. Finally, this section will cover general issues and considerations surrounding the research.

Both behavioural experiments in Chapters 2 and 4 involved a multiple-choice categorical test, where participants had to categorise examples of each of six facial expressions, and for both tests we measured a full confusion matrix. An informal inspection of the pattern of confusions made during the tasks suggests that participants in both experiments behaved similarly in terms of the confusions made between expressions. For example, confusions were frequently made between expressions of anger and sadness, between fear and surprise, and between disgust and anger. These confusions are consistent with those identified by Young et al. (2002) in the design of the Emotion Hexagon test, where participants must identify the dominant emotion in warps between pairs of the most easily confused emotions. No formal comparisons have been conducted between the matrices generated by participants in each Chapter due to the different number of stimuli.

As outlined in Chapter 1, conscious visual perception is not simply a feedforward stimulus-driven process, but is instead the result of an interaction between top-down predictions and bottom-up processing of visual stimuli. Accurate perception is, therefore, thought to necessitate a flexible balance between these top-down and bottom-up processes (O'Callaghan et al., 2017). This view has allowed for recent models to predict symptoms of psychosis (e.g. hallucinations) as an imbalance in this system, with greater importance placed on predictions rather than the sensory input (Adams, Stephan, Brown, Frith, & Friston, 2013; Corlett, Honey, Krystal, & Fletcher, 2011). Furthermore, it has been suggested that imbalances in this predictive coding can explain symptoms in multiple areas of psychopathology, including reduced theory of mind in autism (Friston, Stephan, Montague, & Dolan, 2014).

It may, therefore, be worth taking this view in the investigation of the effect of age on emotion recognition. As we established in Chapter 4, the perception of facial expressions requires the integration of stimulus-based cues with top-down knowledge of emotion concepts, so perhaps age differences in the processing of facial expressions may be (in part) due to an imbalance in the roles of top-down expectations and bottom-up processing of the stimuli.

As examined in Chapter 2, older adults have poorer visual acuity and contrast sensitivity than younger adults, suggesting that there may be age differences in the processing of the shape and surface properties of face stimuli. As such, it could be that greater importance is placed on conceptual information than the stimulus-based cues in older adults. Alternatively, perhaps the age-related reduction in volume of some frontal areas may attenuate the role of top-down information

Future work could perhaps repeat the experimental paradigm as used in Chapter 4, using distinct age groups with the aim of assessing age differences in the contribution of conceptual and stimulus-based cues to the perception of facial expressions. The results of Chapter 4 suggested that conceptual information plays a greater role in explaining perceptual similarities and categorisation errors than the stimulus-based cues. Should older and younger adults differ in the relative roles of conceptual and stimulus-based cues, an interaction would be expected between age group and cue type. It should be noted, however, that this would not necessarily explain the specific impairments in the recognition of anger, fear and sadness, but rather would explain age differences in the patterns of confusions, or perceptual similarities. Future work to further examine this could perhaps use fMRI with RSA to investigate whether conceptual information shapes representations in face processing areas in older adults to a different extent than younger adults. Such research would provide a new perspective on age differences in facial expression processing.

There are, or course, some potential issues to consider for the research within this thesis. For example, our use of the six basic emotions throughout this research is worth discussing. As explained in Chapter 1, the conclusion that there are six universal basic expressions of emotion came from the work of Ekman (e.g. Ekman, 1970; Ekman & Oster, 1979), and these six categories have been used extensively in subsequent research. However, the experience of an emotion is clearly not confined to these six distinct categories, and is instead a much a more subjective and content-rich experience (Barrett, Mesquita, Ochsner, & Gross, 2007). It has been argued that emotions do not have such distinct boundaries, and that evidence that the six basic facial expressions can reliably be identified should not be taken as evidence of these boundaries for emotional experiences (Barrett, 2006).

Cowen and Keltner (2017) used a fully data-driven approach to examine categories of emotional experiences. The researchers probed the emotional states elicited by a large number of short emotionally evocative videos, such as videos of natural disasters, sex acts, deaths, and awkward handshakes. Using self-report methods, the researchers found that participants reliably reported experiencing an emotion that falls into one of 27 distinct categories. Furthermore, Skerry and Saxe (2015) presented participants with stories depicting a character experiencing one of 20 emotions with subtle distinctions. When identifying the emotion, dissociable patterns of activation for each emotional category were elicited in several regions involved with theory of mind. Together, these studies show that both the perception and experience of emotions is not necessarily confined to the six basic emotions as has been used within research. It could be the case that the facial expressions corresponding to the six basic emotions are the easiest to identify, or have the best correspondence between emotional experience and facial expression, although this is a question for future research to assess. Although the emotion categories used throughout the research within this thesis may not have captured a wider range of potential emotional experiences, the results can be used as a basis for the effects observed and can be applied to previous (and likely future) work using these six emotion categories. Perhaps future work could perform similar investigations, using emotion categories with more subtle distinctions.

This raises a further conceptual issue, which is the relationship between the ability to experience an emotion and the ability to process the facial expression corresponding to that emotion. Research has shown that the affective state of an individual provides top-down guidance on visual perception (e.g. Barrett & Bar, 2009). In the domain of facial expression recognition, mood-congruency effects have been found, such that participants who had been primed with a positive mood better recognised facial expressions of happiness than those in a negative mood, who better recognised facial expressions of sadness (Schmid & Mast, 2010). A further example of this relationship comes from individuals with alexithymia, a sub-clinical trait characterised by the difficulty to recognise internal emotional states. Individuals who score high on measures of alexithymia perform more poorly at theory of mind tasks (Moriguchi et al., 2006) and facial expression recognition tasks (Cook et al., 2013). This further demonstrates the relationship between the experience of an emotion and the ability to recognise emotions in others. This trait, and the mood of the participant, was not controlled for within the research within this thesis. Of course, the factors that affect emotion recognition that we measured did not constitute an exhaustive list, however this is one issue that is worth discussing as it may have had implications for the role of conceptual information on facial expression processing. Perhaps future research could examine whether levels of alexithymia affect the role of emotion concepts on the perception of facial expressions. As previously suggested, measuring the similarity of emotion concepts within-subject may provide a more accurate measure of the influence of concepts on facial expression processing, especially given the potential variability introduced by this trait.

To conclude, the research within this thesis further examined several factors that can affect the processing of facial expressions of emotion. The research into the effect of age on emotion recognition further clarified the role of several cognitive factors that may account for the behaviourally observed age differences in emotion recognition. Furthermore, this research demonstrated that age differences in neural response to facial expressions (within regions in which the response declines with age) may occur independently from the recognition of the emotion. The research into the role of emotion concepts and stimulus-based cues highlighted the relative influence of these cues on two behavioural tasks and neural representations. In particular, the research demonstrated the role of top-down conceptual knowledge of emotions on visual perception. Together, these studies pave the way for future research to apply a predictive coding framework to the investigation of age differences in emotion recognition.

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9 Appendix A – Supplementary tables for Chapter 2

Table A1: F ratios, p-values, and effect sizes for each covariate within the ANCOVA model for the recognition of all emotions

Covariate	**Angry**				**Disgusted**			**Fearful**		
	F	**p**	**η_p^2**		**F**	**p**	**η_p^2**	**F**	**p**	**η_p^2**
MR	.693	.407	.008		.505	.479	.006	11.433	.001	.115
DS	2.320	.131	.026		.004	.948	<.001	2.229	.139	.025
GFMT	5.032	.027	.054		1.786	.185	.020	6.652	.012	.070
VS	1.416	.237	.016		.933	.337	.010	.136	.713	.002
CS	.043	.836	<.001		.181	.671	.002	.676	.413	.008

MR = Matrix Reasoning; DS = Digit Span; GFMT = Glasgow Face Matching Test; VA = Visual Acuity; CS = Contrast Sensitivity.

Table A1 (continued)

Covariate	**Happy**			**Sad**			**Surprised**		
	F	**p**	**η_p^2**	**F**	**p**	**η_p^2**	**F**	**p**	**η_p^2**
MR	4.803	.031	.052	.435	.511	.005	1.067	.305	.012
DS	3.564	.062	.039	2.406	.124	.027	.094	.759	.001
GFMT	4.276	.042	.046	.706	.403	.008	.394	.532	.004
VS	.003	.956	<.001	1.185	.279	.013	.045	.832	.001
CS	1.377	.244	.015	.213	.645	.002	.079	.780	.001

MR = Matrix Reasoning; DS = Digit Span; GFMT = Glasgow Face Matching Test; VA = Visual Acuity; CS = Contrast Sensitivity.

10 Appendix B – Supplementary tables for Chapter 3

Table B1: The correlation between activation and three behavioural measures (recognition accuracy, offline reaction time, and online reaction time) within regions showing significant age effects, for each expression.

Contrast	**Hemisphere**	**Region**	**MNI Coordinates**			**Correlation with expression recognition (n=30)**		**Correlation with RT for expression (offline) (n=23)**		**Correlation with RT (online) (n=30)**	
			X	*Y*	*Z*	r	p	r	p	r	p
Angry > Neutral	L	Postcentral gyrus	-42	-25	53	-0.110	0.562	0.327	0.128	0.044	0.818
	L	Anterior cingulate	-9	26	17	0.209	0.268	-0.062	0.778	0.098	0.607
	L	Precuneus	-9	-49	65	0.170	0.368	0.025	0.910	-0.101	0.596
	R	Postcentral gyrus	36	-25	56	0.034	0.859	0.082	0.710	-0.034	0.857
Fearful > Neutral	L	Superior parietal lobule	-21	-58	56	-0.277	0.138	0.132	0.548	0.080	0.674
			-21	-73	50	-0.171	0.367	-0.048	0.826	0.056	0.769
	L	Ventral Dorsal Caudate	-3	-7	-13	0.033	0.864	-0.105	0.634	-0.043	0.821
	L	Putamen	-24	2	-10	-0.089	0.641	0.054	0.808	-0.003	0.989
	R	Superior parietal lobule	21	-67	47	-0.172	0.364	-0.126	0.567	-0.081	0.670
Happy > Neutral	R	Medial precentral gyrus	12	-22	53	0.037	0.847	0.046	0.835	-0.003	0.986
	R	Lateral precentral gyrus	30	-22	56	0.077	0.685	-0.065	0.769	0.002	0.992
	L	Lingual gyrus	-27	-70	8	-0.157	0.408	0.103	0.640	0.011	0.955
	L	Middle cingulate	-15	-7	44	0.146	0.441	0.300	0.164	0.370	0.044
	R	Middle frontal gyrus	30	32	26	-0.316	0.089	0.349	0.102	0.257	0.170
	L	Precentral gyrus	-30	-22	53	0.169	0.371	-0.214	0.328	-0.019	0.919
	L	Superior parietal lobule	-24	-52	56	-0.136	0.472	0.205	0.348	0.183	0.334
	L	Middle temporal gyrus	-48	-40	2	-0.095	0.617	0.309	0.151	0.109	0.567
	R	Middle cingulate	18	8	35	-0.182	0.337	0.353	0.099	0.298	0.110
	L	Angular gyrus	-42	-55	32	0.114	0.549	0.140	0.524	0.014	0.941
	R	Medial postcentral gyrus	6	-37	62	-0.252	0.179	0.399	0.059	0.251	0.182

11 Appendix C – Supplementary tables for Chapter 6

Table C1: The mean and standard deviation of the correlation coefficients, and the results of the Wilcoxon signed tank test, for each model, for each region.

ROI	**Model**	**Mean Rho**	**S.D.**	**Z-stat**	**Alpha (FDR corrected)**	**P**
FFA	Conceptual	0.226	0.299	3.222	8.82E-03	1.27E-03
	Shape	0.139	0.266	2.619		8.82E-03
	Surface	0.013	0.267	0.353		7.24E-01
	Categorical	0.283	0.284	3.723		1.96E-04
	Perceptual	0.289	0.282	3.769		1.64E-04
OFA	Conceptual	0.239	0.351	3.063	2.19E-03	2.19E-03
	Shape	0.051	0.302	1.002		3.16E-01
	Surface	0.079	0.287	1.454		1.46E-01
	Categorical	0.262	0.293	3.610		3.07E-04
	Perceptual	0.224	0.282	3.314		9.21E-04
STS	Conceptual	0.261	0.272	3.860	6.36E-04	1.13E-04
	Shape	0.074	0.279	1.196		2.32E-01
	Surface	0.117	0.321	1.981		4.76E-02
	Categorical	0.294	0.262	3.962		7.43E-05
	Perceptual	0.278	0.304	3.416		6.36E-04
MPFC	Conceptual	0.206	0.349	2.699	8.51E-03	6.97E-03
	Shape	0.118	0.219	2.631		8.51E-03
	Surface	0.049	0.325	0.820		4.12E-01
	Categorical	0.206	0.302	2.915		3.56E-03
	Perceptual	0.250	0.266	3.632		2.81E-04

Table C2: Mean, standard deviation, and the results of the one-sample t-test for the conceptual, shape, and surface models as predictors of the representational structure in each of the 4 regions

Region	**Model**	**Mean**	**S.D.**	**Mean R^2**	**Alpha (FDR corrected)**	**T-test**
FFA	Conceptual	0.296	0.307	0.309	2.296E-05	t(27) = 5.105, p < .001
	Shape	0.092	0.243			t(27) = 1.994, p = .056
	Surface	-0.095	0.257			t(27) = -1.957, p = .061
OFA	Conceptual	0.266	0.375	0.377	8.373E-04	t(27) = 3.758, p = .001
	Shape	0.017	0.323			t(27) = 0.278, p = .783
	Surface	0.002	0.289			t(27) = 0.027, p = .978
STS	Conceptual	0.310	0.293	0.350	5.987E-06	t(27) = 5.607, p < .001
	Shape	-0.006	0.289			t(27) = -0.109, p = .914
	Surface	0.021	0.309			t(27) = 0.364, p = .719
MPFC	Conceptual	0.236	0.350	0.322	1.365E-03	t(27) = 3.570, p = .001
	Shape	0.076	0.250			t(27) = 1.610, p = .119
	Surface	-0.046	0.294			t(27) = -0.834, p = .411

Table B3: Results of the pairwise comparisons between the standardised betas for each predictor, for each region.

Region	**Alpha (FDR corrected)**	**Model comparison**	**T-test**
FFA	0.008	Conceptual-Shape	t(27) = 2.878, p = .008
		Conceptual-Surface	t(27) = 4.902, p < .001
		Shape-Surface	t(27) = 3.075, p = .005
OFA	0.017	Conceptual-Shape	t(27) = 2.535, p = .017
		Conceptual-Surface	t(27) = 2.786, p = .010
		Shape-Surface	t(27) = 0.192, p = .849
STS	0.002	Conceptual-Shape	t(27) = 4.467, p < .001
		Conceptual-Surface	t(27) = 3.455, p = .002
		Shape-Surface	t(27) = -0.275, p = .785
MPFC	0.001	Conceptual-Shape	t(27) = 1.690, p = .103
		Conceptual-Surface	t(27) = 3.557, p = .001
		Shape-Surface	t(27) = 1.724, p = .096