Integration of Emotion from Face and Body in the Human Brain

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A thesis submitted to Cardiff University
for the degree of Doctor of Philosophy

November 2023

Summary of Thesis

This thesis explores the integration of facial expression and body posture information in the human brain. Previous work has shown that facial expressions are biased by the emotion displayed by an accompanying body posture, and vice versa. However, there has been little investigation into this phenomenon beyond neurotypical adults, and there remains conflicting evidence in the literature regarding the hierarchy of integration of facial expression and body posture information in the human brain.

In **Chapter 3**, I investigated the influence of body posture on facial expression perception across the adult lifespan and found that the influence of body posture increases with age and is linked to a decrease in recognition ability for facial expressions across the lifespan. Additionally, I showed that facial expression also biases the perception of body posture across the adult lifespan, but that the degree of this influence remains stable with age.

Chapter 4 compares the influence of body posture on facial expression perception in autistic and non-autistic individuals, finding that reduced facial expression recognition in autistic individuals correlates with a heightened influence of body posture compared with the non-autistic comparison group. This suggests a similar mechanism underpinning integration of facial expression and body posture information in both autistic and non-autistic individuals.

In **Chapter 5**, I used neuroimaging techniques to explore the hierarchy of integration of face and body emotion along the visual processing pathway. I found evidence for integrated face and body emotion representations at multiple sites along the visual processing pathway, including relatively early brain regions.

In summary, the work presented in this thesis contributes to a comprehensive understanding of how emotion cues from face and body are integrated in daily life to construct coherent representations during social interactions.

Acknowledgements

I extend my deepest gratitude to Dr Elisabeth von dem Hagen for her consistent guidance and encouragement throughout my PhD journey. It has been a privilege to learn from and work alongside Elisabeth for four years, and her mentorship has been instrumental in shaping both the trajectory of my research and me as a researcher.

I am also thankful to Dr Christoph Teufel for his invaluable advice and expertise, particularly in the intricate analysis of the psychophysics involved in my empirical work. His insights significantly contributed to the depth and quality of my thesis.

Beyond my core supervisory team, Dr Punit Shah deserves a special thanks for his guidance and collaboration. His expertise in the field of Autism research enriched my work, and made the work in Chapter 4 possible.

A heartfelt appreciation goes out to all the volunteers who generously participated in my studies. I am especially grateful to my friends and colleagues who patiently sat through countless scanning sessions with me.

The completion of this journey wouldn't have been possible without the unwavering support of my loved ones. The love and patience from those close to me were the pillars that made this experience possible, and for that, I am so grateful. You all kept me sane (for the most part!), and I feel incredibly lucky to have had the opportunity to undertake such a fulfilling and challenging academic venture.

Contents

List of Figures

List of Tables

List of Abbreviations

ASD	**A**utism **S**pectrum **D**isorder
ATL	**A**nterior **T**emporal **L**obe
BOLD	**B**lood **O**xygenation **L**evel **D**ependent
EBA	**E**xtrastriate **B**ody **A**rea
EPI	**E**cho **P**lanar **I**maging
FBA	**F**usiform **B**ody **A**rea
FFA	**F**usiform **F**ace **A**rea
fMRI	**f**unctional **M**agnetic **R**esonance **I**maging
IFG-FA	**I**nferior **F**rontal **G**yrus - **F**ace **A**rea
MEG	**M**agnetoencephalography
MNI	**M**ontreal **N**eurological **I**nstitute
MRI	**M**agnetic **R**esonance **I**maging
MVPA	**M**ulti**v**ariate **P**attern **A**nalysis
OFA	**O**ccipital **F**ace **A**rea
PF	**P**sychometric **F**unction
PSE	**P**oint of **S**ubjective **E**quality
RDM	**R**epresentational **D**issimilarity **M**atrix
RF	**R**adio **F**requency
ROI	**R**egion of **O**f **I**nterest

RSA	**R**epresentational **S**imilarity **A**nalysis
STS	**S**uperior **T**emporal **S**ulcus
TPOJ	**T**emporal - **P**arietal - **O**ccipital **J**unction
WCC	**W**eak **C**entral **C**oherence

Chapter 1

General Introduction

1.1 Organisation of the human visual system

The human visual system is characterised by its hierarchical and feedforward organisation (Herzog and Clarke, 2014). Visual information processing begins in the retina, then travels, via the lateral geniculate nucleus (LGN) in the thalamus to the primary visual cortices (V1-V3), where basic visual features like lines and edges are processed. The neurons located in lower visual areas (such as primary visual cortex, V1) have smaller receptive fields and are more sensitive to basic visual features compared with neurons located in higher visual areas, such as inferior temporal cortex (IT). As information travels along the visual pathway, from lower areas to higher areas, more complex features are able to be encoded; V4 neurons encode shapes of stimuli, while the IT stage of the pathway processes high-level features like faces and objects (Fig 1.1) (Herzog and Clarke, 2014).

However, contrary to this feedforward model, which suggests that visual information flows unidirectionally from lower-level to higher-level areas, alternative evidence

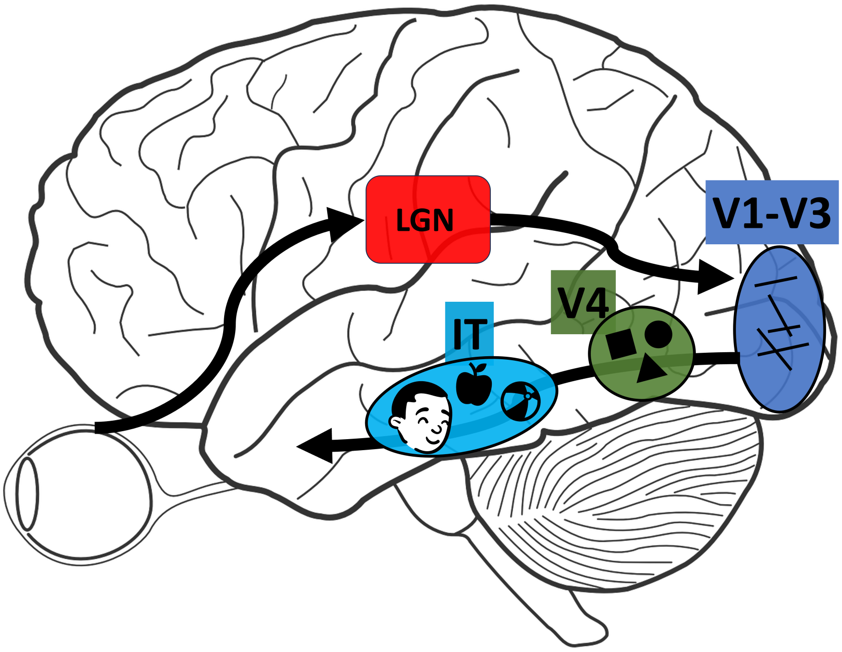


FIGURE 1.1: Hierarchical model of visual processing. This figure shows the feed forward hierarchical organisation of visual processing. Visual information comes through the retina to the LGN, then on to V1 and later visual areas. Earlier visual areas (V1-V3) code basic features like lines and edges. Information is then passed onto V4, where features like shapes can be processed. The information is then passed on to the high-level areas, such as IT, where they can encode more complex features of a stimulus, such as objects and faces.

suggests bidirectional communication between areas (Wyatte et al., 2014). For example, studies utilising techniques like transcranial magnetic stimulation (TMS) and visual backward masking have shown that recurrent feedback circuits engage in visual processing, influencing object recognition within the first 100ms of stimulus onset (Boehler et al., 2008; Mika Koivisto et al., 2011). This rapid feedback, originating within the visual stream itself, plays a crucial role in shaping perception independently of slower attention-mediated processes. This alternative view of human vision emphasises the dynamic interplay between feedforward and feedback processes, challenging the notion of vision as a purely feedforward phenomenon. Incorporating recurrent interactions between lower and higher levels of visual processing could provide a more comprehensive understanding of how visual perception is shaped by both bottom-up sensory inputs and top-down influences (Wyatte et al., 2014).

1.2 Face perception in the human brain

A quick glance at a face can provide a wealth of information on a person's identity, emotional state, attentional focus, gender, and much more. Face perception has been shown to depend on coordinated activity of multiple brain regions that respond selectively to faces (Duchaine and Yovel, 2015), which facilitates the rapid extraction of information shown by a face. An early cognitive model to characterise human face perception was formulated through evidence from neuropsychological and cognitive studies (Bruce and Young, 1986). It proposed that face processing begins with the formulation of a view-centric representation of the face, which feeds into two separate systems for both familiar and unfamiliar faces. The processing of familiar faces relies on a structural code that allows recognition despite changes in pose, expression, and lighting. Whereas the processing of unfamiliar faces relies on static facial representations, which may depend on a different processing route (Bruce and Young, 1986). A key component of this model is that recognition of identity from a face, outlined above, and facial expression recognition are processed independently from each other. The basis for the proposed separability of expression and identity information comes from studies of individuals with prosopagnosia who were able to recognise facial expressions despite impairments in identity recognition, as well as from studies of healthy individuals being able to make judgements on facial expressions irrespective of the familiarity of the face (Duchaine and Yovel, 2015).

The advent of functional MRI (fMRI) provided a neural perspective on face processing, and revealed a region in the fusiform gyrus that showed a greater response to face stimuli compared with control stimuli or non-face objects (Halgren, 2000; Haxby et al., 1999; Kanwisher et al., 1997; McCarthy et al., 1997), referred to as the 'fusiform face area' (FFA) (Kanwisher et al., 1997). The studies that initially identified this face-responsive region all included tasks that focussed on invariant aspects of face perception. However, it has been shown that the magnitude of response in the FFA is reduced when attending to changeable aspects of the face (e.g. eye gaze direction) (Hoffman and Haxby, 2000). This finding prompted the idea that the FFA may not be a one-stop-shop for face perception, but rather plays more of a role in the perception of invariant aspects of the face. The superior temporal sulcus (STS) has also been revealed as a key region in face processing (Eacott et al., 1993; Hasselmo et al., 1989; Heywood and Cowey, 1993; Hoffman and Haxby, 2000; Puce et al., 1998). An early study showed that, in the macaque brain, cells in the STS showed selectivity for facial expressions, whereas cells in IT were more selective for individual identity

(Hasselmo et al., 1989). Further evidence was provided through bilateral STS lesions in macaques resulting in unimpaired performance in face-identity matching tasks but deficits in gaze discrimination (Eacott et al., 1993; Heywood and Cowey, 1993). Studies in humans have yielded a similar pattern of results, with STS showing activation in response to viewing a face in which the eyes or mouth are moving (Puce et al., 1998), along with selective attention to gaze direction showing a stronger response in the left STS compared with selective attention to identity (Hoffman and Haxby, 2000). A further face-selective area in the occipital lobe has also shown up consistently in response to faces (Dubois et al., 1999; Gauthier et al., 2000; Halgren et al., 1999; Kanwisher et al., 1997), and is often referred to as the occipital face area (OFA). Later studies provided further evidence for a role of the OFA in face perception by showing that TMS in the right OFA, but not in adjacent regions, disrupted face perception (Pitcher et al., 2007, 2008).

Haxby and colleagues (2000) proposed a neural model for face processing, with a core system compromised of the OFA, FFA, and STS. Within their model, OFA is proposed to be engaged in the early stages of face processing and sends output to both the FFA (where invariant aspects of faces, such as identity, are represented) and the STS (where variant aspects of faces, such as expression, are represented). Beyond this core network, an extended face network was also proposed within the model, which is focussed on the extraction of other types of information from faces. For example, from the STS, information is shared with the intraparietal sulcus, involved in directing attention in accordance with gaze direction, the auditory cortex, involved in speech perception, and the amygdala/limbic system, involved in processing emotional stimuli (Duchaine and Yovel, 2015; Haxby et al., 2000). More recently, however, in light of emerging findings highlighting the complexity of face processing, it has become apparent that revisions to the Haxby model are necessary (Duchaine and Yovel, 2015). In particular, the anterior temporal lobe (ATL), which in the Haxby model is part of the extended system and was thought to be associated with the representation of biographical and autobiographical knowledge regarding a face. A review of the ATL in face processing (Collins and Olson, 2014) has suggested that the hierarchy of face-selective areas in the brain extends bilaterally from the inferior occipital gyri to the anterior temporal lobes. They argue that this whole system is essential for the accurate processing of faces, with the ATL being at the top of this hierarchy. Facial representations get more complex the further the information moves up the hierarchy, with the ATL acting as a link between viewpoint invariant face representations with features such as person-specific semantic/background knowledge (Collins and Olson, 2014). Figure 1.2 shows a revised core network system, highlighting key areas for this thesis.

Recent research has challenged the conventional view of a strict feed-forward hierarchical model where the OFA serves as a source of input for areas like FFA and STS (for review, see: Atkinson and Adolphs, 2011). The involvement of OFA in higher-level face perception abilities suggests a more interactive neural model. Studies of patients with lesions encompassing the OFA have shown preserved face-selective responses in spared regions of FFA and STS (Rossion et al., 2003; Schiltz et al., 2006; Sorger et al., 2007). Despite the absence of a typical face-selective response in OFA, these patients can discriminate faces from non-face objects, implying alternative processing routes bypassing OFA. However, impairment in tasks requiring high-level face processing, such as identifying faces based on emotional expression or sex, suggests the indispensability of OFA in these functions. Furthermore, functional connectivity analyses

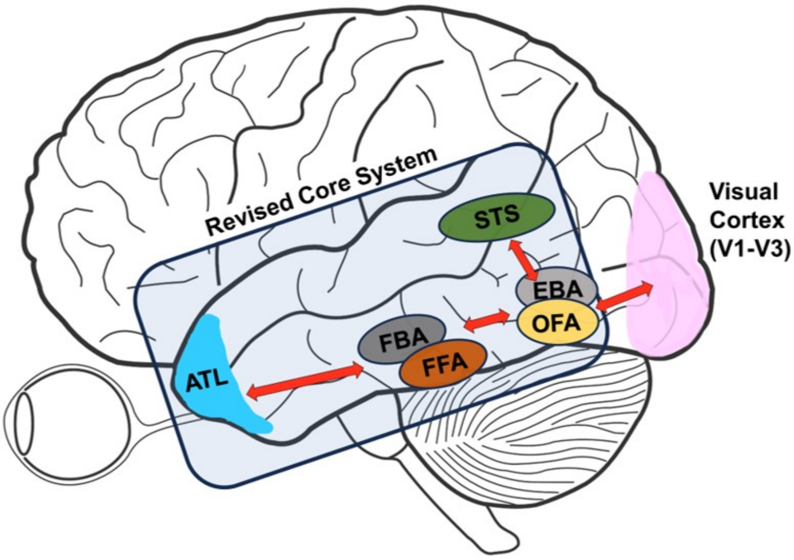


FIGURE 1.2: Adapted illustration of a revised core system from the Haxby model of face perception (Haxby et al. 2000) with the inclusion of areas involved in both face and body perception, namely the extrastriate body area (EBA) and the fusiform body area (FBA), in addition to the traditional face areas. In this model, the occipital face area (OFA) engages in early stages of face processing and sends input to the fusiform face area (FFA) and superior temporal sulcus (STS) for the processing of invariant and variant aspects of faces, respectively. The anterior temporal lobe (ATL) then acts as a link between viewpoint invariant face representations (from the FFA) and features such as person-specific semantic/background knowledge (Collins Olson, 2014).

have revealed direct connections from extrastriate cortical areas to FFA (M. Kim et al., 2006), suggesting alternative pathways for face processing independent of OFA. The intricate interactions within the face-processing network blur the distinction between "early" and "late" processing regions, making it challenging to delineate clear boundaries within the processing stream of faces.

1.3 Facial expression recognition in humans

One key feature that is extracted from faces is expression information. Facial expressions provide us with essential information about someone's emotional state, making them an essential component for social functioning in our everyday lives. There has been a wealth of research into how we recognise facial expressions of emotion, and whether the recognition of these expressions is biologically innate and universal (Darwin, 1872). There have been two leading views on the nature of facial expression recognition: the *basic view* (Ekman, 1993; Ekman et al., 1972; Izard, 1994) and the *continuous view* (J. A. Russell, 1997; J. A. Russell and Bullock, 1986). The *basic view* suggests that there are a selection of basic expressions that are universal to everyone, and that these expressions are created by specific configurations of facial muscles (Ekman, 1993; Ekman et al., 1972; Izard, 1994). This view was adapted from the work of Charles Darwin, who was the first to suggest that emotion expressions in human beings are biologically innate and evolutionarily adaptive, and therefore recognition of these expressions must be universal to all human beings (Darwin, 1872). Darwin (1872) characterised happiness, surprise, disgust, anger, sadness, and fear as being the 6 facial expressions that are universally recognised by all human beings. The *continuous view* suggests that emotions are perceived and expressed on a 2-dimensional scale of valence and arousal (J. A. Russell, 1997; J. A. Russell and Bullock, 1986). This model has two stages: first, both valence and arousal are subconsciously and rapidly read from a face. This is followed by a process in which they are translated into specific emotion categories, where the surrounding contextual information would also be integrated into perception of the face (J. A. Russell, 2003). These models, although different, are not necessarily mutually exclusive.

To gain a comprehensive understanding of how emotions are represented in the brain, it is imperative to integrate insights from both the *basic* and *continuous* views. The *continuous* view acknowledges the multidimensional nature of emotions, recognising the nuanced interplay of individual experiences and environmental factors at play during social interactions. Conversely, the *basic view* provides valuable specificity by identifying discrete facial expressions corresponding to universally recognised emotions. By combining the flexibility of the *continuous view* with the clarity of the *basic view,* we can develop a more adaptive framework for recognising emotions in diverse social contexts, which is essential for the work in this thesis. This integrated approach allows for the recognition of discrete emotions while also considering the dynamic nature of emotional experiences within wider contexts, ultimately enhancing our understanding of how emotions are processed in the brain.

The recognition of prototypical facial expressions has been well studied (e.g. A. J. Calder et al., 2000; Calvo and Lundqvist, 2008; Recio et al., 2013). These studies have found that recognition performance for all expressions is generally above 70%, with reliable discrimination among the six basic emotions (Calvo and Nummenmaa, 2016). Another common finding among these studies is that responses for happy faces were faster and more accurate compared with all other emotional faces, followed by surprised, angry, sad, disgusted, and fearful faces (Calvo and Nummenmaa, 2016). Functional MRI (fMRI) provides a neural perspective on facial expression recognition and has been used to assess whether specific brain areas show selectivity to facial expression. The posterior STS (pSTS) has been shown to play a role in the processing of facial expression (Baseler et al., 2014; Engell and Haxby, 2007). Studies have revealed that pSTS exhibits a stronger response to all basic expressions compared to neutral facial expressions, and shows sensitivity to changes in expression intensity (R. J. Harris et al., 2012).

Multivariate methods have expanded our ability to study phenomena like facial expressions by considering patterns of brain activity across multiple voxels. This approach allows us to detect distributed patterns in response to stimuli. One notable multivariate technique, known as Representational Similarity Analysis (RSA) (Kriegeskorte et al., 2008), operates by mapping data into a Representational Dissimilarity Matrix (RDM), which illustrates relative differences between pairs of stimuli. The ability to map data from any source into an RDM, makes RSA indifferent to the data source, enabling direct comparisons across multiple modalities or sources. Muukkonen et al. (2020) harnessed RSA to compare neural representations of faces using Electroencephalography (EEG) and fMRI, exploring the spatio-temporal dynamics of facial expression processing. They discovered that early EEG time windows (around 130ms) highly correlated with fMRI data from V1, while later time windows (around 190ms) correlated with data from lateral occipital, FFA, and the temporal-parietal-occipital junction (TPOJ) (Muukkonen et al., 2020). They also found that facial expression intensity was also represented in the TPOJ, suggesting that this area is involved in decoding facial expression intensity (Muukkonen et al., 2020). Expanding on this work, Muukkonen et al. (2022) employed dynamic facial expression stimuli with varying intensity and expression types. They included behavioural measures in their model RDMs, utilising participant ratings of the intensity of angry, happy, or surprised facial expressions in videoclips. This approach revealed that a region in the inferior frontal lobe, which they refer to as the inferior frontal gyrus-face area (IFG-FA), exclusively processes emotion expression intensity, whereas the OFA, STS and FFA process both expression intensity and expression type (Muukkonen and Salmela, 2022). In a related earlier study (Wegrzyn et al., 2015), a different multivariate approach, Multivariate Pattern Analysis (MVPA), was employed to investigate the neural mechanisms underlying facial expression perception. Researchers employed a classifier to assess how effectively various brain regions could decode specific expressions. The classifier was trained on responses from a specific number of trials for each facial expression, providing it with information about the patterns of brain activity associated with each expression. Subsequently, the classifier's performance was tested in each region of interest. Results revealed that the FFA, anterior temporal regions, and STS exhibited the highest classification accuracies across all expressions, suggesting that these areas are involved in the decoding of facial expressions. Collectively, these studies underscore the power of multivariate neuroimaging techniques, like MVPA and RSA, in unravelling the intricate neural processes underlying facial expression perception.

MVPA and RSA are both valuable techniques for analysing brain activity patterns, yet they serve distinct purposes. MVPA primarily aims at decoding or classifying brain activity patterns to accurately predict the category or condition of a stimulus. In essence, it focuses on making precise predictions regarding experimental conditions based on brain activity. On the other hand, RSA delves into analysing similarities between representations of stimuli in the brain using correlation-based metrics. Its primary strength lies in its ability to compare these similarities across different modalities, offering a broader exploration of neural patterns (Kriegeskorte et al., 2008). In the context of this thesis, RSA was chosen for its unique capabilities. Unlike MVPA, RSA enables comparisons across various modalities and sources of data. This choice aligns with the thesis's objective of integrating behavioural and neuroimaging components to comprehensively understand face and body emotion integration. By leveraging RSA, I could explore not only how different brain regions process facial expressions and body postures but also how these processes interact with behavioural data. This holistic approach facilitated a deeper investigation into the underlying neural mechanisms and their relationship with behavioural outcomes. Therefore, the decision to focus on RSA was driven by its capacity to provide a broader and more integrative perspective on face and body integration.

1.4 Body posture recognition in humans

Research into facial expression recognition has been extensive, but the study of emotional body language remains relatively unexplored, despite its significance in our daily interactions (De Gelder, 2006). The limited research into body posture recognition shows high recognition abilities across emotions (Atkinson et al., 2004; De Gelder and Van Den Stock, 2011; Hadjikhani et al., 2009).

Ekman (1965) conducted initial investigations into the role of bodies as conveyors of emotions (Ekman, 1965). Early studies on body perception aimed to determine whether they undergo configural processing akin to facial expressions and whether there exists a dedicated neural circuitry responsible for this function (De Gelder, 2006). A prominent method employed to investigate configural processing is the inversion effect, which revealed significantly impaired recognition of inverted bodies compared to upright ones (Reed et al., 2003; Robbins and Coltheart, 2012). Recent MRI findings indicate that cortical areas responsive to bodies exhibit a preference for processing whole-body stimuli over body parts (Brandman and Yovel, 2014). However, bodies communicate a wealth of social information, encompassing posture, movement, and emotional expression. Research into the neural networks responsible for processing this information underscores the attribute-dependent nature of neural representation (De Gelder, 2006). De Gelder (2006) proposed a conceptual framework, the ’two-systems’ model of emotion-behaviour connectivity, suggesting parallel processing through a subcortical reflex-like network and a cortical visuomotor perceptual route. These systems are interconnected with frontal regions involved in body awareness.

Initial fMRI studies (Downing et al., 2001) revealed the existence of the extrastriate body area (EBA) near the middle occipital gyrus, responding selectively to bodies and exhibiting minimal response to faces. Recent research (Brandman and Yovel, 2014; Reed et al., 2003; Robbins and Coltheart, 2012) affirmed this, showcasing the EBA’s "inversion effect", with the EBA preferentially responding to upright bodies. Further fMRI inquiries identified two more body-selective areas: the fusiform body area (FBA) and the superior temporal sulcus (STS) (De Gelder et al., 2015). Although some overlap exists between FBA and FFA, their activations to bodies and faces are distinct, with FBA primarily responding to headless or faceless bodies (Peelen and Downing, 2005). Notably, EBA activation correlates with the proportion of a body posture shown, suggesting part-based processing, while FBA’s activation increases with whole bodies, implying a different processing mechanism (J. C. Taylor et al., 2007).

The STS plays a crucial role in body processing by responding to both biological motion and static images depicting body motion. When transcranial magnetic stimulation (TMS) is applied to the STS, observers exhibit a reduced ability to recognise different body postures, underscoring the STS’s importance in recognising and distinguishing body postures in our social interactions (Candidi et al., 2011). The evidence discussed here and in the previous section on facial expressions implicates the role of the STS in both face and body processing. Specifically, research highlights specialised responses within the STS to facial expressions, gaze direction for faces, and bodily movements. For instance, anterior portions of the STS are implicated in decoding emotional cues conveyed through facial expressions, while certain subregions demonstrate sensitivity to changes in gaze direction, reflecting their role in processing social signals related to attention and intention via the face (Deen et al., 2015). Moreover, posterior portions of the STS show specialisation in perceiving and understanding bodily movements, indicating their involvement in decoding social cues conveyed through body movements. Notably, the precise boundaries between these functional subregions may vary across individuals and studies, posing challenges to achieving precise delineation between face and body stimuli.

1.5 Social cues in context

So far, I have discussed the perception of facial expressions and body postures in isolation. However, this fails to capture the reality of social perception in our everyday social lives, because these cues are usually embedded within a wider context and not encountered in isolation. Previous studies have shown the importance of context in the processing of facial expressions. For example, visual scenes in which a facial expression is shown (Lee et al., 2012; Righart and De Gelder, 2008; Righart and de Gelder, 2006; Van den Stock and de Gelder, 2012), vocal expressions accompanying facial expressions (De Gelder and Vroomen, 2000), and accompanying body posture (Aviezer et al., 2008; Meeren et al., 2005) have all been shown to influence how facial expressions are perceived. The term 'context' can take on many forms in the literature, but in the work discussed and carried out in this thesis, ‘context’ will refer to an accompanying affective body posture when making emotion judgements about a face (Chapter 3, Experiment 1; Chapter 4; Chapter 5), or an accompanying facial expression when making emotion judgements about a body (Chapter 3, Experiment 2).

Previous research has shown that the recognition of facial expressions is influenced by the body posture with which they are presented (Aviezer et al., 2008; Meeren et al., 2005). Similarly, to a lesser extent, the recognition of body posture can also be influenced by the accompanying facial expression (Lecker et al., 2020). For instance, a disgusted facial expression is more likely to be categorised as “angry” when it is displayed alongside an angry body posture, as opposed to when it is presented with a disgusted body posture (Aviezer et al., 2008). The observed interplay between facial expressions and body postures underscores the importance of studying them in tandem to gain a more comprehensive understanding of how we perceive and interpret emotional cues in real-world contexts. Meeren et al., 2005 found that when participants were asked to categorise the emotion displayed in facial expressions presented in either congruent (e.g., fearful face on a fearful body posture) or incongruent (e.g., fearful face on an angry body posture) conditions, the observers’ judgement of facial expression became biased towards the emotion displayed by the accompanying body posture. This suggests that facial expression recognition becomes biased in the direction of the emotion shown by surrounding body context. During the task, simultaneous measurements of EEG revealed that the P1 amplitude, believed to originate from early extrastriate visual areas (e.g. OFA), exhibited a notably higher magnitude in response to incongruent stimuli (Meeren et al., 2005). This suggests a swift extraction of information related to congruency between face and body cues in the visual processing pathway. Aviezer et al. (2008) also demonstrated the influence that body posture has on facial expression recognition, and investigated whether this degree of influence is modulated by the perceptual similarity between the facial expression and associated body posture. They discovered that anger and disgust emotions were most perceptually similar, leading observers to more frequently judge a disgusted face as the emotion conveyed by the body when it was shown in the context of an angry body posture compared to sad or fearful postures (Aviezer et al., 2008). In this 2008 study, the concept of perceptual similarity was derived from Susskind et al. (2007). In this 2007 study, they utilised computational modelling to investigate how the human brain distinguishes between different facial expressions. Their findings revealed that distinct brain regions aid in recognising individual emotions while also detecting similarities between expressions. This implies that the visual resemblance of two expressions can impact our emotional comprehension of them. The computational model proposed by the researchers suggested that facial expression similarity may arise from shared visual features rather than emotional or somatic factors (Susskind et al., 2007). This differentiation clarifies their discussion of perceptual similarity from valence similarity, which focuses on the emotional polarity of expressions, and expression ambiguity, which pertains to interpretational variability. In this thesis, taking perceptual similarity into account during stimulus creation was essential. Maintaining perceptual similarity between the original facial expressions and their morphed transitions was vital for crafting stimuli that accurately conveyed the intended emotions. By incorporating perceptual similarity into the morphing procedure, I could capture the subtle nuances of facial expressions with precision, enabling a detailed exploration of how contextual cues interact with perceptual features to shape emotional interpretation. Ultimately, integrating perceptual similarity into the morphing process boosts the ecological validity of the stimuli and enhances the validity and reliability of the research findings presented in this thesis.

Lecker et al., 2020 explored the bidirectional nature of this influence by studying how facial expressions impact body posture categorisation. This study involved isolated facial expressions, body postures, and whole person stimuli, with observers making emotional judgements on these stimuli. The results demonstrated mutual influence between faces and body postures, with facial expressions being more susceptible to contextual influence than body postures (Lecker et al., 2020)).

Individuals vary in performance in cognitive tasks (Boogert et al., 2018), with facial expression recognition ability being no exception (Palermo et al., 2018). These variations can provide insight into the cognitive mechanisms underlying the variations between individuals, as they often reflect real perceptual, visual and neural differences that modulate perception (Boogert et al., 2018). Demonstrating the importance of studying these individual differences in perception, Ward et al. (*in prep*) revealed that the degree of body posture's influence on facial expression recognition was linked to an observer's ability to discriminate isolated facial expressions. The study demonstrated that a lower precision in isolated facial expression representations led to a stronger influence of body posture on facial expression perception (Ward et al. *in prep*). This result suggests a potential mechanism regulating the extent of body posture's influence on facial expression perception.

Understanding the integration of face and body cues is crucial because it can illustrate how our brains process sensory inputs to construct our perception of the world. It remains unclear how these emotional signals are integrated in the human brain. There are conflicting accounts regarding the stage of the visual processing hierarchy where integration takes places, with some suggesting an early site for integration (Aviezer et al., 2008, 2011; Foster et al., 2021, 2022; Meeren et al., 2005; Pitcher et al., 2012) and others suggesting a later site (Fisher and Freiwald, 2015; Harry et al., 2016; Hu et al., 2020; Song et al., 2013; Teufel et al., 2019). For example, in support of early integration, behavioural findings have demonstrated the influence of body posture remains consistent even when a concurrent memory task is introduced alongside the categorisation task described in Aviezer et al., 2008 (Aviezer et al., 2011), suggesting that the integration of these cues takes place automatically at an early site along the processing pathway. Conversely, evidence for later integration is supported by research showing that adaptation to facial expressions is unaffected by accompanying body posture (Teufel et al., 2019). This indicates a later site for integration of these cues because adaptation is thought to occur in later visual areas (like FFA), with these cues only being integrated after this adaptation site in the visual processing pathway.

Neuroimaging studies investigating the integration of face and body cues have also yielded mixed results, with Peelen et al., 2010 finding evidence for STS encoding emotional information regardless of cue modality while Harry et al., 2016 only identified common coding of face and body cues in the ATL. However, Song et al., 2013 found increased neural responses in the FFA, but not the OFA for face-body stimuli. To reconcile these discrepancies, a distributed model for face and body integration offers a more nuanced perspective Foster, 2022, which emphasises distinct brain regions being responsible for integrating different properties of a stimulus (e.g. identity, expression). This leaves conflicting accounts, across behavioural and neuroimaging studies, regarding the hierarchy of integration for face and body cues. This highlights a need to develop a more detailed and nuanced account for how these cues are combined along the visual processing pathway, with the focus of this thesis being on emotion signal integration.

1.6 Emotion Perception Overview

The recognition of facial expressions and body postures plays a crucial role in our social interactions, providing essential cues about others' emotional states and intentions. The *basic view* (Ekman, 1993; Ekman et al., 1972; Izard, 1994) the *continuous view (J. A. Russell, 1997)* offer two complementary perspectives on how we interpret these cues, with the former highlighting discrete, universally recognised expressions and the latter emphasising the multidimensional nature of emotions. Combining insights from both views allows for a more adaptive framework for understanding emotional perception, acknowledging both the specificity of basic expressions and the contextual nuances conveyed through continuous dimensions of valence and arousal. Examination of the neural mechanisms underlying facial expression perception revealed several key brain regions. Studies utilising multivariate techniques like MVPA and RSA have shed light on these areas. The fusiform face area (FFA), anterior temporal regions, and superior temporal sulcus (STS) have consistently shown high classification accuracies across different expressions in MVPA studies (Wegrzyn et al., 2015). Meanwhile, RSA analyses have revealed correlations between facial expression processing and regions such as the inferior frontal gyrus-face area (IFG-FA), occipital face area (OFA), and the temporal-parietal-occipital junction (TPOJ) (Muukkonen and Salmela, 2022; Muukkonen et al., 2020). These findings underscore the involvement of these brain regions in decoding and representing facial expressions, emphasising their significance in facial expression perception.

The exploration of emotional body language remains underdeveloped compared to facial expression recognition, despite its significance in daily interactions. Early investigations by Ekman (1965) paved the way for understanding how bodies convey emotions, leading to studies on configurable processing and dedicated neural circuitry, exemplified by the inversion effect (Reed et al., 2003; Robbins and Coltheart, 2012) and MRI findings on cortical areas like the extrastriate body area (EBA) and the fusiform body area (FBA). Recent research highlights the role of the superior temporal sulcus (STS) in processing body cues, including its involvement in decoding emotional cues and bodily movements (Candidi et al., 2011). However, challenges persist in delineating functional subregions within the STS and understanding the precise mechanisms of face and body processing.

The investigation into facial expressions and body postures in isolation fails to capture the complexity of social perception in everyday interactions. Previous studies emphasise the significant influence of context on facial expression recognition (Aviezer et al., 2008; Meeren et al., 2005), highlighting the importance of studying these cues together. Research demonstrates a bidirectional influence between facial expressions and body postures (Lecker et al., 2020), with context shaping the perception of both cues. Individual differences in cognitive abilities also modulate the extent of this influence, suggesting a mechanism regulating the integration of face and body cues. However, conflicting accounts exist regarding the stage of integration (e.g., Foster et al., 2021; Harry et al., 2016; Meeren et al., 2005; Song et al., 2013) in the visual processing hierarchy, necessitating further research to develop a nuanced understanding of how these cues are combined in the brain. Overall, this thesis contributes to the ongoing exploration of emotion signal integration, offering insights into the intricate mechanisms underlying social perception.

1.7 Facial expression recognition across adult lifespan

Previous research has consistently shown a decline in facial expression recognition abilities as individuals age (A. J. Calder et al., 2003; Mill et al., 2009; Olderbak et al., 2019; Ruffman et al., 2008; Rutter et al., 2019; Sasson et al., 2010; West et al., 2012). These age-related deficits could potentially be attributed to general cognitive decline, as some studies have indicated a link between general intelligence and expression recognition (Hildebrandt et al., 2015; Lewis et al., 2016; Schlegel and Scherer, 2016). However, a recent study (Connolly et al., 2021) delved into the relationship between facial expression recognition, facial identity recognition, and general intelligence across a broad age range (18 to 88 years). Their findings revealed that, while all three measures declined with age, the decline in expression and identity recognition persisted even when controlling for general intelligence. This suggests that cognitive decline may not entirely account for these age-related decrements in face perception (Connolly et al., 2021).

Despite a general deficit in facial expression recognition in older adults, the degree of impairment varies for different emotions (A. J. Calder et al., 2003; Noh and Isaacowitz, 2013; Ruffman et al., 2008). Older adults have been shown to struggle with recognising negative emotions such as anger, sadness, and, to a lesser extent, fear (D. M. Isaacowitz et al., 2007). It is important to consider factors such as potential attention bias in older adults, particularly in their inclination towards positive emotions (D. Isaacowitz et al., 2006; Mather and Carstensen, 2003; Ruffman et al., 2008). Some studies suggest that older adults may initially avoid negative information in their attention processing (Mather and Carstensen, 2003). Contrary to this though, a meta-analysis revealed that older adults actually frequently exhibit lower accuracy when judging positive emotional faces but not when judging disgusted faces (Ruffman et al., 2008). These results challenge the idea that older adults only show deficits when judging negative emotions, or that there is a broad positivity bias driving age-related recognition differences. To gain a more precise understanding of how these deficits manifest in older adults, it is important to utilise stimuli that more closely reflect the way in which stimuli are encountered in daily life. In this regard, it is essential to also consider older adults' ability to recognise body postures and their perception of integrated face and body representations compared to younger adults. This will aid in gaining a clearer picture of how emotion perception from face and body cues varies across the adult lifespan.

1.8 Body Posture Recognition Across Adult Lifespan

The majority of research on emotion perception throughout the adult lifespan has primarily focussed on facial expression recognition abilities as people age. However, the limited exploration of how age impacts the recognition of emotional body postures suggests that there is a similar decline in this ability, akin to what is observed in facial expression recognition (Abo Foul et al., 2018; Montepare et al., 1999; Ruffman et al., 2009). Montepare et al., 1999 examined older and younger adults' judgements of dynamic emotional body gestures and movements. They found that both younger and older adults were able to recognise all emotions portrayed by the stimuli above chance level, but older adults consistently showed lower accuracy, particularly when viewing negative emotions (Montepare et al., 1999). Similarly, Ruffman et al., 2009 asked younger and older adults to make emotional judgements on dynamic body movement stimuli. In this study they showed that younger adults had higher accuracy when identifying angry and happy body movement compared to older adults, but no significant difference was observed between the two groups when recognising sadness, fear, or disgust (Ruffman et al., 2009).

1.9 Influence of Context Across Adult Lifespan

To my knowledge, only two studies have looked at the influence of body posture on facial expression perception in older adults compared with younger adults (Abo Foul et al., 2018; Noh and Isaacowitz, 2013). Noh and Isaacowitz, 2013 measured recognition of facial expressions, as well as scanning patterns, of older and younger adults viewing angry or disgusted facial expressions in either neutral, congruent, or incongruent conditions. They found that older adults were influenced more by body context than younger adults, and that older adults were more likely to fixate on the context region of the stimulus in the initial moments of stimulus presentation (Noh and Isaacowitz, 2013). Abo Foul et al., 2018 built upon this previous work and presented participants with incongruent face-body composites displaying sadness, anger, fear, and happiness. They found that older adults were more influenced by body posture than the younger adults in their sample, which they suggest is down to an increased social expertise in older adults (Abo Foul et al., 2018; Hess, 2006). Their social expertise account states that older adults show adaptive social functioning as a result of their cumulative social experience over the lifespan, which leads them to prioritise the 'whole picture' when perceiving a social stimulus (Hess, 2006).

However, an alternative explanation for the heightened influence of body posture in older adults could be linked to the well-documented decline in facial expression recognition abilities with age (A. J. Calder et al., 2003; Mill et al., 2009; Olderbak et al., 2019; Ruffman et al., 2008; Rutter et al., 2019; Sasson et al., 2010; West et al., 2012). Ward et al., 2023 looked at facial expression discrimination abilities and the influence of body posture on facial expression perception in children and adolescents. They found a decreased influence of body posture as children got older, which was concurrent with an increase in facial expression discrimination ability. This raises the possibility that a comparable mechanism may be governing the influence of body posture among older adults, with the decline in facial expression recognition ability leading to a heightened reliance on body posture. To further explore this possibility, it is essential to study recognition ability in older adults using more subtle expression stimuli. This approach would provide the necessary sensitivity in measurements to detect individual differences among observers. These subtle differences in facial expression recognition ability could then be linked to the extent of influence that body posture subsequently exerts on the perception of facial expressions.

1.10 Emotion Perception Across Adult Lifespan Overview

Previous research consistently indicates a decline in facial expression recognition abilities as individuals age (e.g., A. J. Calder et al., 2003; Mill et al., 2009; Olderbak et al., 2019). Despite potential links between general intelligence and expression recognition, recent findings suggest that cognitive decline may not entirely explain age-related decrements in face perception (Connolly et al., 2021). Interestingly, while older adults generally struggle with recognising negative emotions, such as anger and sadness, their perception of emotion varies across different emotions (A. J. Calder et al., 2003; Noh and Isaacowitz, 2013; Ruffman et al., 2008). Factors like attention bias towards positive emotions may influence these patterns. Utilising stimuli reflecting real-world encounters is crucial to understanding how emotion perception varies across the adult lifespan, including the recognition of body postures and integrated face-body representations.

Research suggests a decline in the recognition of emotional body postures with age (Abo Foul et al., 2018; Montepare et al., 1999; Ruffman et al., 2009), similar to facial expression recognition. Older adults consistently show lower accuracy, particularly when identifying negative emotions portrayed by dynamic body movements. While studies have primarily focused on facial expression recognition, examining emotional body posture recognition across the lifespan provides valuable insights into age-related changes in emotion perception.

Studies investigating the influence of body posture on facial expression perception in older adults reveal intriguing findings (Abo Foul et al., 2018; Noh and Isaacowitz, 2013). Older adults appear to be more influenced by body context than younger adults, possibly due to increased social expertise or a decline in facial expression recognition abilities. Understanding the mechanisms underlying the heightened influence of body posture in older adults necessitates further exploration, particularly regarding the relationship between facial expression discrimination ability and the extent of body posture influence.

1.11 Facial expression recognition in Autism

Autism is characterised as a pervasive developmental disorder identified by the onset of difficulties in social interactions, communication, and engaging in repetitive patterns of behaviours, interests, and activities (Lai et al., 2014). To capture the dimensional nature of this developmental disorder, the term 'autism spectrum disorder' (ASD) is often used (American Psychiatric Association, 2013). However, throughout this thesis, the terminology 'Autism' and 'autistic individuals' will be used, to align with the preferred terminology within this population (Bury et al., 2020; Kenny et al., 2016; Lei et al., 2021). The worldwide prevalence of Autism is estimated to be 1-2%, with males being affected at a rate of 2-3 times higher than females (Baron-Cohen et al., 2009; Hsu et al., 2012; Idring et al., 2012; Y. S. Kim et al., 2011; Mattila et al., 2011; G. Russell et al., 2014; Saemundsen et al., 2013). The increased prevalence of Autism in males may be attributed, in part, to camouflaging observed in autistic females. Camouflaging involves compensating for their symptoms, particularly social ones, and can manifest at any point in development (Livingston and Happé, 2017), which can result in delayed diagnoses compared to males (Baron-Cohen et al., 2013). Autistic individuals often exhibit challenges in understanding social cues and communication (American Psychiatric Association, 2013). Researchers have investigated their ability to recognise emotions, as difficulties in grasping emotional signals from face and body cues could be a contributor to their social difficulties. Previous research has found a reduction in autistic individuals' facial expression recognition ability compared to non-autistic comparison groups (Ashwin et al., 2006; Corden et al., 2008; Howard et al., 2000; S. Wallace et al., 2008). Notably, there have also been studies that have found no differences between autistic individuals and non-autistic comparison groups (Adolphs et al., 2001; Neumann et al., 2006; Ogai et al., 2003). This conflict in results may arise from factors such as alexithymia (Keating and Cook, 2020), underdeveloped mechanisms for recognising facial expressions (Lozier et al., 2014), differences in stimuli used (such as expressions of non-autistic individuals being used in most cases, rather than expressions from autistic individuals), stimulus intensity, and other variables such as age or IQ (Keating and Cook, 2020).

The variability in the intensity of facial expressions utilised in studies may contribute to the inconsistent findings regarding differences in facial expression recognition abilities between autistic individuals and non-autistic comparison groups. Previous research has emphasised that the intensity of facial expressions presented as stimuli can significantly impact recognition abilities (Ogai et al., 2003; G. L. Wallace et al., 2011; N. Wong et al., 2012). Support for this comes from studies using 100% intensity/prototypical facial expressions finding no difference in recognition ability in autistic individuals compared with non-autistic individuals (Baron-Cohen et al., 1997; Castelli, 2005; Fonseca et al., 2009; Jones et al., 2011; Neumann et al., 2006), whereas a recent study by Wang and Adolphs et al., 2001 used facial expressions morphed between fear and happiness, and found that autistic individuals had reduced recognition abilities compared to a non-autistic comparison group. This could be a potential reason for the discrepancy we see in the literature, with sensitivity in measurement methods being a crucial element to capture these differences.

1.12 Body posture recognition in Autism

A large focus has been placed on how autistic individuals differ in terms of facial expression recognition, but to understand the root of their difficulties in social communication it is important to also consider body posture recognition ability in this population. Research so far into the recognition of body posture in autistic individuals compared with non-autistic individuals has garnered mixed results (Mazzoni et al., 2022). In a 2014 study (Libero et al., 2014) stick figures representing either actions or emotions were presented to a group of autistic individuals and a group of non-autistic individuals. Participants were asked to determine either what action the figure was performing or what emotion it conveyed, depending on the condition presented. Interestingly, the results showed no significant differences in accuracy or reaction times between the group of autistic individuals compared with the non-autistic comparison group (Libero et al., 2014). An earlier study (Hadjikhani et al., 2009) required both autistic and non-autistic individuals to match body stimuli representing emotions (emotion condition) or actions (neutral condition) without facial expressions. The results of this study showed that non-autistic individuals outperformed autistic individuals in matching neutral body postures, but that the opposite was true for performance in matching emotional body posture (Hadjikhani et al., 2009). This finding suggests that reduced matching abilities in the autistic individuals are specific to emotional stimuli, due to non-autistic individuals only showing improved matching abilities for the emotional stimuli and being outperformed by the autistic group for neutral stimuli.

1.13 Social cues in context in Autism

Facial expression recognition for isolated faces in autistic individuals is important to understand in the context of the social/communication difficulties that are seen in those with Autism (American Psychiatric Association, 2013). However, as mentioned previously, faces are rarely encountered in isolation, making the influence of surrounding context equally, if not more, important to investigate in autistic individuals to further understand the social/communication differences associated with this diagnosis.

Frith (1989) introduced ‘central coherence’ to refer to the tendency of non-autistic individuals to process sensory information in a holistic manner, focussing on the big picture over the details. This differs in autistic individuals, who exhibit ‘weak central coherence’ (WCC), prioritising a more local processing style for stimuli, rather than a global one. Evidence for WCC, or a more local processing style, is seen through autistic individuals showing better performance in the embedded figures task compared with non-autistic observers (Ropar and Mitchell, 1999). Further evidence for WCC in autistic individuals comes from studies that found them to be less susceptible to visual illusions than non-autistic individuals (F. G. Happé, 1996; Ropar and Mitchell, 1999, 2001).

Notably, this tendency towards a local processing style in autistic individuals does not extend to face stimuli however, with autistic individuals showing an intact face inversion effect (Tavares et al., 2016; Weigelt et al., 2012), and typical performance in the parts-whole task compared with non-autistic individuals (Weigelt et al., 2012), suggesting intact holistic processing in Autism. This discrepancy between the weak central coherence shown in autistic individuals for non-face stimuli compared with the global style adopted for face stimuli becomes interesting when considering how surrounding context may influence how autistic individuals perceive a facial expression compared with non-autistic individuals. To my knowledge, only one study has investigated the influence of body context on facial expression perception in autistic individuals. This study (Brewer et al., 2017) found that body posture had a significant influence on facial expression categorisation for both the autistic group and the non-autistic group of observers, with no difference in the degree of influence between the groups (Brewer et al., 2017). This result is interesting because previous research has shown that the degree of influence that body posture has on facial expression perception in typical adults is linked to discrimination ability for isolated facial expressions, with a lower discrimination ability leading to a higher influence of body posture (Ward et al. *in prep*). In the Brewer et al., 2017 study, they found no difference in the recognition of facial expressions when comparing autistic observers to non-autistic observers. If the mechanisms regulating the integration of face and body cues in autistic individuals are the same as those in non-autistic individuals, then the absence of differences in how body posture influences facial expression perception between these groups could be accounted for by their comparable abilities to recognise isolated facial expressions in this study.

Considering the existing understanding of autistic individuals' tendency towards local processing and the link between facial expression discrimination and body posture influence in non-autistic individuals, two conflicting perspectives arise regarding the role of body posture in Autism. The first suggests that the observed lower facial expression discrimination in Autism might heighten the influence of body posture, potentially explaining the absence of differences found in a previous study (Brewer et al., 2017), which also reported no distinction in facial expression recognition between autistic and non-autistic groups. The second perspective proposes that the local processing tendency in Autism may diminish the influence of body posture. Resolving this ambiguity is important for a deeper understanding of how social challenges manifest at a perceptual level among autistic individuals. It is key to determine whether this mechanism operates in a similar fashion to what has been shown previously in non-autistic children and adolescents (Ward et al., 2023), and non-autistic adults (Ward et al. *in prep*).

1.14 Emotion Perception in Autism Overview

Autism, characterised by challenges in social interactions and communication, often involves difficulties in recognising emotions from facial expressions (Lai et al., 2014). While some studies report reduced facial expression recognition abilities in autistic individuals compared to non-autistic groups (e.g., Ashwin et al., 2006), others find no significant differences (e.g., Adolphs et al., 2001). Factors such as alexithymia, stimulus intensity, and methodological variations may contribute to these discrepancies. Sensitivity in measurement methods, particularly regarding the intensity of facial expressions presented, is crucial for accurately capturing differences in recognition abilities (Keating and Cook, 2020).

Understanding body posture recognition in autistic individuals complements research on facial expression recognition. Mixed findings exist in this domain (Mazzoni et al., 2022), with some studies showing no significant differences between autistic and non-autistic groups in recognising emotions conveyed through body postures (Libero et al., 2014). However, autistic individuals may exhibit specific difficulties in matching emotional body postures compared to neutral ones, highlighting the importance of considering different types of stimuli in research on social perception in Autism.

While isolated face perception in autistic individuals has been studied, the influence of surrounding context, like body posture, is equally important to investigate. Autistic individuals typically exhibit a "weak central coherence" favouring local processing over global perception (F. G. Happé, 1996; Ropar and Mitchell, 1999, 2001). However, this does not extend to facial stimuli, where holistic processing appears intact. One study found that body posture significantly influences facial expression categorisation in both autistic and non-autistic individuals, suggesting similarities in integration mechanisms (Brewer et al., 2017). Conflicting perspectives emerge regarding the role of body posture in autistic individuals compared to non-autistic individuals: whether it heightens or diminishes its influence in these groups due to differences in facial expression discrimination and/or processing styles. Clarifying this ambiguity is crucial for understanding social challenges among autistic individuals at a perceptual level.

1.15 Aims and overview of thesis

This thesis investigates the integration of facial expression and body posture information in the brain. Specifically, the thesis first studies the mechanisms underpinning the influence of body posture on facial expression perception across the lifespan and among autistic individuals, and secondly investigates the hierarchy of integration of face and body emotion signals along the visual processing pathway.

In **Chapter 3** Experiment 1, I evaluated observers spanning the adult lifespan in their discrimination abilities for isolated facial and body emotion cues, as well as their susceptibility to the influence of body posture on facial expression perception. Experiment 2 in this chapter replicated Experiment 1 but focused instead on how facial expressions influence body posture perception across the adult lifespan. The central question in this chapter addresses whether an individual's discrimination abilities for isolated facial expressions and body postures can explain variations in the influence of body posture (Experiment 1) or facial expression (Experiment 2) across the adult lifespan. Experiment 1 revealed that the influence of body posture on perception increases with age, and this increase is associated with a decline in facial expression discrimination ability with age. In Experiment 2, I found a reciprocal relationship, with facial expressions also influencing the perception of body posture, although to a lesser extent. Interestingly, I found that the influence of facial expression on body posture remains consistent across the adult lifespan in Experiment 2. This constancy could possibly be attributed to stable discrimination abilities for isolated body postures observed in this experiment.

In **Chapter 4**, autistic and non-autistic individuals were compared in their discrimination abilities for isolated facial expressions and isolated body postures, and in their susceptibility to the influence of body posture on facial expression perception. The central question revolves around whether the reduced facial expression recognition in autistic individuals results in a more pronounced contextual influence, akin to non-autistic individuals. The findings of this chapter revealed that autistic individuals exhibited lower discrimination abilities for facial expressions compared to the non-autistic comparison group, and crucially, this reduced ability was associated with a greater influence of body posture in autistic individuals. This suggests that the influence of body posture on facial expression perception in autistic individuals is modulated by their isolated facial expression discrimination abilities, consistent with previous research in non-autistic adults (Chapter 3, Experiment 1; Ward et al. *in prep*), children, and adolescents (Ward et al., 2023).

In **Chapter 5**, I addressed the hierarchy of integration of face and body emotion information along the visual processing pathway. By using a combination of RSA, fMRI, and perceptual discrimination data, I found evidence for integrated face and body emotion representations in the FFA, STS, and ATL. These findings indicate that such integrated representations arise relatively early in the processing pathway rather than being confined to later stages of visual processing.

Chapter 2

General Methods

2.1 Behavioural data collection

The quantification of the relationship between physical stimuli and their subjective perception was first termed ‘psychophysics’ by Gustav Theodor in 1860 (Kingdom and Prins, 2009). Psychophysics is a sub-discipline of Psychology and has been crucial in studying early sensory systems (Read, 2015), which has facilitated knowledge in how to accurately quantify the relationship between the physical (objective) world and human perception (subjective) (Lu and Dosher, 2013). In this thesis, psychophysical methods were used to measure the sensitivity of the visual perceptual system, specifically to measure discrimination of emotion signals from the face and body.

In this thesis, I employ the psychophysical approach to investigate the precise relationship between physical stimuli and the resulting changes in an observer′s perception. The primary tool for my analysis is the Psychometric Function (PF). By systematically manipulating physical stimuli and measuring the subsequent alterations in perception, I gain insight into the connection between input and percept. This research employs these measurements to explore specific perceptual processes, such as social perception, emotional categorisation, and the integration of cues from both facial expressions and body postures. My goal is to discern how these processes vary across different populations, including individuals across the adult lifespan, neurotypical adults, and autistic individuals. Additionally, I integrate neuroimaging techniques to study how the integration of facial expressions and body postures occurs within the visual processing pathway. To facilitate a deeper understanding of the psychophysical measures obtained in this thesis, I will provide a brief overview of the various components of a PF.

A PF relates quantitative stimulus properties to the probability of a particular percept (Read, 2015) and can be characterised by four parameters: the threshold (α), slope (β), guess rate and lapse rate (Kingdom and Prins, 2009). The threshold (α) and slope (β) are the two parameters of interest in characterising the underlying sensory mechanisms involved in perception throughout this thesis. Both parameters can be seen with an example PF below (Fig 2.1). The Point of Subjective Equality (PSE) is the measure of (α) used throughout this thesis. The PSE depicts the stimulus level (e.g. facial expression morphs from anger to disgust) at which the stimulus is equally likely to be perceived as either stimulus category (e.g. anger or disgust).

(β), the slope of the PF, represents the rate of change in an observer's responses. The guess rate, representing the likelihood of participants making random or uninformed responses, is crucial in tasks involving ambiguous stimuli, where participants may resort to guessing rather than relying solely on perception (Kingdom and Prins, 2009).

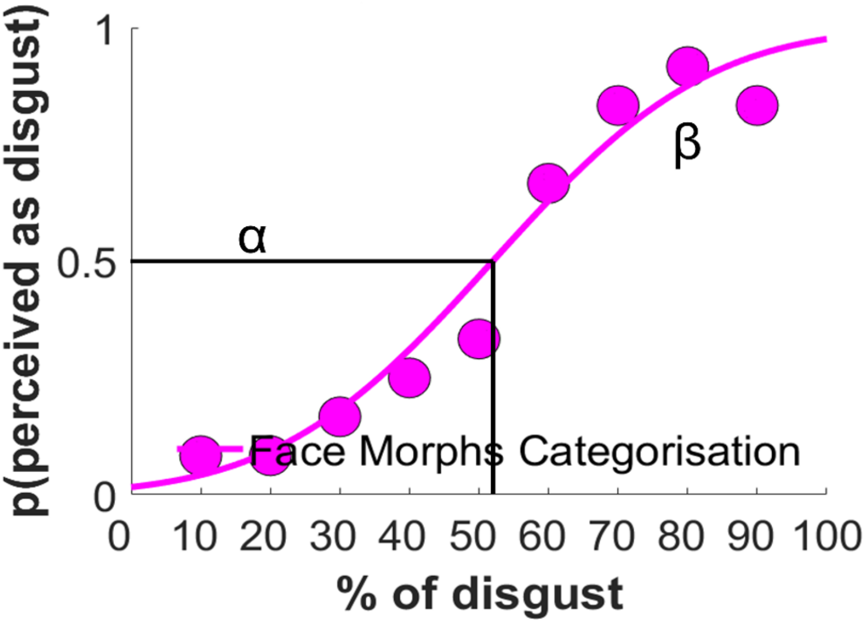


FIGURE 2.1: Example of Psychometric Function with threshold (α) and slope (β), two key measures from a psychometric function.

The lapse rate characterises the observer's tendency to respond independently of the stimulus. In the experimental procedures outlined in this thesis, the guess rate was determined through the employed paradigm, while the lapse rate was set at 0.03. This choice was informed by simulations demonstrating the enhanced robustness of fitting procedures with low fixed lapse rates, such as the one utilised in this thesis (Kingdom and Prins, 2009).

In order to acquire the data needed to create the PFs for each observer from an online platform, I used the Methods of Constants (Laming & Laming, 1992). This is a psychophysical technique, first described in 1860 (Fechner, 1860), used to determine the threshold at which a stimulus becomes detectable. It involves presenting a set of stimuli spanning a range of intensities multiple times in a random order to the participant. I had to create a behavioural task that was compatible with the JavaScript syntax and functionalities required to host the experiment online. Although JavaScript libraries have now been developed to run a selection of adaptive procedures online (Kuroki and Pronk, 2022), these were not available during the time period in which I was creating my online psychophysical research. In the Methods of Constants, the level of a certain property of a stimulus (e.g. facial expression morph) are not related from one trial to the next, but are instead presented randomly (Gescheider, 1997). In my study, the number of repetitions of each stimulus were kept constant between participants, which allowed an accurate detection threshold for each stimulus to be obtained. This method prevents the observer from being able to make predictions about the next stimulus that will be presented, and as a result the rates of expectation and habituation in the observer will be reduced. This method allows for a full sampling of the PF. Although this method is ideal for reducing habituation/expectation rates in observers, it does require a larger number of trials, and therefore longer experiment duration, compared to an adaptive procedure.

Psychophysical methods, as described here, give researchers a means to quantify human perception of the visual world. These tools are essential for determining how sensory information is encoded and how this sensory information is represented in perceptual judgements. The changes seen across varying stimulus intensity are related to changes in how sensory neurons encode that physical stimulus, making this methodology very valuable in both quantifying perception and providing insight into related brain function.

2.2 Magnetic Resonance Imaging

Magnetic Resonance Imaging (MRI) relies on the principles of nuclear magnetic resonance, which involves the behaviour of hydrogen nuclei (protons) within the body. To understand how MRI works, it is important to first outline the properties of Hydrogen (H1) atoms and the Larmor frequency (Tubridy and McKinstry, 2000). Hydrogen atoms are abundant throughout the human body in the form of water and various organic molecules. Each nucleus in these hydrogen atoms exhibits a property known as 'precession' (Westbrook and Talbot, 2018). In this context, precession refers to the continuous circular or spinning motion of the proton's magnetic moment around the direction of an applied magnetic field (B0). The precession occurs at a rate known as the Larmor Frequency, which is a fundamental parameter in MRI. The Larmor Frequency is essential in MRI as it determines the resonance condition required for the system to absorb and emit radiofrequency (RF) energy. When an RF pulse is applied to the system at the Larmor Frequency, it causes protons to temporarily shift from their aligned state, generating RF signals as they return to equilibrium. These RF signals are then detected and recorded by the MRI scanner's receiver coils, forming the basis of the MR signal, which is further processed to create detailed anatomical images. It is important to note that protons in different tissue types relax at different rates after the RF pulse is applied. This phenomenon, known as relaxation, is what provides the contrast in MR images. By exploiting variations in relaxation times, MRI can distinguish between different types of tissue.

To construct an MRI image, magnetic field gradients are applied in addition to the primary B0 field. These gradients create variations in the resonance frequency based on their location, essentially "tagging" different areas within the body. This tagging selectively excites a region of tissue and introduces variations in frequency and phase within that area. These variations allow for the creation of a three-dimensional image sensitive to the local magnetic environment, which reflects different tissue properties.

2.3 Functional MRI (fMRI)

Functional MRI (fMRI) relies on the magnetic properties of blood, specifically the differences in magnetic susceptibility between oxygenated and deoxygenated blood, to detect changes in brain activity. This technique, known as Blood Oxygenation Level-Dependent (BOLD) imaging, was first described in the early 1900's and is now widely used to non-invasively capture spatial changes in neural activity in the brain (Ogawa et al., 1990). Oxygenated blood, known as oxyhaemoglobin, is formed during respiration when oxygen binds to the haemoglobin component of red blood cells. It has no unpaired electrons in this oxygenated state. However, when oxygen is released and deoxyhaemoglobin is formed, the molecule becomes strongly paramagnetic due to the presence of unpaired electrons. This results in a difference in the magnetic susceptibility of the blood compared to the surrounding brain tissues, leading to variations in the MR signal decay (Glover, 2011). When a specific region of the brain is activated, both the local cerebral blood flow and oxygenation concentration change. These alterations lead to differences in the MR signal decay. It's crucial to understand that BOLD contrast is not solely determined by blood oxygenation; it also depends on physiological factors such as blood flow, volume, and vasculature (Arthurs and Boniface, 2002). Early research has indicated a linear relationship between changes in BOLD responses and underlying neural activity (Logothetis, 2003). Furthermore, studies that simultaneously record electrophysiological data and fMRI data have demonstrated that BOLD changes correspond to the neural changes induced by a stimulus (Hillman, 2014).

2.4 Representational Similarity Analysis

Traditional univariate neuroimaging methods have been fundamental in the study of neural activity, primarily concentrating on assessing overall differences in brain activity between various experimental conditions. Univariate methods provide valuable insights into the average or amplitude of brain activity in response to different experimental conditions. However, these methods may not capture the nuanced patterns of activity that are linked to behaviours and cognitive processes in brain regions. Recently, there has been a shift towards multivariate approaches, such as representational similarity analysis (RSA) (Kriegeskorte et al., 2008). RSA allows researchers to explore the intricate dynamics of brain networks and better relate brain activity patterns across multiple voxels to behaviours and cognitive functions. RSA permits an examination of the nuanced differences in how the brain represents various stimuli within different regions. The core of RSA involves creating a 'Representational Dissimilarity Matrix' (RDM). This matrix is a symmetrical representation where each element measures how dissimilar brain response patterns are when exposed to different pairs of stimuli. Essentially, it quantifies how different the brain's response patterns are when presented with different stimuli (Fig 2.2). These dissimilarity values in the RDM can be seen as distances in a multivariate space for those stimuli within the region of interest (ROI), the whole brain, or a defined mask (Nili et al., 2014). By examining these dissimilarity patterns, researchers gain insights into the underlying neural representations and whether a specific brain region can distinguish between various stimuli or conditions. RSA isn't limited to a single data source; RDMs can be created from any data where the dissimilarity between stimulus pairs can be measured. This allows RSA to directly compare data from multiple sources, such as fMRI, EEG, and MEG. Additionally, RDMs can be created based on computational models or theoretical hypotheses, known as model RDMs. Comparing these model RDMs with neural RDMs (constructed from neuroimaging response patterns) provides a means to evaluate the validity of cognitive theories and computational models in explaining observed brain activity patterns.

Within this thesis, RSA is used to describe the dissimilarity between patterns of brain activity in response to different stimuli, such as facial expression morphs and body posture morphs. The specific approach I used is referred to as a 'searchlight' analysis, a technique that systematically investigates localised brain regions throughout the whole brain or within a specified mask. In this thesis, the searchlight was carried out within the visual processing pathway. This method involves creating small, overlapping spheres (the 'searchlights') that are moved across the visual processing pathway. Within each searchlight, neural activity patterns are examined to understand how different regions within the visual processing pathway represent and respond to each stimulus. By applying RSA in a 'searchlight' manner, a detailed understanding of the fine-grained neural representations for each stimulus is achieved, without needing to pre-define regions of interest.

In this thesis, I use RSA to investigate how the brain processes different stimulus types, including faces, bodies, and whole-person stimuli, as well as the integration of emotion information. To understand the neural responses to the different stimulus types,

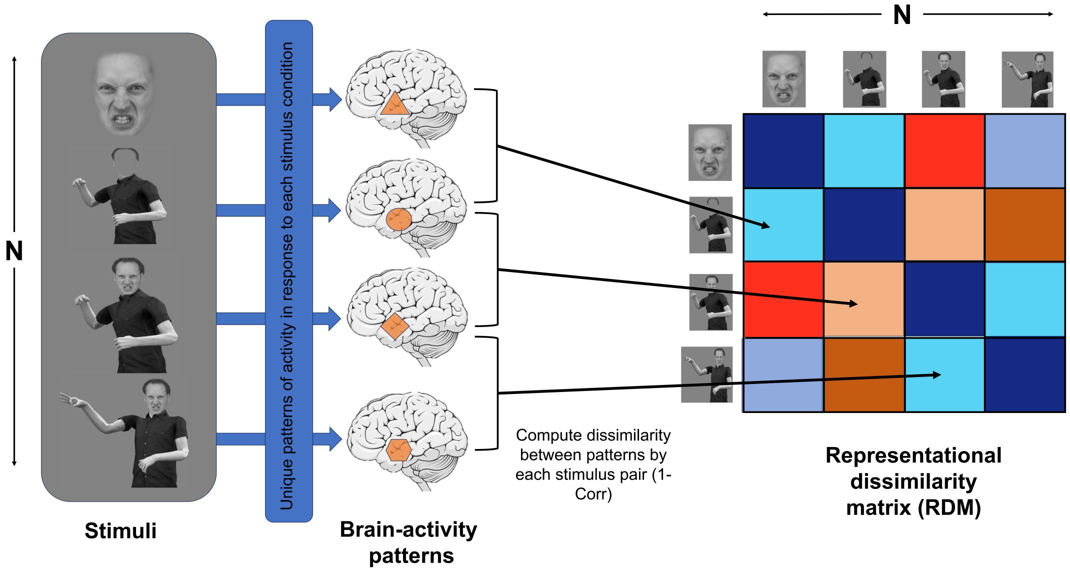


FIGURE 2.2: Creating representational dissimilarity matrix (RDM) from brain activity patterns elicited by a stimulus. Each stimulus causes a unique pattern of activity in a brain area. The dissimilarity of patterns between each stimulus is calculated by performing 1-Correlation between each pair of stimuli. These dissimilarity values are then entered into an RDM indicating the dissimilarity in activity patterns between each pair of stimuli.

I developed categorical model RDMs. These models were designed to examine how the brain distinguishes between stimuli containing faces and those containing bodies, emphasising the categorical nature of these representations. A separate investigation was made into how the brain integrates emotional information from facial expression and body cues. For this purpose, I constructed two distinct models. The first model, known as the "isolated emotion cue model", focussed solely on the representation of isolated emotional information, without integrating contextual emotional information like body posture. In contrast, the "integrated emotion cue model" explored how the brain represents emotional information when body context has been integrated with facial expression information. To build these models, I utilised data from a behavioural emotion discrimination task as the basis for modelling the brain's responses to these emotional cues. Creating these model RDMs allows for a unified approach to compare information across various sources, including neural, behavioural, and conceptual data, all within the same representational space. This approach facilitates the discovery of brain regions related to face and body perception and integration by calculating the correlation between neural RDMs and the categorical model RDMs, as well as between neural RDMs and the isolated/integrated emotion cue models.

In short, RSA bridges the gap between neural activity and behaviour, which is a key objective of this thesis. It will facilitate my exploration of brain activity patterns in relation to specific perceptual and conceptual representations. The multivariate and spatially precise nature of RSA makes it a powerful tool for investigating neural representations for the goals of my research. It can provide insights into face and body cue integration within the visual processing pathway.

Chapter 3

Facial expression and body posture perception across adult lifespan.

3.1 Introduction

As mentioned in the introduction to this thesis, body posture has an influence on how facial expressions are categorised (Aviezer et al., 2008; Meeren et al., 2005), with the precision at which an observer can discriminate between facial expressions being a determining factor in how much influence body posture exerts over the categorisation of the facial expression (Ward et al. *in prep*). Older adults exhibit larger influence of body posture over facial expressions compared with younger counterparts (Abo Foul et al., 2018), and have been shown to have poorer facial recognition abilities compared with younger adults (A. J. Calder et al., 2003; Ruffman et al., 2008; Sullivan and Ruffman, 2004). The two experiments conducted in this study aim to characterise, using sensitive psychophysical methods, how the influence of context (body posture or facial expression) changes across the adult lifespan, and whether any changes can be linked to the discrimination abilities for the target cue (facial expressions or body postures).

Facial expressions are rarely encountered in isolation, which makes the wider context in which a face is perceived an important factor to consider when studying social perception. Previous studies have shown that facial expression recognition can be biased towards the emotion displayed by an incongruent body posture it is seen with (Aviezer et al., 2008, 2012; Hassin et al., 2013; Meeren et al., 2005). Aviezer et al., 2008 demonstrated that an observer is more likely to categorise a disgusted face as 'angry' when it is presented with an angry body posture, an effect which was shown to increase with the perceptual similarity between the target facial expression and the facial expression associated with the emotional context provided by the body posture (Aviezer et al., 2008). This perceptual phenomenon has also been shown to persist even when the observer is asked to ignore the body posture and make their judgements based only on the facial expression (Aviezer et al., 2011). Interestingly, a recent study has demonstrated that the degree of influence that body posture has over facial expression recognition is modulated, at least in part, by an observers ability to precisely discriminate between facial expressions in isolation (Ward et al. *in prep*). Taken together, these studies suggest that body posture will exert more influence over facial expression when there is higher confusability between the target facial expression and the emotion associated with the body posture or lower ability to precisely discriminate between isolated facial expressions, the observer will rely more heavily on body posture.

The maximum age of observers in the studies mentioned so far has been 35 years old, despite there being evidence for differences in social perceptual abilities between younger and older adults (A. J. Calder et al., 2003; Ruffman et al., 2008; Sullivan and

Ruffman, 2004). Specifically, older adults show a consistent decline in the recognition of angry, sad, and fearful facial expressions compared with younger adults (A. J. Calder et al., 2003; Sullivan and Ruffman, 2004), reduced recognition in older adults are also seen for happy and surprised facial expressions, but the reductions for these expressions were lower than for the previously mentioned expressions (Ruffman et al., 2008). With differences in facial expression recognition being consistently observed in older adults, it is important to consider how facial expression recognition is influenced by body posture in older adults. Noh and Isaacowitz, 2013 first addressed this in their study into the influence of body posture on facial expression recognition across the adult lifespan. They found that older adults showed significantly reduced accuracy compared with younger adults when face and body emotions were incongruent (e.g. an angry facial expression on a disgusted body posture), as well as being more likely to categorise the face as expression the emotion shown by the body context (Noh and Isaacowitz, 2013). A more recent study (Abo Foul et al., 2018) also compared the influence of body posture on facial expression perception in younger and older adults. They found that older adults were more biased towards the body emotion when making emotional judgements about the face, as well as significantly impaired in recognising isolated faces and bodies compared with younger adults (Abo Foul et al., 2018). Both of these studies reveal an age-related increase in the degree of influence that body posture has on facial expression recognition, with the authors suggesting that this could be due to a greater 'social-expertise' in older adults (Abo Foul et al., 2018; Noh and Isaacowitz, 2013). This social expertise theory (Hess, 2006) posits that older adults lend more attention to relevant social cues, which then allows them to adopt adaptive strategies in a given social situation. However, given the prototypical expressions used, there was a high recognition of emotions in both the older and younger adults. This makes it more difficult to conclusively argue for older adults' social expertise being the cause of this increased influence of body posture with ageing, when other factors, such as decreasing facial expression discrimination ability with ageing, could play a key role in modulating this.

While research into the influence of body posture on facial expression perception has consistently shown that body posture biases the perception of the facial expression towards that expressed by the body (Abo Foul et al., 2018; Aviezer et al., 2008; Meeren et al., 2005; Noh and Isaacowitz, 2013), the bidirectionality of this relationship has not been investigated as thoroughly. In other words, does facial expression influence the perception of body posture in a similar fashion to how body posture influences the perception of facial expression? To my knowledge, only one study has explored this bidirectionality (Lecker et al., 2020). They found that, although facial expression did influence the recognition of body postures, body posture had a stronger biasing influence over facial expression recognition than the other way around (Lecker et al., 2020). This suggests that the influence that facial expressions and body postures have on the recognition of the other is bidirectional but asymmetrical in nature, with body posture having a stronger influence over facial expressions. This study only investigated this bidirectionality in a young adult sample using prototypical emotional stimuli, which limited their ability to explore what may be modulating this bidirectionality and how it might change across the adult lifespan.

The current study consisted of two experiments: the first investigated the influence of body posture on the categorisation of facial expressions across the adult lifespan, and the second investigated the influence of facial expression on the categorisation of body postures across the adult lifespan. Unlike previous research to date, facial expression and body posture morphs were used (as opposed to prototypical emotional stimuli) in this present study. This methodological difference allowed me to use more sensitive psychophysical methods to quantify both observers' discrimination ability for the isolated facial expressions and isolated body postures, as well as the degree of influence that body posture has on facial expression (Experiment 1) and vice versa (Experiment 2).

3.2 Experiment 1

3.2.1 Methods

Observers

A total of 128 adult observers (65 male; age in years (mean ± std): 44.8 ± 19.3), with an age range of 18-77 were recruited via Prolific (www.prolific.co) after undergoing multiple participant certification processes ("Prolific", 2014). Consent was obtained for each observer before the commencement of the study via an online Qualtrics form ("Qualtrics", 2005), which would exit the study completely if consent was not provided. The study was approved by the School of Psychology Ethics Committee. Participants were paid for their participation through Prolific.

Stimuli

Male facial expressions expressing anger and disgust were selected from the NimStim (Tottenham et al., 2009) and Radboud (Langner et al., 2010) faces database. Four Caucasian male faces were selected, and their angry and disgusted facial expressions were morphed together for each of the 4 identities using FantaMorph software [FantaMorph

Pro, Version 5]. This created a morph continuum between angry and disgusted facial expressions for each identity. The facial expression morphs in this morph continuum changed in increments of 10% (10-90%), resulting in 9 facial expression morphs between anger and disgust for each identity. To create the body posture morph stimuli, a motion capture suit and a Unity 3D game engine was used (Haas, 2014). A male adult actor was instructed to pose in certain body postures expressing anger and disgust (based on the poses used in Aviezer et al., 2008 study), whilst wearing a motion capture suit with motion trackers distributed over the whole body (Fedorov et al., 2018). The Unity 3D game engine was then used to visualise the body postures captured by the actor in the motion capture suit. Four unique body postures were produced by the actor displaying slightly different poses, the body composition and clothing given to each of these unique postures were also different – resulting in four "identities". Weighted averages of these angry and disgusted body postures were then used to produce body posture morphs between anger and disgust for each of the four identities. As with the facial expression morphs, the body posture morphs changed in increments of 10% (10-90%), resulting in 9 morph levels per identity. The face and body stimuli were then combined (GNU Image Manipulation Program, Version 2.10) to create whole-person stimuli for each separate identity. For the experiment, the 100% body postures (either 100% angry or 100% disgusted) were combined with each facial expression morph for each identity. For each identity, there were 9 facial expressions morphs shown on a fully angry body posture, and 9 facial expression morphs shown on a fully disgusted body posture. This created 36 unique whole-body stimuli (9 per identity) for the facial expression on angry body posture condition, and 36 unique whole-body stimuli for the facial expression on disgusted body posture condition. The facial expressions shown in isolation were matched in size to the facial expressions that were shown with a body posture in the whole person condition.

Procedure

The study was conducted online, and stimuli were presented using PsychoPy (Jonathon Pierce and MacAskill, 2018), and hosted on Pavlovia (www.pavlovia.org). Participants accessed the task via an online link. Participants could only take part in the study if they were accessing the link via a desktop computer or laptop, to keep the presentation of stimuli as consistent as possible.

There were three conditions (face-only, body-only, and a whole-person condition), which were presented in a randomised order for each participant. No significant differences in performance were observed for different condition orders, which suggests that condition order did not have an impact on how participants performed in each task. For each trial, participants were presented with a stimulus and asked to make a judgement on whether the stimulus was disgusted or angry. Each unique stimulus was repeated 3 times in each condition, such that there were 12 stimuli presented per morph level (4 identities x 3 repeats). There was a total of 108 trials in the face-only and body-only conditions, and 216 trials in the whole-person condition (108 trials for the facial expression morphs on a fully angry body posture, and 108 trials for the facial expression morphs on a fully disgusted body posture). Stimulus presentation was pseudorandomised for each condition: two orders were made for each condition (the order of stimuli to be presented within a condition was assigned at the onset of each condition for each participant), to ensure that the same identity was never shown in two consecutive trials. This was implemented to avoid habituation of the same identity in participants, which could reduce sensitivity to expressions of a particular identity with repeated exposure over multiple consecutive trials. Before each condition, there was a practice session consisting of 10 trials to ensure the participant knew what was expected of them in each task.

In each trial (Fig 3.1), a stimulus was presented for 1.5 seconds on a grey background, and participants were free to respond after the stimulus had been on the screen for 1 second. For the face-only and body-only conditions, participants were asked to categorise the facial expression and body posture, respectively, as being either angry (keypress 'A') or disgusted (keypress 'D'). In the whole-person condition, participants were instructed to ignore the body posture and judge whether the facial expression was angry or disgusted. A prompt would appear if no response was made after 2 seconds, reminding participants of the response options. Progression to the next trial only occurred once the participant had responded. There was an interstimulus interval of 2 seconds.

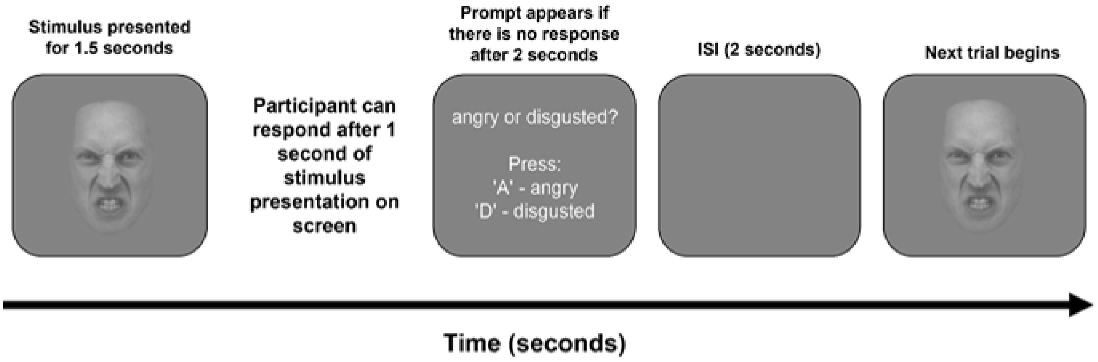


FIGURE 3.1: Example trial. Example stimulus from face-only condition, but trial structure was identical for all conditions.

Data Analysis

Psychometric functions based on a cumulative Gaussian were fitted to estimate each observer's point of subjective equality (PSE) and discrimination ability (indexed by the slope parameter) for each condition. These were fitted using MATLAB R2019b with the Palamedes toolbox (Kingdom and Prins, 2009). Lapse rate was fixed at 0.03 and guess rate at 0. A psychometric function was fitted to data from each condition for each observer, resulting in 4 plots per observer (Fig 3.2): psychometric function fitted to responses in face-only condition, the body-only condition, and two psychometric functions for the whole-person condition – one for facial expressions morphs shown on a 100% angry body posture, and one for facial expression morphs shown on a 100% disgusted body posture.

The slope parameter from the psychometric function in the face-only and body-only conditions provided me with a measure of discrimination ability for facial expression and body posture, respectively. The difference in PSE values between the two psychometric functions plotted for the whole-person condition provided a quantifiable measure of the influence that body posture has on facial expression categorisation. Examples of the psychometric functions produced from a single observer are shown in Figure 3.2. The steeper the slope of the psychometric function, the better the discrimination ability is in that observer for that cue (better ability to precisely recognise subtle difference between the morphs of the cue).

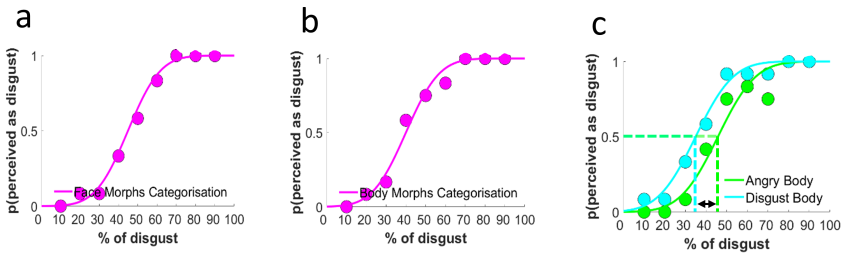


FIGURE 3.2: Example psychometric functions from an observer in experiment 1: (a) face-only, (b) body-only, (c) whole-person condition. Key measures include: the slope values from (a) and (b) as a measure of discrimination ability, and the difference in PSE from (c) as a measure of influence of body posture on facial expression categorisation (indicated by the dotted lines and arrow). Each circle represents the average response of 12 trials at a given morph level.

To ensure that every observer included in the analysis was engaged in and able to perform the task, I excluded any observer with a slope below 0.5 in the face-only condition (29 excluded. 20 male; age in years (mean ± std): 49.7 ± 20.3). Participants with a slope below 0.5 exhibited a poor ability to discriminate even the prototypical examples of the emotion stimuli. This raises the possibility of them not understanding or engaging with the task at hand. With this possibility in mind, these participants were excluded from the analysis. I then identified age-specific outliers by age group (18-30, 31-40, 41-50, 51-60, 61-70, 71+). Exclusions were done by age grouping to account for age-related differences in facial expression recognition with age (for meta-analysis see: Ruffman et al., 2008). Due to the non-normal distribution of the data, inter-quartile range was used to identify outliers as 2 IQR's above the 3rd quartile within each age-group. This led to 5 more observers being excluded (2 from 18-30, 3 from 61-70). An additional 7 observers were excluded following visual inspection of the remaining participants' data. These 7 observers either responded as the body posture only within the whole-person condition (potentially indicating a misunderstanding of the task, which was to categorise the facial expression and ignore the body) or they displayed chance performance in the whole-person condition. A summary of the total number of exclusions per age-group can be found in Figure 3.3.

This left a sample size of 85 observers for data analysis (37 male; age in years (mean ± std): 44.7 ± 18.7) with an age range of 18 to 77 (Fig 3.4). Some observers within this sample had PSE change values larger than 1 but were not excluded due to their overall data quality, suggesting they were engaging with the task. To visualise these PSE change values in my plots, the PSE changes were all ranked between 1 and 85, and then rescaled so all values fit between 0 and 1. The data from this sample was non-normally distributed, so non-parametric statistical tests were used throughout.

A PSE change value larger than 1 indicates a substantial shift in perception between conditions (face displayed on an angry body compared to a disgusted body). Such changes could raise concerns as they might reflect significant variability or inconsistency in participants' responses, potentially compromising the reliability of the results. Prior to participant inclusion, visual inspections of the data were crucial to ensure that large PSE change values were primarily influenced by the experimental manipulation rather than inconsistencies in participant responses. This step aimed to enhance the reliability and validity of the study's outcomes. For both Experiment 1 and Experiment 2, the results were affected by the inclusion or exclusion of participants with a PSE change value larger than 1. However, the primary reason for this alteration lies in the demographic composition of the participant sample, with my research question relying on the variations in PSE change and perceptual measures across the lifespan in my sample. Specifically, excluding participants with a PSE change value larger than 1 would result in the disproportionate removal of older participants from the sample. Given that the study aims to investigate age-related changes in perceptual processing, the complete exclusion of older participants would substantially diminish the representativeness of age groups across the lifespan. So, while the exclusion of participants with large PSE change values may yield more consistent results in terms of perceptual responses, it would come at the cost of sacrificing the diversity and comprehensiveness of the participant sample, particularly in capturing age-related nuances in perceptual processing. It is important to note that, as well as visual inspections of the data, age-specific exclusion criteria were also implemented to address these concerns. Applying blanket exclusion criteria based solely on PSE change values above 1 would not only disproportionately affect older participants but would also fail to account for potential age-related variations in perceptual processing. Therefore, by adopting age-specific exclusion criteria, the study aimed to preserve the integrity of the participant sample while ensuring a balanced representation of participants from different age cohorts. While the exclusion of participants with a PSE change value larger than 1 may indeed lead to more uniform results, it is essential to recognise that this approach would compromise the overarching goals of the study by eradicating significant portions of the older participant demographic.

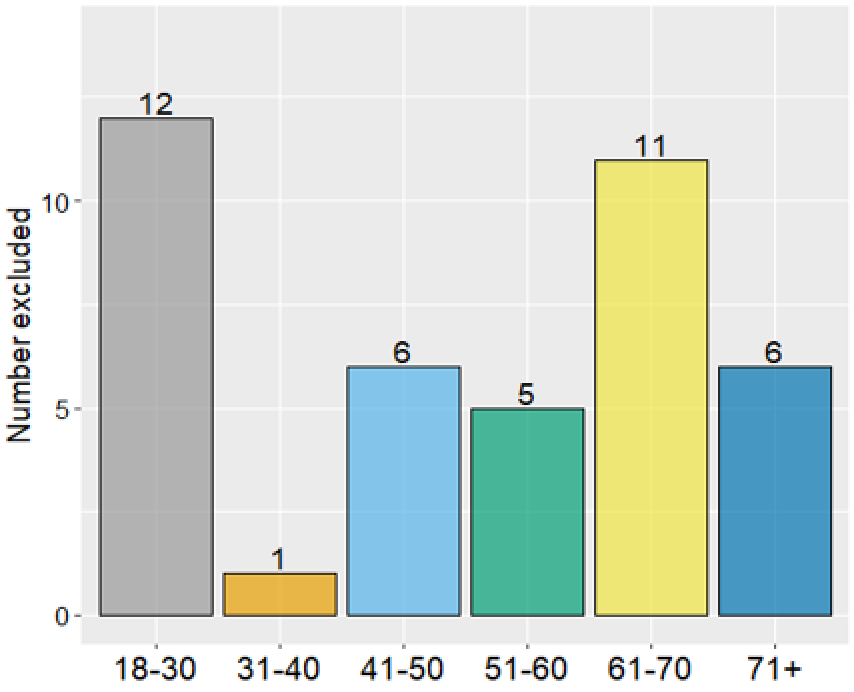


FIGURE 3.3: Summary of exclusions from Experiment 1 by age-group. There were 41 exclusions in total (26 male; age in years (mean ± std): 49.2 ± 20.5).

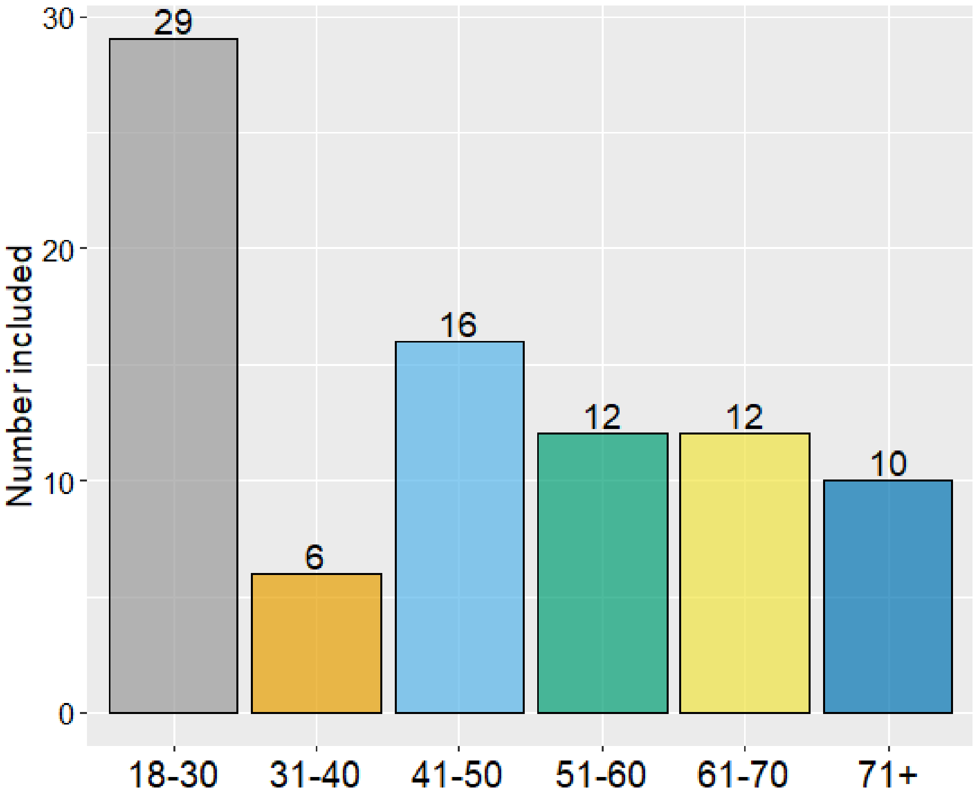


FIGURE 3.4: Summary of included participants from Experiment 1 by age-group. There were 85 participants in total (37 male; age in years (mean ± std): 44.7 ± 18.7).

3.2.2 Results

Influence of body posture on facial expression categorisation

The PSE change, the difference between the PSE for facial expressions displayed on an angry body posture vs. a disgusted body posture, was used as a measure of the influence of body posture in each participant. The PSE for facial expressions displayed on an angry body (Mdn = 0.71) was significantly higher than the PSE for facial expressions displayed on a disgusted body (Mdn = 0.33) (Fig 3.5a – bar; Wilcoxon signed rank test W = 4861, $p < 0.001$). Figure 3.5b shows the change in PSE value between when the face shown on angry body and when the face is shown on a disgusted body posture for each observer (two linked points per observer).

Therefore, body posture had a significant influence on facial expression categorisation in my sample overall.

A post-hoc power analysis showed an achieved power of 0.80, indicating an 80% chance of detecting true differences in PSEs between facial expressions on angry and disgusted body postures, given the observed effect size.

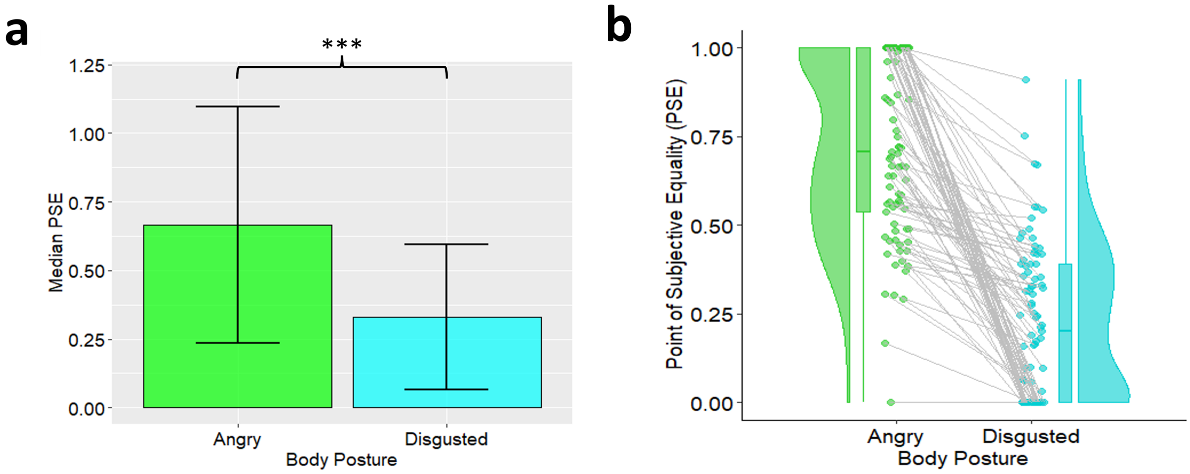


FIGURE 3.5: Visualisation of influence of body posture on facial expression perception. a) Bar plot showing the median PSE of categorisation of facial expressions shown on angry body postures (green) and disgusted body postures (blue). Error bars represent the IQR. *** $p<0.001$. b) A visual representation of the influence of body posture. Raincloud plot showing the difference in PSE of categorisation of facial expressions shown on angry body postures (green) and disgusted body postures (blue). Each data point represents an observer, with lines linking the same observer in each condition. For the sake of the visualisation, PSE values above 1 were capped at a value of 1, and PSE values less than 0 were capped at 0.

Relationship between facial expression discrimination ability and age

There was a significant negative relationship between facial expression discrimination ability (the slope of the psychometric function in the face-only condition) and age (Fig 3.6; rs = -0.25, p = 0.019), suggesting that older adults are worse at discriminating facial expressions.

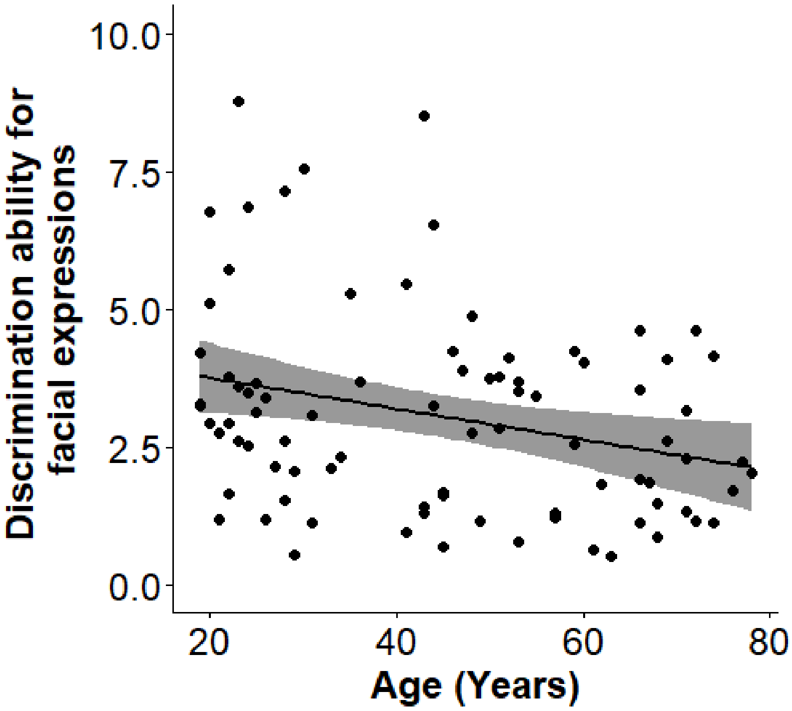


FIGURE 3.6: Scatterplot showing the relationship between discrimination ability of facial expressions (the slope of the psychometric function in the face-only condition) and age in my sample. The 95% confidence interval is shown with grey shading.

A post-hoc power analysis evaluated the sensitivity of the observed correlation between facial expression discrimination ability and age. The achieved power was 0.68

(n = 85), indicating that the study may have been underpowered to detect smaller effects. Caution is warranted in interpreting the correlation strength, and future research with larger sample sizes may provide more robust conclusions.

Relationship between body posture discrimination ability and age

No relationship was observed between body posture discrimination ability (the slope of the psychometric function in the body-only condition) and age (Fig 3.7; rs = -0.047, p = 0.67), suggesting that body posture discrimination ability is stable across the adult lifespan.

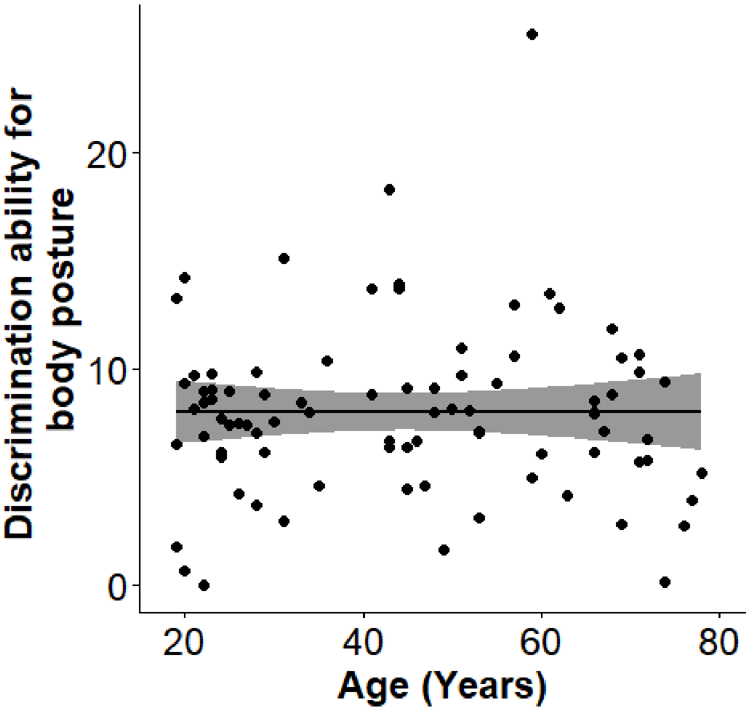


FIGURE 3.7: Scatterplot showing the relationship between discrimination ability of body posture morphs (the slope of the psychometric function in the body-only condition) and age in my sample. The 95% confidence interval is shown with grey shading.

Relationship between influence of body posture and age

There was a significant positive relationship between the influence of body posture on facial expression categorisation (PSE change) and age (Fig 3.8; rs = 0.26, p = 0.018), suggesting older adults are more influenced by body posture in their categorisation of facial expression in the whole person condition.

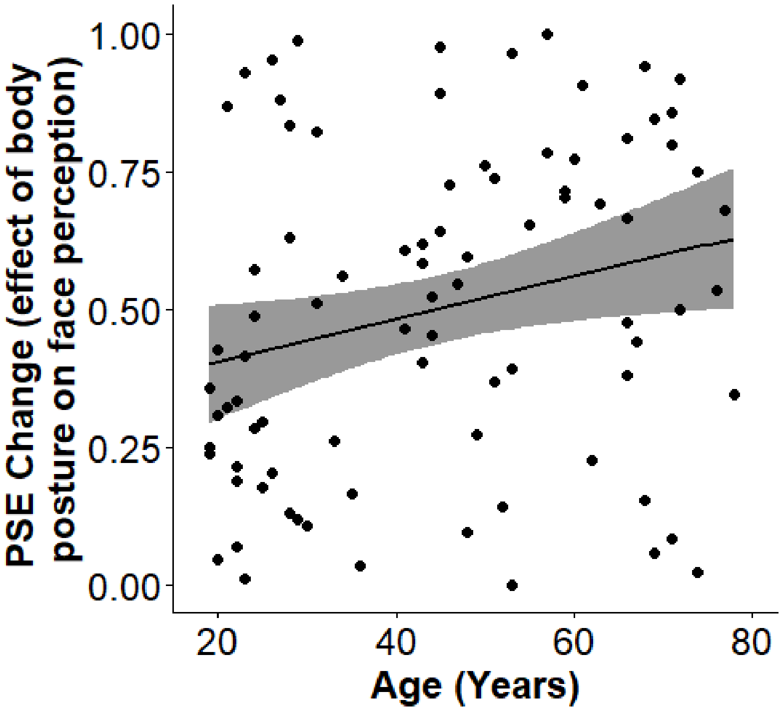


FIGURE 3.8: Scatterplot showing the relationship between influence of body posture on facial expression categorisation (PSE change) and age in my sample. The 95% confidence interval is shown with grey shading.

A post-hoc power analysis evaluated the relationship, revealing an achieved power of 0.7 (n = 85). The study may have been underpowered to detect smaller effects. Caution is warranted in interpreting the correlation, and future research with larger samples may provide more conclusive results.

Relationship between degree of influence of body posture and discrimination ability for facial expressions

There was a significant negative relationship between the influence of body posture on facial expression categorisation (PSE change) and discrimination ability for facial expressions (Fig 3.9; rs = -0.45, $p < 0.0001$), suggesting that a worse discrimination ability for facial expressions is linked with a greater influence of body posture on facial expression categorisation.

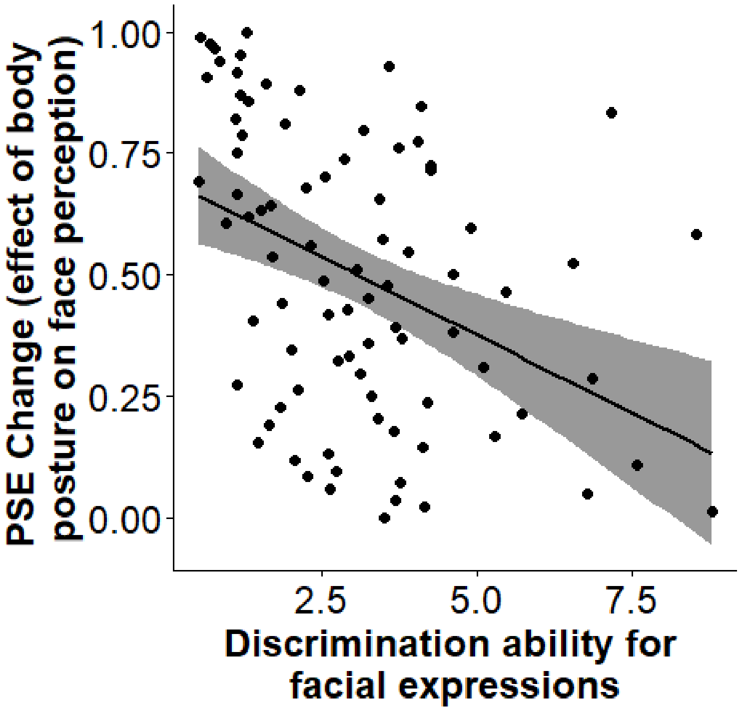


FIGURE 3.9: Scatterplot showing the relationship between influence of body posture on facial expression categorisation (PSE change) and discrimination ability for facial expressions (the slope of the psychometric function in the face-only condition) in my sample. The 95% confidence interval is shown with grey shading.

A post-hoc power analysis found an achieved power of 0.99 (n = 85), indicating a high probability of detecting the observed correlation coefficient of -0.45. The statistically significant negative relationship observed is supported by the high achieved power, providing strong confidence in the reliability of the findings.

3.2.3 Results Summary - Experiment 1

Experiment 1 showed that categorisation of facial expressions was biased by body posture, and that this influence of body posture increased with ageing. Interestingly, I showed that the influence of body posture was modulated by an observer's discrimination ability for isolated facial expressions. In keeping with this pattern of results, I also found that discrimination ability for facial expressions significantly decreased across the adult lifespan. The relationship between discrimination ability for facial expressions and the influence of body posture, suggests that the decreased discrimination ability with ageing could be driving the increased influence of body posture across the adult lifespan.

3.3 Experiment 2

3.3.1 Methods

Observers

A total of 138 adult observers (69 male; age in years (mean ± std): 44.4 ± 18), with an age range of 18-79 were recruited via the same methods as Experiment 1. Ethics, consent, and payment details were also identical to Experiment 1.

Stimuli

The stimuli used were identical to Experiment 1 for the face-only and body-only conditions. To create the whole-person stimuli for Experiment 2, the face and body stimuli were again combined (GNU Image Manipulator Program, Version 2.10), but unlike Experiment 1, 100% facial expressions (either 100% angry or 100% disgusted) were combined with body posture morphs for each identity. There were 9 body posture morphs shown with a fully angry facial expression, and 9 body posture morphs shown with a fully disgusted facial expression (Fig 3.10). This created 36 unique whole-body stimuli (9 per identity) for the body posture displayed with an angry facial expression condition, and 36 unique whole-body stimuli for the body posture displayed with a disgusted facial expression condition.

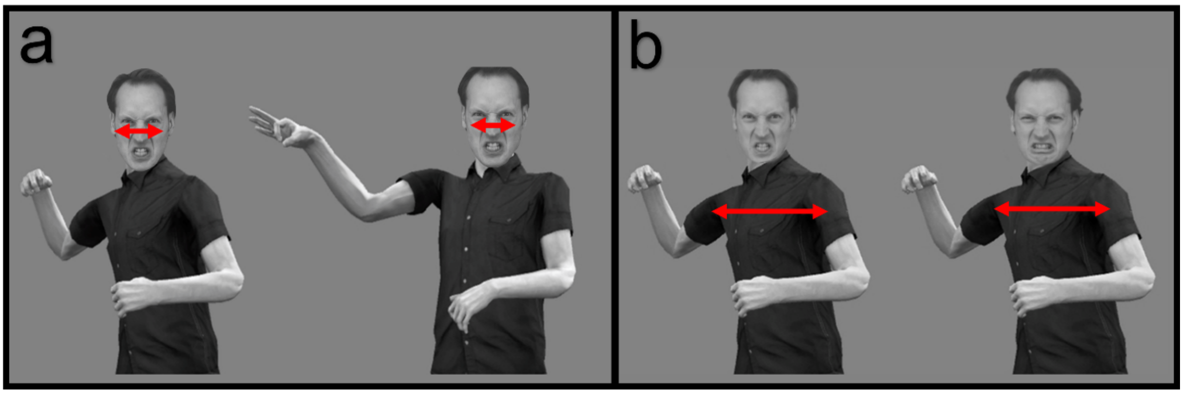


FIGURE 3.10: Schematic representation of whole-person stimuli used in Experiment 1 (a) and Experiment 2 (b). a) Whole-person stimuli in Experiment 1 showed facial expression morphs on either a fully angry or fully disgusted body posture. b) Whole-person stimuli in Experiment 2 showed body posture morphs with either a fully angry or fully disgusted facial expression.

Procedure

The design was identical to Experiment 1. However, for the whole-person condition, participants were instructed to ignore the facial expression and judge whether the body posture was angry or disgusted. Like Experiment 1, a prompt would appear if no response was made after 2 seconds, reminding the participants of the response options. Progression to the next trial only occurred once the participant had responded.

Data Analysis

Data analysis and exclusion criteria were identical to Experiment 1: slope below 0.5 in face-only condition (38 excluded, 18 male; age in years (mean ± std): 47.6 ± 17.7), age-specific outliers (1 exclusion in 18-30 group). An additional 3 observers were excluded following visual inspection of the remaining participants' data. These 3 observers either responded as the facial expression only within the whole-person condition (potentially indicating a misunderstanding of the task, which was to categorise the body posture and ignore the facial expression) or they displayed chance performance in the whole-person condition. A summary of the total number of exclusions per age-group can be found in Figure 3.11.

This left a sample size of 96 observers for data analysis (47 male; age in years (mean ± std): 42.9 ± 18.1) with an age range of 18 to 79 (Fig 3.12). Some observers within this sample had PSE change values larger than 1 but weren't excluded due to their overall data quality, suggesting they were engaging with the task. To visualise these PSE change values in my plots, the PSE changes were all ranked between 1 and 96, and then rescaled so all values fit between 0 and 1. Data was non-normally distributed, so non-parametric statistical tests were used throughout. The use of non-parametric tests also meant that the outcomes of the statistical tests were less likely to be affected by any of the larger PSE change values. Statistical analyses were carried out with the software R (The R Foundation for Statistical Computing).

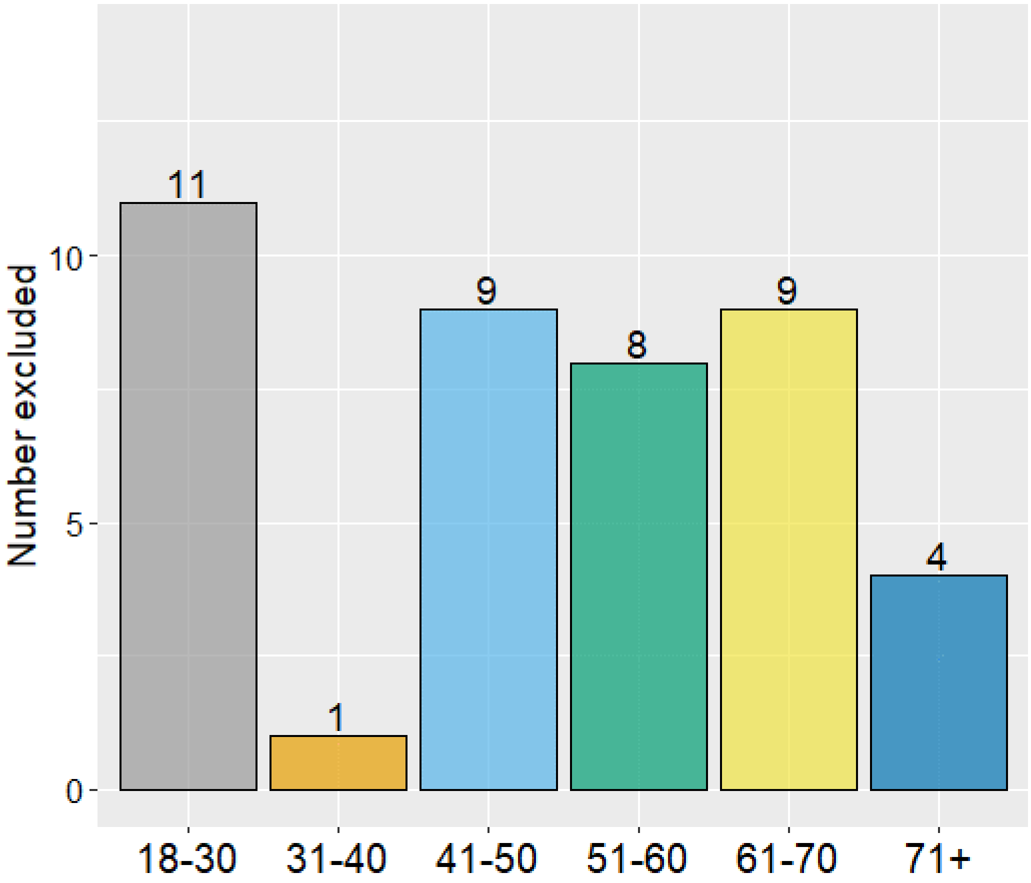


FIGURE 3.11: Summary of exclusions from Experiment 2 by age-group. There were 42 exclusions in total (19 male; age in years (mean ± std): 47.9 ± 17.5).

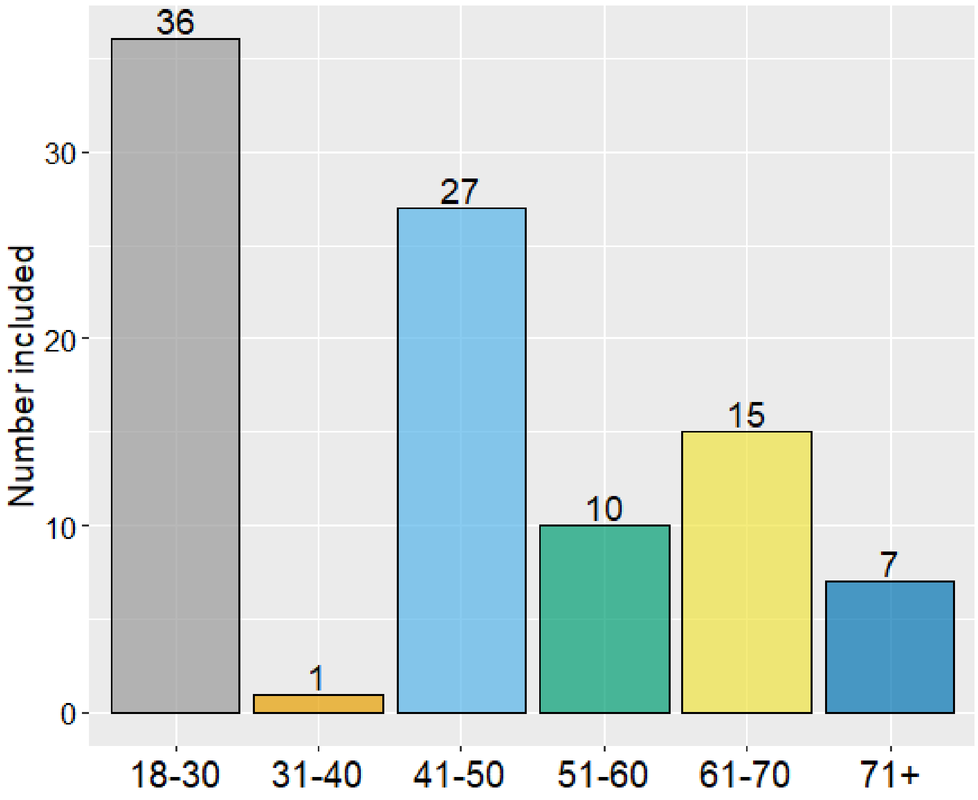


FIGURE 3.12: Summary of included participants from Experiment 2 by age-group. There were 96 participants in total (47 male; age in years (mean ± std): 42.9 ± 18.1).

3.3.2 Results

Influence of facial expression on body posture categorisation

The PSE change, the difference between the PSE for body postures displayed with an angry facial expression vs. a disgusted facial expression was used as a measure of the influence of facial expression on body posture perception in each participant. The PSE for body postures displayed with an angry facial expression (Mdn = 0.45) was significantly higher than the PSE for body postures shown with a disgusted facial expression (Mdn = 0.41) (Fig 3.13(a) - bar: Wilcoxon signed rank test W = 5673, p-value = 0.0057). Figure 3.13(b) shows the change in PSE value between when the body is shown with an angry facial expression and when the body is shown with a disgusted facial expression for each observer (two linked data points per observer). This suggests that facial expression has a significant influence on body posture categorisation.

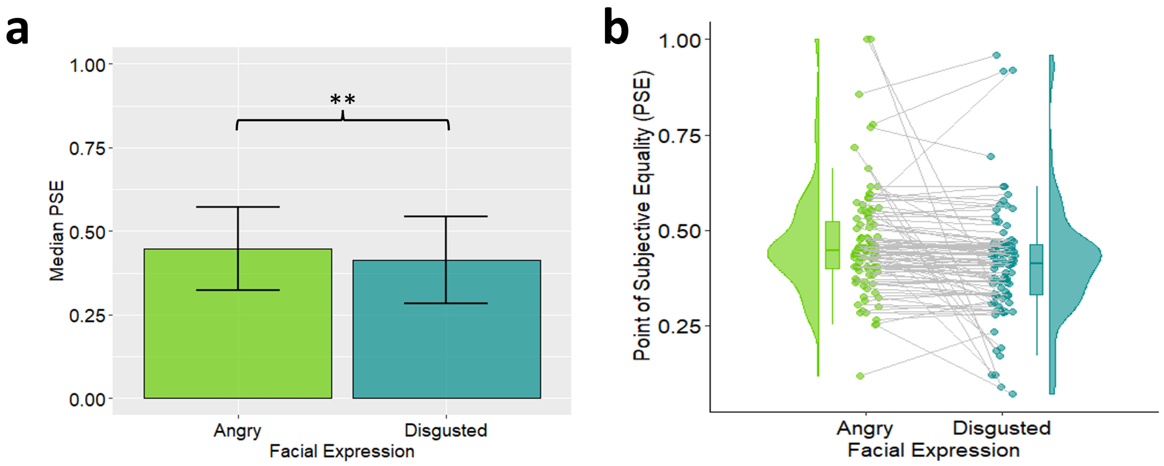


FIGURE 3.13: Visualisation of influence of facial expressions on body posture. a) Bar plot showing the median PSE of categorisation of body postures shown with angry facial expressions (green) and disgusted facial expressions (blue). Error bars represent the IQR. ** $p<0.01$. b) A visual representation of the influence of facial expression. Raincloud plot showing the difference in PSE of categorisation of body postures shown with angry facial expressions (green) and disgusted facial expressions (blue). Each data point represents an observer, with lines linking the same observer in each condition. For the sake of the visualisation, PSE values above 1 were capped at a value of 1, and PSE values less than 0 were capped at 0.

A post-hoc power analysis showed an achieved power of 0.79, indicating an 79% chance of detecting true differences in PSEs between body postures displayed with either angry or disgusted facial expression, given the observed effect size. Despite the statistically significant difference in PSEs, while the 0.79 achieved power suggests sensitivity to detect the effects, caution is needed in interpreting the results. Further research with larger samples is advisable to validate and generalise the findings.

Relationship between body posture discrimination and age

No significant relationship was found between discrimination ability for body postures and age (Fig 3.14; rs = -0.028, p = 0.78).

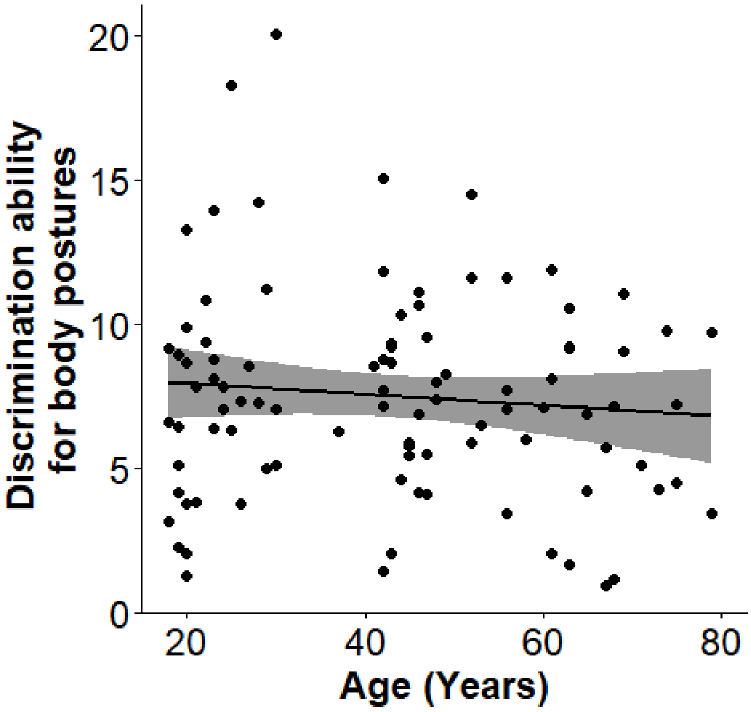


FIGURE 3.14: Scatterplot showing the relationship between discrimination ability for body postures (the slope of the psychometric function in the body-only condition) and age. The 95% confidence interval is shown with grey shading.

Relationship between influence of facial expression on body posture and age

No significant relationship was found between the influence of facial expression on body posture categorisation (PSE change) and age (Fig 3.15; rs = -0.085, p = 0.41). This result would suggest that although facial expression does have a significant influence on body posture categorisation, this influence doesn't change with age.

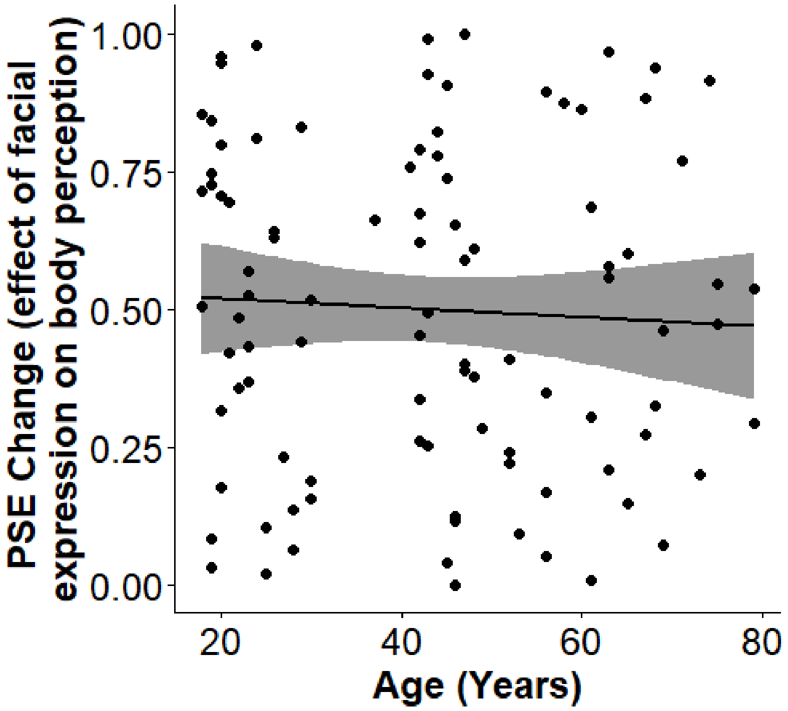


FIGURE 3.15: Scatterplot showing the relationship between the influence of facial expression on body posture categorisation (PSE change) and age. The 95% confidence interval is shown with grey shading.

Relationship between degree of influence of facial expression and discrimination ability for body postures

No significant relationship was found between the influence of facial expression on body posture categorisation (PSE change) and age (Fig 3.16; rs = -0.18, p = 0.08). However, a trend is apparent, where higher discrimination ability for body postures leads to less reliance on facial expression in making the body posture judgment.

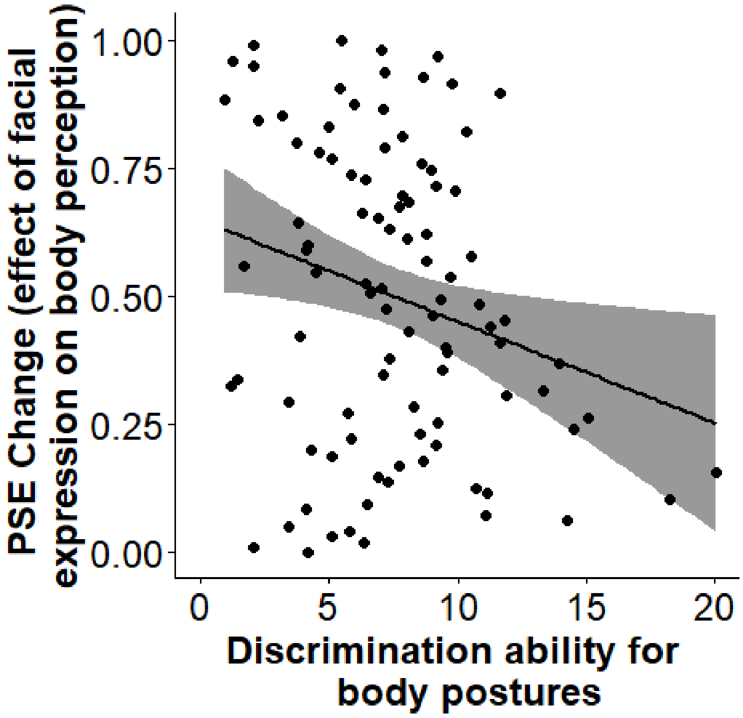


FIGURE 3.16: Scatterplot showing the relationship between the influence of facial expressions on body posture categorisation (PSE change) and discrimination ability for body postures (slope of psychometric function in the body-only condition). The 95% confidence interval is shown with grey shading.

3.3.3 Results Summary - Experiment 2

Experiment 2 showed that categorisation of body postures was biased by facial expressions, but that the degree of influence did not change across the adult lifespan. However, similar to Experiment 1, there was a trend between the precision of the representation of the isolated cue and the influence that the other cue then had in the whole-person condition. Here, the higher discrimination ability for body postures resulted in less reliance on facial expression in making the body posture judgement. This relationship was further supported by the fact that both discrimination ability for body postures and the influence of facial expressions on body posture did not change with age.

3.4 Comparing Experiment 1 and 2

3.4.1 Contextual Influence

In Experiment 1, I found that body posture had a significant influence on facial expression categorisation, and biased categorisation towards the emotion being portrayed by the body. In Experiment 2, I found that facial expression had a significant influence on the categorisation of body postures, and biased categorisation towards the emotion portrayed in the facial expression. This indicates a bidirectional influence of face and body emotion cues in making judgments about the other, with both cues being able to influence the categorisation of the other. However, body posture had a significantly larger impact on facial expression categorisation than facial expressions did on the categorisation of body postures (Fig 3.17 - bar: Wilcoxon rank-sum test W = 6279, p < 0.001).

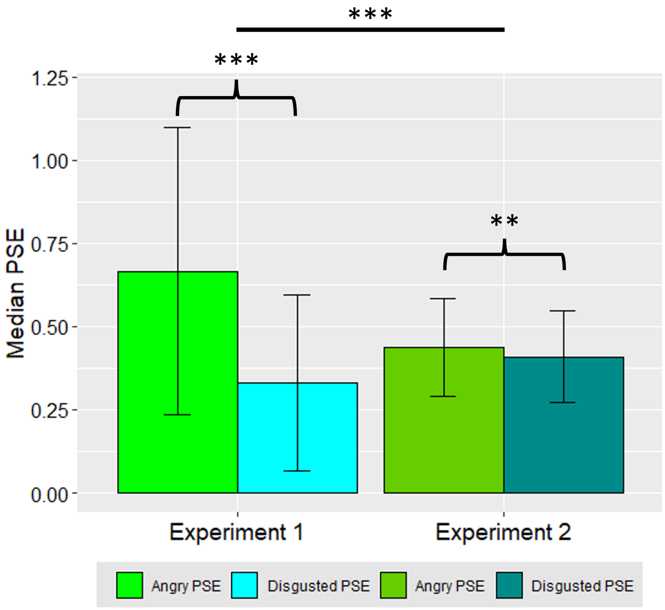


FIGURE 3.17: Bar plot showing the median PSE of categorisation of facial expressions shown on angry body postures (Experiment 1 – green) and disgusted body postures (Experiment 1 – blue) and the median PSE of categorisation of body postures shown with angry facial expressions (Experiment 2 – green) and disgusted facial expressions (Experiment 2 – blue). Error bars represent the IQR. ** p<0.01 *** p<0.001.

3.4.2 Replicability of findings

To assess the replicability of the relationship between facial expression discrimination ability and age in Experiment 1, the same analysis was run for the sample in Experiment 2. Interestingly, the same relationship was not found in the Experiment 2 sample, with no relationship seen between facial expression discrimination ability and age in this sample (Fig 3.18; rs = 0.022, p = 0.83).

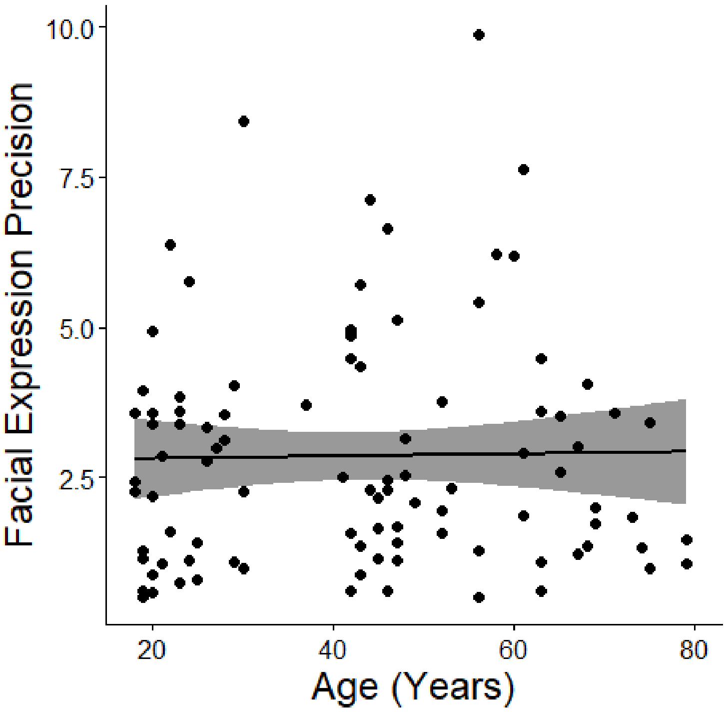


FIGURE 3.18: Scatterplot showing the relationship between discrimination ability of body posture morphs (the slope of the psychometric function in the body-only condition) and age in my sample. The 95% confidence interval is shown with grey shading.

3.5 Discussion

The current study consisted of two experiments; the first explored the influence of body posture in the categorisation of facial expressions across the adult lifespan. Unlike previous studies, I investigated this parametrically over a larger, continuous age range, and used a more sensitive psychophysical approach to assess discrimination ability. I found that body posture has a significant influence on how a facial expression is categorised and that this influence increases across the adult lifespan. I also found that discrimination ability for facial expressions decreases across the adult lifespan. However, it is important to exercise caution in interpreting these findings, as the same relationship was not replicated in Experiment 2, which utilised identical parameters but involved a different group. So, while the decline in discrimination ability in Experiment 1 is noteworthy, further investigation is warranted to understand the variability observed across Experiment 1 and 2. Interestingly, this was not mirrored by a decline in discrimination ability for body postures across the adult lifespan, which suggests that the decreased discrimination ability for facial expressions is unlikely to be a reflection of general cognitive or perceptual decline in older adults. The results of Experiment 1 are consistent with previous studies (Abo Foul et al., 2018; Noh and Isaacowitz, 2013) that showed an increased influence of body posture in older adults compared with younger adults when judging prototypical emotional face and body stimuli. However, in my study, I also found that a lower discrimination ability for isolated facial expressions was significantly linked to a higher influence of body posture, which suggests that the degree of influence that body posture has is modulated, at least in part, by an observer's ability to precisely categorise facial expressions. This result provides insight into a possible mechanism for the increased reliance on body posture in older adults; the influence of body posture increases as their discrimination ability for isolated facial expressions decreases across the adult lifespan.

Experiment 2 investigated the influence of facial expression on the categorisation of body posture across the adult lifespan. Here, I showed that facial expressions have a significant influence over how body postures are categorised, but that this influence doesn't change across the adult lifespan. In Experiment 2, I was also able to show the trend that influence of facial expressions increased as precision of discrimination for isolated body cues decreased in my sample. Meaning that Experiment 2 also supports the idea that the precision of individual cues drives the influence of contextual factors. When comparing Experiment 1 and Experiment 2, the influence of body posture on facial expression categorisation was significantly higher than that of facial expression on body posture categorisation. This result demonstrates the bidirectional yet asymmetrical nature of the relationship between emotion signals from the face and body.

A key finding in Experiment 1, that older adults are more influenced by body posture than younger adults, is consistent with previous studies (Abo Foul et al., 2018; Noh and Isaacowitz, 2013). These previous studies used a selection of prototypical facial expressions and body postures, and I was able to show the same pattern of results, but with a large, continuous sample of healthy adults. Looking at age-related changes across the full range of ages in Experiment 1, allowed me to observe how individual differences are distributed across the whole age-range in my study. This provided a more informative picture of these changes *throughout* the adult lifespan, rather than making a comparison between defined groups of older and younger adults. Consistent with previous findings of emotional recognition deficits in older adults (Abo Foul et al., 2018; A. J. Calder et al., 2003; Sullivan and Ruffman, 2004), I found a significant reduction in facial expression recognition abilities across the adult lifespan. I found no reduction in discrimination ability for body postures across the adult lifespan, which is contrary to a previous finding that there is a reduction in recognition of both facial expressions and body postures in older adults compared to younger adults, and that recognition ability does not significantly differ between face and body cues in either age group (Abo Foul et al., 2018). However, the prototypical stimuli used in their study could be the reason that no significant difference is seen between the recognition of faces and bodies, due to ceiling effects being reached in both the older and younger adults (Abo Foul et al., 2018). Experiment 1 speaks directly to this issue and shows that, using sensitive psychophysical measures, there was a significant difference in discrimination ability for isolated face and body cues across all ages in my sample, with the discrimination ability for body posture being significantly higher (Wilcoxon signed rank test W = 6279, $p < 0.001$). This indicates that, within my sample, the decrease in recognition ability for faces is not due to a general perceptual or emotional recognition deficits, but it is specific to faces and body posture must act as a clearer source of emotional information across all ages.

Consistent with a previous study that found a link between facial expression discrimination ability and influence of body posture in adults (Ward et al. *in prep*), I found a significant relationship between decreasing facial expression discrimination ability with age and increasing influence of body posture across the adult lifespan. The consistency of this relationship across the adult lifespan, suggests that the increased influence of body posture seen in older adults is likely driven by a decreased discrimination ability for facial expressions with age. This provides evidence against the suggestion of social expertise as a potential reason for the increased influence of body posture observed in older adults (Abo Foul et al., 2018; Noh and Isaacowitz, 2013). Within this theoretical framework, older adults rely more on surrounding contextual cues due to their employment of adaptive social strategies, as a result of their accumulated social experience (Hess, 2006). My results suggest that older adults rely more heavily on cues from body posture to compensate for their reduced discrimination ability for facial expressions. So, rather than older adults adopting adaptive strategies due to accumulated social experience (Abo Foul et al., 2018; Noh and Isaacowitz, 2013), they have instead adapted to compensate for a decrease in their ability to recognise isolated facial expressions with increasing age.

As mentioned previously, the bidirectionality of these effects have not been widely explored. A recent study (Lecker et al., 2020) investigated this bidirectionality using 4 prototypical facial expressions and body postures (anger, disgust, fear, and happiness), which were combined to make whole-body composites. In their study, they found that this relationship was bidirectional, with body posture exerting a stronger influence over facial expression than vice versa (Lecker et al., 2020). In Experiment 2, I also investigated this bidirectionality but with a larger age range (18 to 79 years old) and with more sensitive psychophysical methods. As in Experiment 1, this allowed me to investigate this influence parametrically over a large, continuous age range, unlike previous research (Lecker et al., 2020). Consistent with Lecker et al., 2020, my study confirms that facial expressions significantly influence body posture categorisation. Additionally, I observed that this influence remains consistent across the adult lifespan. The implementation of a sensitive psychophysical approach, along with the use of facial expression and body posture morphs, facilitated an examination of individual differences in the relationship between facial expression influence on body posture and the discrimination ability for body postures. Notably, I found a similar trend to that seen in Experiment 1; better discrimination ability for body posture was linked to a lower influence of facial expressions on body posture categorisation in Experiment 2.

Across adulthood and into old age (Experiment 1 and 2), a consistent trend emerges: the degree of influence that a surrounding emotional cue (from either the face or body) has on target stimulus categorisation is linked to the observer's ability to discriminate the target cue in isolation. In Experiment 1, when participants assessed only facial expressions in a whole-person stimulus, greater influence from the surrounding body posture occurred when their isolated facial expression discrimination was poorer. Experiment 2 showed a similar pattern but in the opposite direction: higher influence from facial expressions in a whole person stimulus, even when asked to assess only body posture, correlated with lower isolated body posture discrimination abilities. This pattern may explain the asymmetrical nature of this bidirectional influence between facial and body emotional signals. Body posture acts as a more reliable cue than facial expressions, leading observers in Experiment 2 to rely less on the surrounding context cue (facial expression) when judging body posture in the whole person condition. This is in line with the maximum-likelihood principle, which predicts a sensory cue's reliability will determine how much that cue will contribute to the integrated representation (Ernst and Banks, 2002). It appears that although my experiments are dealing with high-level social signals, they seem to follow the same integration as low-level vision; poor discrimination ability in the isolated cue will cause that cue to contribute less to the integrated representation, leaving the surrounding context cue to contribute more to the integrated whole-person.

The study has some limitations to consider. Firstly, no measure of general cognitive function was recorded for the observers in either experiment, making it difficult to completely rule out general cognitive decline as a factor influencing the results observed across the adult lifespan. However, the decline in discrimination ability for facial expressions (but not body posture) suggests that the perceptual changes are specific to face stimuli rather than a result of general perceptual or cognitive decline. Secondly, the absence of eye-tracking data prevents a definitive conclusion regarding whether older adults fixated on the correct cue in the whole-person condition. Nevertheless, a strong positive relationship between discrimination ability in the whole-person condition and isolated cue conditions (Experiment 1: rs = 0.66, $p < 0.001$. Experiment 2: rs = 0.49, $p < 0.001$) provides evidence that observers made judgments based on the instructed cue. Collecting eye-tracking data in future studies could offer additional insights into scanning patterns across the adult lifespan and their association with contextual influence. Additionally, concerns about statistical power and false positives should be acknowledged. While efforts were made to maximise statistical power, such as maintaining as large a sample size as possible, the risk of false positives remains a pertinent concern, especially in the context of multiple correlational analyses. This underscores the importance of cautious interpretation and validation of my findings, particularly when conducting numerous statistical tests. Another limitation is the use of male identities only throughout this study. This was due to only male body posture morphs being produced by my collaborators (Fedorov et al., 2018), which restricted the investigation of whole-person body perception to male in this study, due to only having male body postures to combine with the facial expressions. The use of only morphs between anger and disgust for face and body stimuli may limit the generalisability of the findings to other emotional expressions. Again, this is due to the use of body posture morphs in this study, with anger (raised fist) and disgust (holding up something in disgust) body morphs being able to morph with each other convincingly. However, given their perceptual similarity and high recognisability, the study serves as a reliable starting point for investigating this effect across a wider range of emotional expressions and provides robust initial results for these two expressions. Another limitation to consider is the use of young adult facial expressions only. This could introduce a potential own-age bias in the recognition abilities of the participants and could be a potential factor in older adults exhibiting lower facial expression recognition abilities compared to younger participants. A final limitation to consider is the use of Caucasian stimuli only, and the lack of data collected on the ethnicity of each participant online, which could create a potential own-race bias in recognition that has gone unaccounted for. To address this, further research should record the ethnicity and race of each participant and look at whether this affects different age groups equally, or whether it is a factor in the difference in recognition ability in older adults. Future research should collect eye-tracking data whilst the participant does the categorisation task, to ensure that the observer is attending to the target cue. Expression morphs from a wider range of emotions could also be used in future studies, to see whether these patterns we see can be generalised across more emotional expressions.

This chapter bolstered existing literature by conducting a parametric investigation over a broader age range, allowing for a nuanced understanding of age-related changes in emotion perception, particularly in ageing individuals. By employing a more sensitive psychophysical approach, I was able to discern significant influences of body posture on how facial expressions are perceived, with this influence notably increasing across the adult lifespan. This comprehensive approach not only confirms previous findings but also unveils previously unexplored nuances in the interplay between body posture and facial expression categorisation, offering valuable insights into the emotional processing mechanisms that may impact the social interactions and well-being of ageing individuals. Understanding these mechanisms aids in the understanding of emotional recognition and communication skills in older adults, ultimately enhancing their quality of life as they navigate social interactions and relationships.

3.6 Chapter Summary

To summarise, this chapter demonstrates the bidirectional relationship between face and body emotion cues when viewing a whole-person. Experiment 1 demonstrated the influence of body posture on facial expression categorisation and how this influence increases across the adult lifespan. Discrimination ability for facial expressions decreased with age in my sample, whilst no change was seen in the discrimination ability for body postures. This suggests age-related perceptual change that is specific to facial expressions, and not reflective of a general perceptual decline with age. A negative relationship was observed between the influence of body posture and the discrimination ability of facial expressions in the isolated cue condition in Experiment 1. A similar trend was seen in Experiment 2, where the influence of facial expression on body posture categorisation was investigated. A significant influence of facial expression on body posture categorisation was found, although it was not shown to change across the adult lifespan. A negative relationship was observed between the influence of facial expression and the discrimination ability for body postures in the isolated cue condition. My results challenge the social expertise theory and point towards older adults showing a larger influence of surrounding cues to compensate for a reduced discrimination ability for isolated cues, rather than as an adaptive strategy developed through social experience.

Chapter 4

Influence of body on facial expression perception in Autism.

4.1 Introduction

The accurate recognition and response to affective states of others is essential for optimal social cognition and communication in our everyday social lives. Autism Spectrum Disorders (ASD), henceforth Autism, refers to a group of neurodevelopmental disorders, which are often characterised by difficulties in social cognition and communication (American Psychiatric Association, 2013). These difficulties in social cognition include reduced facial expression recognition abilities relative to non-autistic people (although there have been mixed findings; For reviews, see: Keating and Cook, 2020; Lozier et al., 2014; Uljarevic and Hamilton, 2013). In our everyday lives, however, we rarely encounter facial expressions on their own; they are typically accompanied by a body posture. Research has shown that the perception of facial expressions can be significantly influenced by body posture in non-autistic adults (Aviezer et al., 2008; Meeren et al., 2005). For example, a disgusted facial expression is more likely to be categorised as angry when displayed with an angry body posture (Aviezer et al., 2008). Moreover, there are large individual differences in the extent of the influence of body posture on facial expression perception (Teufel et al., 2019), with some individuals showing a large influence of body posture and others showing little to no influence of body posture. A recent study in children and adolescents (Ward et al., 2023) found that the influence of body posture on facial expression perception decreases with age, concurrently with improved facial expression discrimination ability, such that younger children had reduced facial expression discrimination ability and showed a greater influence of body posture in making judgements on facial expression. This relationship in non-autistic children raises interesting questions regarding the influence of body posture in individuals who have difficulties in facial expression perception, such as autistic individuals. Studying the influence of body posture in autistic individuals could help deepen our understanding of the difficulties in social cognition associated with Autism, by investigating how they differ from non-autistic individuals. To my knowledge, only one study to date has investigated the influence of body context on facial expression perception in Autism. Brewer et al., 2017 found a significant influence of body posture on facial expression categorisation in both non-autistic and autistic adults, but they found no difference in the degree of influence that body posture had on facial expression perception between groups. Their findings suggest that autistic adults are influenced by body posture to a similar degree as non-autistic adults when perceiving facial expressions. These results are particularly interesting in the context of Ward et al.'s (2023) findings; the latter would suggest that autistic individuals should show a greater influence of body posture compared with non-autistic individuals, due to their difficulties in facial expression recognition

(Keating and Cook, 2020; Lozier et al., 2014; Uljarevic and Hamilton, 2013; Wang and Adolphs, 2017). It is also unclear how, or indeed if, body posture might influence the integration of emotion signals from face and body. A facial expression and a body posture together form a whole person. A prominent theory of information processing in Autism, the weak central coherence (WCC) theory (Frith, 1989), posits that autistic individuals show a preference towards a local processing style (Frith, 1989). For instance, autistic observers display improved performance on an embedded figures task compared with non-autistic observers (Ropar and Mitchell, 1999), where individuals are asked to find a simple form/shape embedded within a larger, complex figure. A preference towards local processing however also suggests that autistic individuals focus less on the integrated whole. Within this framework then, body posture could be expected to have less influence on the perception of facial expressions in autistic observers compared with non-autistic observers. This provides conflicting predictions regarding the influence of body posture on facial expression perception in autistic individuals. First, weaker facial expression discrimination precision often seen in autistic individuals should lead to a stronger influence of body posture, and conversely, second, weak central coherence in autistic individuals should lead to a weaker influence of body posture on facial expression perception. Here, using precise psychophysical methods, a novel means to measure body posture discrimination precision, and a larger sample size, I conducted an online study to investigate the relationship between discrimination precision of isolated facial expressions and isolated body postures, and the influence of body posture on facial expression perception in autistic and non-autistic adults.

4.2 Methods

4.2.1 Observers

This study was conducted online, and all participants were recruited through Prolific (Prolific Team, 2019). The sample of autistic individuals, as well as the matched non-autistic controls in this study were taken from a larger, curated sample, created by a group of researchers through Prolific (E. C. Taylor et al., 2022). This sample was created through multiple participant certification processes; they were all UK residents and had received a clinical diagnosis of ASD according to DSM or ICD criteria (American Psychiatric Association, 2013; World Health Organization, 2019). This diagnosis was received from an independent healthcare professional in a recognised clinical setting, when the participant was either a child or an adult. In line with previous studies that have recruited large samples of clinically diagnosed autistic people (Farmer et al., 2017; Grove et al., 2013; Milne et al., 2019), participants provided detailed information about their diagnosis (e.g. ASD, Asperger syndrome), their diagnosing clinician (e.g. Psychiatrist, Psychologist) and the location of the diagnosis. These details surrounding their diagnosis were also confirmed by the individual at multiple time points during the screening process. Individuals who had self-identified as autistic or those seeking a diagnosis were not eligible to participate. Many participants had also recently participated in autism research (Clutterbuck et al., 2021), including in-person studies (E. C. Taylor et al., 2021). This sample also contained a non-autistic sample, which was closely matched with the ASD sample on age, sex, and IQ. IQ was assessed using the International Cognitive Ability Resource (ICAR; Condon and Revelle, 2014). The ICAR test is a well-validated measure for online use, comprising matrix reasoning, three-dimensional rotation, verbal reasoning, and letter and number series. From this curated sample, we recruited a total of 78 autistic adult observers (34 male; age in years (mean ± std): 30.7 ± 9.3), with an age range of 18-58. A total of 73 non-autistic adult observers (35 male; age in years (mean ± std): 32.9 ± 10.6), with an age range of 19-62. Both the autistic and non-autistic samples used in this study were closely matched on age, sex, and general cognitive ability. This study was approved by Cardiff University School of Psychology Ethics Committee. Participants provided informed consent according to the Declaration of Helsinki. Consent was obtained via an online Qualtrics form (Qualtrics, Provo, UT). Participants were paid for their participation through Prolific.

4.2.2 Stimuli

Identical to stimuli used in Chapter 3, section 3.2.1.

4.2.3 Design

Identical to design used in Chapter 3, section 3.2.1.

4.2.4 Data Analysis

Identical to analysis and exclusion criteria applied in Chapter 3, section 3.2.1, apart from exclusions relating to age group.

Following exclusions, 44 autistic observers (13 male; age in years (mean ± std): 31.4 ± 9.2) and 53 non-autistic observers (24 male; age in years (mean ± std): 33.6 ± 10.5) were included in the analysis. After exclusions, both groups were still matched on IQ (Wilcoxon rank-sum test: $W = 1092.5$, $p = 0.595$), age (Wilcoxon rank-sum test:$W =$

1025, p = 0.174), and sex (Wilcoxon rank-sum test: W = 2, p = 0.8). Statistical analyses were carried out with the software R (The R Foundation for Statistical Computing). Data were non-normally distributed, so a Mann-Whitney U Test was used to examine group differences.

4.3 Results

4.3.1 Influence of body posture on facial expression perception

The PSE change, the difference between the PSE values for facial expressions displayed on an angry body posture vs. a disgusted body posture, was used as a measure of the influence of body posture in each participant. In the autistic sample, the PSE for facial expressions displayed on an angry body (Mdn = 0.676) was significantly higher than the PSE for facial expressions displayed on a disgusted body (Mdn = 0.414) (Fig 4.1 (top); Wilcoxon signed rank test W = 1781, $p < 0.001$). In the non-autistic comparison group, the PSE for facial expressions displayed on an angry body (Mdn = 0.672) was significantly higher than the PSE for facial expressions displayed on a disgusted body (Mdn = 0.362) (Fig 4.1 (bottom); Wilcoxon signed rank test W = 2626, $p < 0.001$), suggesting that both the autistic and the non-autistic comparison group showed a significant influence of body posture on facial expression perception. The PSE change in the autistic sample (Mdn = 0.625) however was significantly higher than the PSE change in the non-autistic comparison group (Mdn = 0.343) (Wilcoxon rank-sum test W = 1440, $p = 0.048$), pointing towards a greater influence of body posture on facial expression perception in the autistic sample relative to the non-autistic sample.

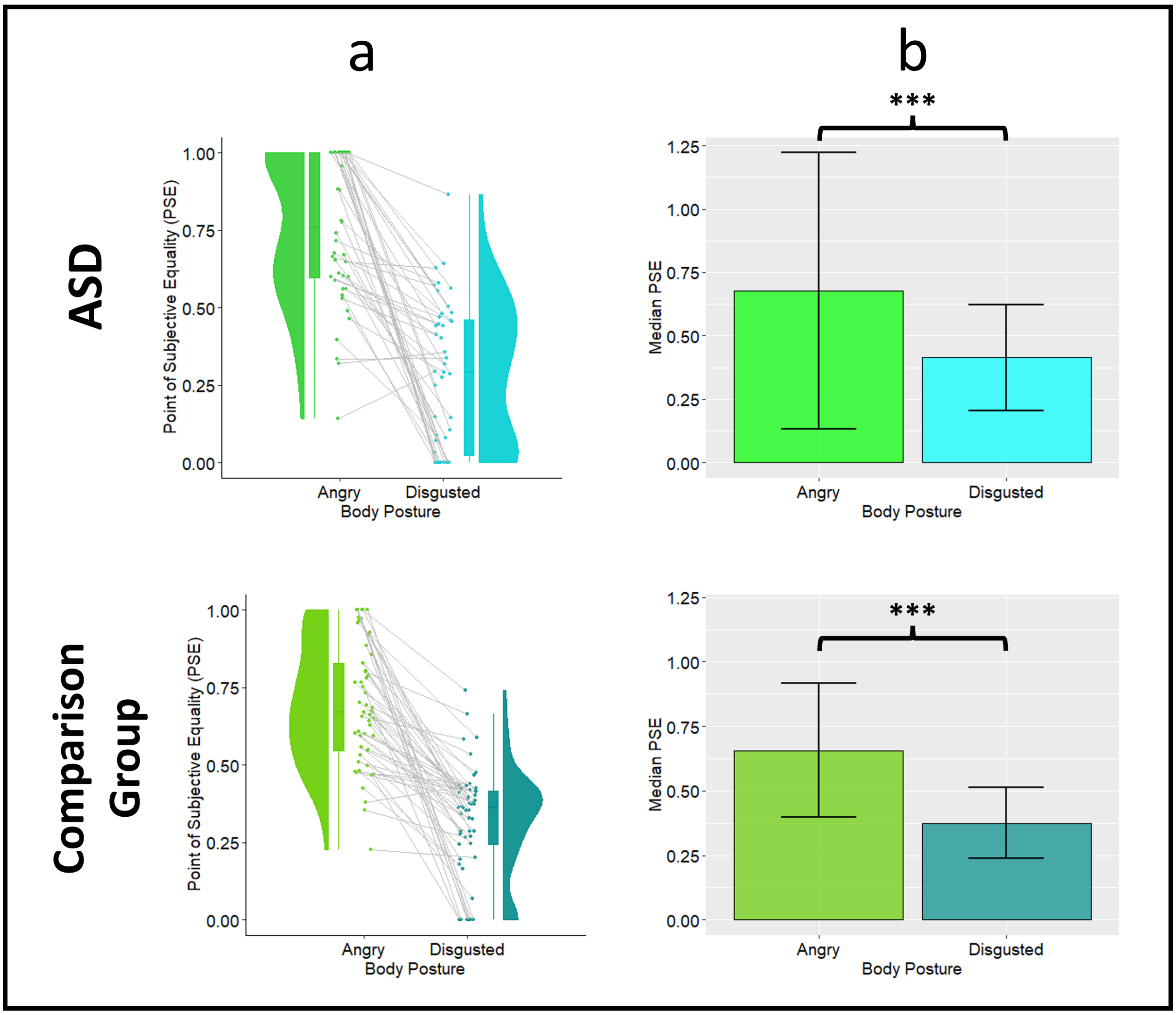


FIGURE 4.1: Figure showing the influence of body posture in the autistic (ASD) and non-autistic comparison group. (a) Raincloud plots showing the difference in PSE of categorisation of facial expressions shown on angry body posture (green) and disgusted body postures (blue). Each data point represents an observer, with lines linking the same observer in each condition. For the sake of visualisation, PSE values above 1 were capped at a value of 1, and PSE values less than 0 were capped at 0. (B) Bar plots showing the median PSE of categorisation of facial expressions shown on angry body postures (green) and disgusted body postures (blue). Error bars represent the IQR. Top – Autistic individuals, Bottom – Non-autistic individuals. *** $p<0.001$.

A post-hoc power analysis evaluated the sensitivity of the observed differences between the PSEs of facial expressions shown with an angry body posture or disgusted body posture in autistic and non-autistic groups. Achieved power was 0.98 (n = 44) for the autistic group and 0.99 (n = 53) for the non-autistic group, indicating a statistically significant association in both.

4.3.2 Facial Expression Discrimination Ability

Facial expression discrimination, as measured by the slope of the psychometric function in the face-only condition, was significantly higher in the non-autistic sample (Mdn = 2.636) than in the autistic sample (Mdn = 2.048) (Fig 4.2; Wilcoxon rank-sum test: W = 820, p = 0.012). This suggests that observers in the non-autistic comparison group had a higher discrimination ability for facial expressions than observers in the autistic sample.

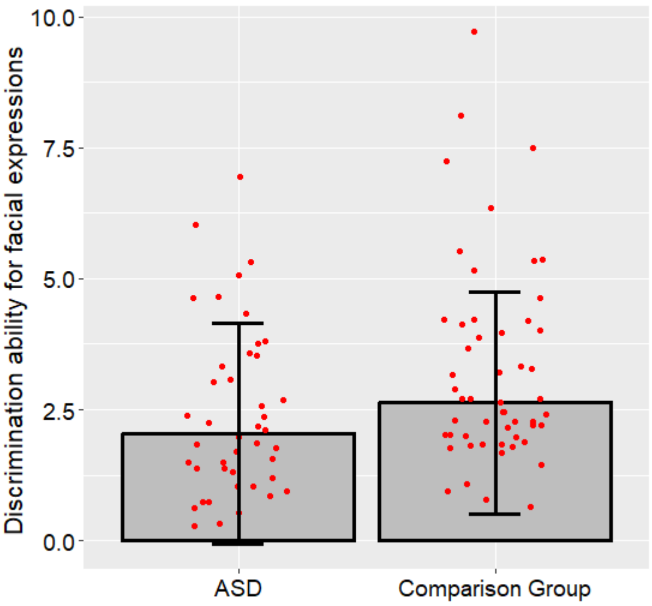


FIGURE 4.2: Bar plot showing the discrimination ability for facial expressions (slope of psychometric function in face-only condition) in the autistic (ASD) and non-autistic comparison groups. Each data point represents one observer. The bar represents the median for that sample. The error bar represented the IQR.

A post-hoc power analysis evaluated the sensitivity of the observed differences between the facial expression discrimination abilities in autistic and non-autistic groups.

The achieved power was 0.68. While this level of power is considered moderate, it suggests that my study may have been underpowered to detect smaller effects.

There was no difference in body posture discrimination ability between the two groups for the isolated body posture condition (Fig 4.3; Wilcoxon rank-sum test: W=1000, p=0.23).

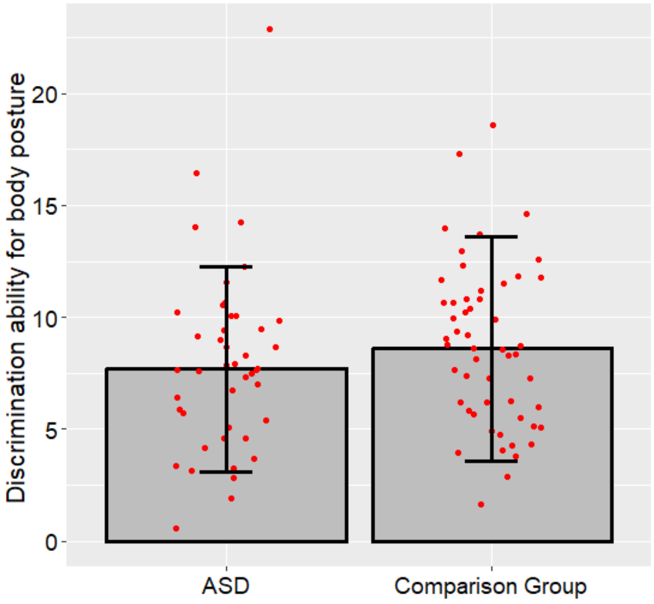


FIGURE 4.3: Bar plot showing the discrimination ability for body postures (slope of psychometric function in body-only condition) in the autistic (ASD) and non-autistic comparison group. Each data point represents one observer. The bar represents the median for that sample. The error bar represented the IQR.

4.3.3 Relationship between facial expression discrimination ability and the influence of body posture on facial expression categorisation

There was a significant negative relationship between facial expression discrimination ability and the influence of body posture on facial expression categorisation in both the autistic group (Fig 4.4(a); rs = -0.39, p = 0.0094) and the non-autistic comparison group (Fig 4.4(b); rs = -0.30, p = 0.028). These correlations were not statistically different from each other (z = -0.4665, p-value = 0.6409).

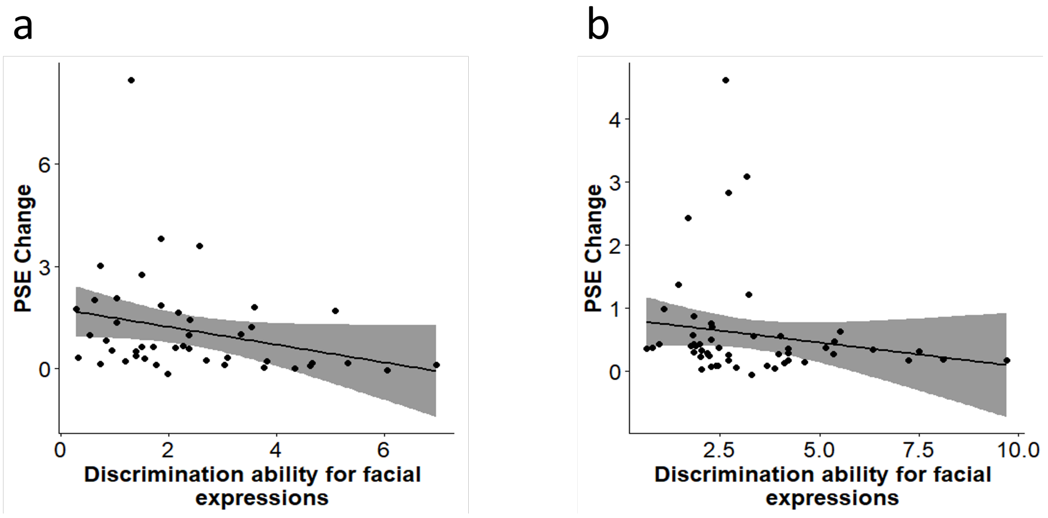


FIGURE 4.4: Scatterplots showing the relationship between discrimination ability for facial expressions (slope of psychometric function in the face-only condition) and influence of body posture on facial expression categorisation (PSE Change). Observers with PSE change values above 1 included. A significant negative relationship was seen in both the (a) Autistic (ASD) group and (b) non-autistic comparison group. The 95% confidence interval is shown with grey shading.

A post-hoc power analysis evaluated the sensitivity of the observed correlation between facial expression discrimination ability and body posture influence in autistic and non-autistic groups. Achieved power was 0.76 (n = 44) for the autistic group and 0.6 (n = 53) for the non-autistic group.

The relationship remained significant even when observers with a PSE change greater than 1 were excluded in both the autistic sample (Fig 4.5(a); rs = -0.54, p = 0.0034) and the non-autistic comparison group (Fig 4.5(b); rs = -0.30, p = 0.043). These correlations were not statistically different from each other (z = -1.1886, p-value = 0.2346).

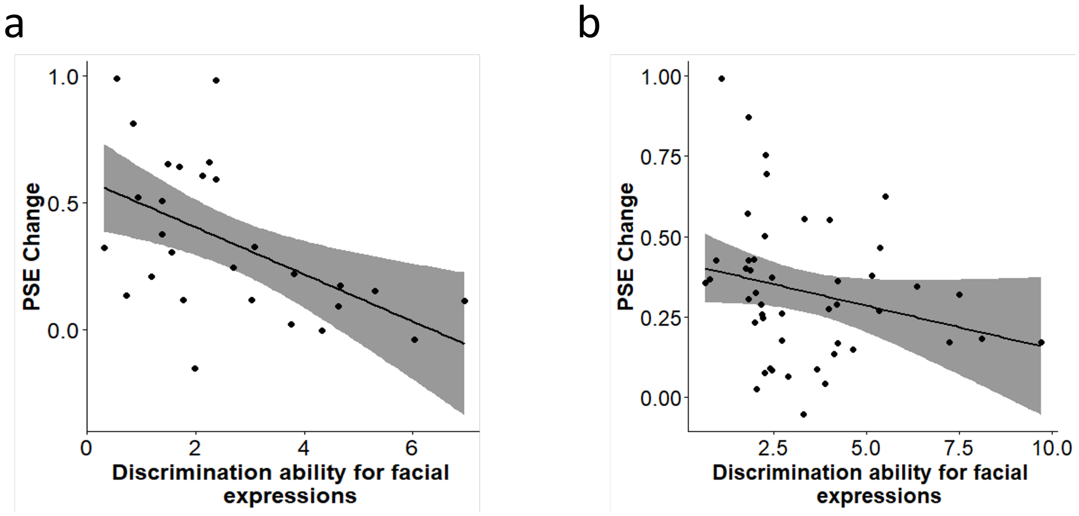


FIGURE 4.5: Scatterplots showing the relationship between discrimination ability for facial expressions and influence of body posture on facial expression categorisation (PSE Change) when participants with PSE above 1 excluded. Each point represents a participant. The 95% confidence interval is shown with grey shading.

A post-hoc power analysis was conducted to evaluate the sensitivity of the observed correlation between facial expression discrimination ability and the influence of body posture in the autistic and non-autistic groups. The analysis revealed an achieved power of 0.86, indicating a 86% chance of detecting the observed correlation coefficient of -0.54, assuming the observed sample size of 28 and a significance level of 0.05 in the autistic group. For the non-autistic group, the analysis revealed an achieved power of 0.55, indicating a 55% chance of detecting the observed correlation coefficient of -0.30, assuming the observed sample size of 47 and a significance level of 0.05.

4.4 Discussion

The current study investigated factors driving the influence of body posture on facial expression perception in autistic and non-autistic adults. I found that body posture has a significant influence on facial expression perception in both groups, but the autistic group showed a significantly greater reliance on body posture in making judgements of facial expressions compared with the non-autistic group. Alongside this group difference in the influence of body posture, I also found reduced precision of isolated facial expression representations, but no difference in precision of isolated body posture representations, in autistic observers compared with non-autistic observers, suggesting that facial expression discrimination difficulties in Autism may not be reflective of generally reduced emotion discrimination abilities. Within each group, the precision of isolated facial expression representations was significantly related to the influence of body posture on facial expression perception, with lower precision leading to an increased influence of body posture. Taken together with the significantly lower precision of facial expression representations in the autistic group compared with the non-autistic comparison group, this suggests that the precision of facial expression representations is likely a key factor in the increased reliance on body posture in making judgements of facial expression in the autistic group.

My finding of a significant influence of body posture on facial expression categorisation is consistent with the findings of previous research (Aviezer et al., 2008; Brewer et al., 2017; Meeren et al., 2005). However, I found that the influence of body posture is significantly greater in the autistic group compared with the non-autistic group, which is interesting when considered in the context of the Weak Central Coherence (WCC) theory, which posits that autistic observers might be expected to show a weaker influence of body posture compared with the non-autistic group, due to their preference for a local over global processing style. In my whole-person task, observers were instructed to ignore the body posture and to make their judgements based on the facial expression only, to ensure that I was measuring the influence that body posture has on facial expression perception specifically. These instructions, combined with the predictions based within the WCC theory, could be expected to lead to an attenuated influence of body posture in autistic observers. However, my results suggest the opposite: autistic observers were more influenced by body posture when recognising facial expressions than non-autistic individuals. It therefore seems unlikely that WCC is a primary factor in determining the influence that body posture has on facial expression recognition. Instead, my findings point towards the importance of facial expression discrimination ability in driving the influence of contextual cues. However, without an independent measure of WCC in the current study, I cannot exclude WCC also playing a role in the influence of body posture on facial expression perception.

Research on facial expression recognition in autistic individuals has produced conflicting results, with some studies finding difficulties in autistic compared to non-autistic observers and others finding no differences (For reviews, see: Keating and Cook, 2020; Uljarevic and Hamilton, 2013). One potential factor contributing to these inconsistencies may be the type of facial expression stimuli used. Studies that rely on stereotypical 100% facial expressions may not be sensitive enough to detect subtle difference between autistic and non-autistic groups due to ceiling effects associated with using these stimuli (Keating and Cook, 2020). In my study, the use of facial expression morphs allowed me to characterise facial expression recognition in a more sensitive manner. The reduced precision of facial expression representations that were observed in autistic individuals is consistent with the results of a previous study by Wang and Adolphs, 2017, who also used facial expression morphs between emotions to study facial expression recognition in autistic and non-autistic adults and found a similarly reduced precision in autistic individuals.

The only previous study to compare the influence of body posture on facial expression perception between autistic and non-autistic groups (Brewer et al., 2017) found no difference in the influence of body context between the autistic group and the non-autistic group, as well as no difference in the discrimination ability for facial expressions between the samples. These findings sharply contrast with my results, however there are some methodological differences between the Brewer et al., 2017 study and the present one, which could account for the discrepancies in results. First, the sample size of my study for both groups was almost double that in Brewer et al., 2017. Second, Brewer et al.'s (2017) study was based on the discrimination of facial expression for one male identity only, compared with four male identities used in my study.

My results are therefore more likely to be generalisable to facial expression recognition across identities. Interestingly and consistent with my results, Brewer et al., 2017 reported a significant relationship between facial expression discrimination precision and the influence of body posture in their autistic group. However, they did not find evidence for a similar relationship in their non-autistic comparison group. Again, this difference in results could be due to the aforementioned methodological difference in sample size and stimuli used.

There are a few limitations in the current study, which need to be discussed. The first being that no eye-tracking data was collected for this study, which leaves the possibility that the autistic individuals were avoiding looking at the face more than the non-autistic individuals. However, in my autistic group, I found a significant positive relationship between discrimination ability in the isolated facial expression condition and the average discrimination ability in the whole-person condition (where the observer is instructed to make judgements on the face only, and ignore the body) (rs = 0.42, p = 0.0048). This suggests that autistic individuals were making their judgements based on the facial expression in the whole-person condition, rather than avoiding the face and focussing on the body posture only. The second is the limited number of emotional expressions used in this study (just anger and disgust). However, due to the perceptual similarity between anger and disgust, these two emotional expressions show the most robust effect of body context compared to other emotions I could have used (Aviezer et al., 2008). A robust influence of body posture was important for maximising sensitivity to individual differences within and between our two groups of observers. A methodological consideration for future studies, is that no direct measure of bias towards local processing was collected. This limits my ability to determine whether WCC plays a role in modulating the degree of influence that body posture has on facial expression categorisation. An embedded figures task could be added to this current methodology to provide a direct measure of central coherence in these participant samples. A final limitation to consider is that a large portion of autistic individuals were excluded after applying the exclusion criteria, which could compromise the generalisability of these findings. This raises concerns regarding whether the exclusion criteria effectively captured the diversity within autistic populations and whether adjustments might be required to ensure a more inclusive approach in future studies. Another factor to consider is whether the task is suitable for autistic individuals, as it is possible that the task's design or demands posed challenges for a considerable portion of the autistic individuals, leading to their exclusion. With this limitation in mind, future research would benefit from refining the inclusion criteria to better capture the diversity within autistic individuals and exploring alternative methodologies or task adaptations that accommodate the unique characteristics of autistic individuals. This would not only enhance the inclusivity of the study but would also contribute to a more comprehensive understanding of social perception in Autism.

These results underscore the importance of considering individual differences and sensory sensitivities in the perception of social cues among autistic individuals, paving the way for tailored interventions and support strategies aimed at enhancing emotion recognition skills and social functioning in this population. By elucidating the distinct patterns of influence observed in Autism, this study contributes valuable insights to the growing body of literature on social cognition in Autism, offering a foundation for future research endeavours that are aimed at developing a deeper understanding of social cognition in Autism.

4.5 Chapter Summary

In summary, my results demonstrate both the differences and commonalities between autistic individuals and non-autistic individuals regarding the perception of face, body and whole-person emotion stimuli. A significant difference was found in discrimination ability for facial expressions between autistic and non-autistic individuals, as well as a significant difference in the influence that body posture has on facial expression perception with autistic individuals showing a significantly higher influence than non-autistic individuals. Across each group, I found that observers with lower facial expression discrimination ability showed an increased influence of body posture, and those observers with a higher discrimination ability for facial expressions showed a decreased influence. These results highlight that similar principles may govern the integration of facial expression and body posture information in autistic individuals as in non-autistic individuals. By elucidating the parallels in social stimuli perception between autistic and non-autistic individuals, my study enhances the understanding of the underlying processes in Autism, advancing the knowledge base for more targeted investigations into what could be causing the difficulties in social cognition seen in autistic individuals.

Chapter 5

Integrated Representations of Face and Body Emotion in Visual Processing Pathways

5.1 Introduction

Previous chapters of this thesis investigated how face and body emotion cues are integrated to form a complete perception of a person's emotional expression. I was able to show that body posture has significant effects on facial expression perception across the adult lifespan (Chapter 3) and in autistic individuals (Chapter 4). However, the neural mechanisms underlying this integration in the human brain remain unclear, with some debate about the locus of this integration along the visual processing hierarchy. Several competing accounts exist regarding the integration of face and body cues in the human brain: some researchers have proposed an early integration (Aviezer et al., 2008; Foster et al., 2021, 2022; Pitcher et al., 2012), while others have suggested integration in later stages of the processing hierarchy (Fisher and Freiwald, 2015; Harry et al., 2016; Hu et al., 2020; Song et al., 2013; Teufel et al., 2019). More recently, a distributed model for face and body integration has also been proposed (Foster, 2022) with different stages of the processing hierarchy proposed to be involved depending on the information being integrated from face and body (e.g. identities, and emotional expressions).

One potential issue in resolving this debate lies in accurately identifying what constitutes ’early’ and ’late’ areas in the visual processing system. The delineation of these areas can be complex due to variations or limitations in the methodologies used. Additionally, the dynamic nature of neural processing suggests that the progression of information along the visual pathway may not adhere to linear temporal or spatial hierarchies. One approach to mitigate this challenge involves adopting a multi-modal methodology, integrating spatial and temporal measurements within a single experiment. For example, conducting both MEG and fMRI sessions for each participant would enable comprehensive recording of both the spatial and temporal dynamics of stimulus responses.

Meeren et al. (2005) was one of the earliest studies to provide evidence for early-stage integration of face and body emotion cues. In their study, electrophysiological recordings were made while observers judged the emotions of face-body stimuli that were either congruent or incongruent. They found a larger increase in the P1 occipital component in response to incongruent face-body pairs compared to congruent pairs, suggesting that this early peak (between 80-130ms) is sensitive to the congruency of face and body emotion (Meeren et al., 2005). A study by Aviezer et al., 2011, building upon earlier research (Aviezer et al., 2008), asked observers to categorise facial expressions while ignoring the body posture of a whole-person stimuli. They added a concurrent memory task to increase cognitive load during the categorisation. Despite the addition of cognitive load, they found that body posture still influenced the perception of facial expressions, which the authors suggested is indicative of integration of face and body emotion cues being an automatic process (Aviezer et al., 2011), occurring in early stages of the visual processing hierarchy. A more recent study by Foster et al., 2022 investigated the integration of viewpoint information from face and body. They used MVPA techniques to determine whether brain response patterns to different face viewpoints could also apply to brain response patterns evoked by different body orientations, and vice versa. The presence of such generalised brain patterns across face and body viewpoints would imply common coding for viewpoint. They found that a region at the intersection between the OFA and EBA in both hemispheres encoded viewpoint information, regardless of whether the information originally came from a face or body. Their results suggest that certain information from face and body is processed and commonly coded at an early stage of the face and body processing pathway (Foster et al., 2022).

However, several studies have provided support for integration occurring in later stages of processing (Fisher and Freiwald, 2015; Harry et al., 2016; Song et al., 2013; Teufel et al., 2019). Fisher and Freiwald, 2015 used fMRI to investigate whether face areas (or face patches) in macaques show a different level of response to whole-agent stimuli compared with individually presented faces and bodies. They found that whole-agent selectivity developed from posterior to anterior visual areas in the macaque brain, suggesting that face and body integration occurs more anteriorly along the visual processing pathway in the macaque brain (Fisher and Freiwald, 2015). Harry et al., 2016 found stronger responses to faces and bodies in the ATL in humans, than to other categories such as spiders or fruits. Using MVPA techniques, they observed a positive correlation in the response pattern for faces and bodies in the ATL, and a negative correlation in the mid-fusiform region for the same stimuli. This suggests common coding of face and body information in the ATL, but not in the fusiform gyrus, indicating increased integration of face and body cues from posterior to anterior regions. Consistent with the idea of hierarchical integration along the visual processing pathway, Song et al., 2013 investigated response differences to isolated faces or bodies and face-body combinations in posterior regions (OFA, EBA) and more anterior regions (FFA, FBA) of the visual processing pathway. They found an increased response to face-body stimuli compared to isolated faces in the FFA, but no significant difference in the OFA. Similarly, there was an increased response to face-body stimuli compared to isolated bodies in the FBA, with no significant difference in the EBA (Song et al., 2013). This suggests hierarchical integration of face-body stimuli, with whole-agent processing occurring in more anterior regions. Teufel et al., 2019 provided further evidence for a hierarchical account of face and body integration. They found that adaptation to facial expressions was unaffected by the accompanying body posture context, implying that integration of face and body cues occurs downstream from sites of facial expression adaptation. As the sites of these adaptation aftereffects are thought to be located in higher-level visual areas (e.g. FFA), their results suggest that integration occurs beyond these areas, such as in the ATL.

This current study addressed the conflicting accounts regarding the hierarchy of face and body emotion integration along the visual processing pathway, using the influence of body posture on facial expressions identified in previous chapters as a behavioural indicator for this integration. I utilised RSA to determine the extent to which brain activity patterns along the ventral visual pathway, as measured by fMRI, represent isolated emotion cues or integrated emotion cues. If a brain area processes integrated emotions, its activity patterns should match more closely with an integrated emotion cue model compared to an isolated emotion cue model. Based on previous research, a higher correlation between an integrated emotion cue model and brain activity patterns in anterior visual processing regions, such as the ATL, as opposed to an isolated emotion cue model, would support the concept of late integration of face and body emotion signals. Conversely, a higher correlation with an integrated model in posterior regions, like the OFA, would lend support for early integration accounts. If both posterior and anterior regions show higher correlation with an integrated emotion cue model than an isolated emotion cue model, this would provide evidence for integrated emotion cues throughout the visual processing hierarchy.

5.2 Methods

5.2.1 Observers

A total of 34 neurotypical participants (9 male; age in years: 24 ± 5), with an age range of 19-38 were recruited to take part in the present study. All participants had normal or corrected-to-normal vision and were either affiliated with Cardiff University or someone who was familiar with psychological research. All experimental protocols were approved by Cardiff University School of Psychology Ethics Committee and were in line with the Declaration of Helsinki. All participants provided informed consent and were fully debriefed at the end of testing. Participants received £35 for taking part in the study. Following data exclusions, which are detailed below, the remaining sample consisted of 22 participants (8 male; age in years (mean ± std): 25 ± 4), with an age range of 19-37.

5.2.2 Behavioural Testing

Stimuli

All participants completed the same online psychophysical behavioural task as detailed in Chapter 3, section 3.2.1. The only difference was the size of the face stimuli shown in this version of the task; larger face stimuli were used to match the size of the face stimuli shown in the scanner. This change ensured consistency between the stimuli used to collect the behavioural and scanning data, both of which are used in the main analyses of this study. This meant that, unlike in Chapters 3 and 4, the size of the facial expressions in isolation were bigger than the facial expressions shown with the body posture in the whole person condition. To minimise discrepancies between the scanner and behavourial testing screens, participants were required to access the study link exclusively via a desktop computer or laptop.

Design

The behavioural portion of the study was conducted online, and stimuli were presented using PsychoPy (Jonathon Pierce and MacAskill, 2018) and hosted on Pavlovia (www.pavlovia.org). Participants accessed the task via an online link. Participants could only take part in the study if they were accessing the link via a desktop computer or laptop, to keep the presentation of stimuli as consistent as possible. As in Chapters 3 and 4, the participants were presented with 4 stimulus types, across 3 tasks (face-only, body-only, face morphs on either an angry or disgusted body posture). For each trial, participants were presented with a stimulus and asked to make a judgment on whether the stimulus was disgusted or angry. There were 2 stimulus presentation orders for each stimulus type, which were randomly assigned by the experimenter.

5.2.3 MRI Acquisition

fMRI acquisition

Whole-brain echo-planar imaging (EPI) gradient echo data was acquired on a 3T Siemens Magnetom MRI scanner (Siemens Healthcare, Erlangen, Germany) (TR/TE=2000/30ms; resolution=2x2x2mm; 64 slices; multi-band factor=4) with an acquisition time (TA) of 9min 50sec for the functional localiser task and 14min 38sec for each of the three RSA runs. The slice angle for the acquisition was positioned along the anterior commissure and posterior commissure to minimise signal drop out from the temporal regions. A high-resolution MP2RAGE structural scan (TR/TE=2100/3.24ms; resolution=1x1x1mm; TA=7min 52sec) was also acquired (Marques et al., 2010).

Functional localiser task

Participants were presented with grey-scale stimuli of faces, houses, bodies, and objects projected onto a Perspex screen, which was then viewed through a mirror mounted on the MRI head coil. Male and female neutral body postures were presented, as well as male and female facial expressions. Angry, disgusted, sad, fearful, happy, and neutral faces were shown. The stimuli were presented in category blocks: faces, bodies, houses, and objects. There were two stimulus presentation orders, and these were counterbalanced across participants. 16 images were displayed in each block, with each image being displayed for 800ms with a 200ms inter-stimulus interval. A block of fixation followed each stimulus category block, where a black fixation cross (15secs) followed by a red fixation cross (1sec) was displayed on a mean grey screen. The fixation cross turning red was an indication to the participant that the next block was about to start. There were four blocks of each stimulus category in total, meaning that 64 trials per stimulus category were presented overall in this task. Participants were instructed to respond using a key press when the same stimulus was presented twice in succession (1-back task). The number of trials where the same stimulus was shown on two consecutive trials varied between 0 and 3 per block. Button responses were recorded using a right-hand MR compatible button box. The average accuracy across participants was also recorded (percentage accuracy (mean ± std): 83.1 ± 11.5). The 1-back task was administered as the first task during the scan session. Participants were instructed verbally and through written instructions on the screen, and their understanding of the task instructions was confirmed verbally before beginning the task. No practice trials were provided.

RSA task

The main task performed while the participant was in the scanner was split into three identical scans. Participants were presented with the same grey-scale stimuli of faces, bodies, and whole people shown in the behavioural task in this study, but only morph levels of 10%, 30%, 50%, 70%, and 90% disgust were shown in the scanner. Within each of the three runs, there were 40 trials per stimulus type (facial expressions, body postures, facial expressions on an angry body posture, and facial expressions on a disgusted body posture). Each stimulus was displayed for 1000ms, followed by a jittered fixation cross (2000-4000ms). The average jitter time was 3000ms for all participants. An additional 40 trials in each run were presented with a green dot somewhere on the stimulus (stimuli from all 4 stimulus types were used for these dot probe trials). Participants were asked to respond using a key press when they saw the dot appear on a stimulus. The attentional task ensured that participants paid attention to the stimuli. Button responses were recorded using a right-hand MR compatible button box. Seven participants were excluded due to less than 60% accuracy in this attentional task. The average accuracy for the remaining participants was 91.8% ± 8.8%. In total, across all runs of the experiment, there were 600 trials presented (120 per stimulus type and 120 attention dot trials).

5.2.4 Behavioural Data Analysis

Identical to analysis and exclusion criteria applied in Chapter 3, section 3.2.1, apart from exclusions relating to age group.

2 participants were excluded from analyses due to a poor fit of the psychometric functions in their behavioural data.

5.2.5 fMRI Analysis

fMRI pre-processing

fMRI data pre-processing was carried out using Statistical Parametric Mapping (SPM12; Wellcome Department of Imaging Science, London, UK; www.fil.ion.ucl.ac.uk/spm) operating in Matlab. All functional data was first unwarped using the B0 field map generated from a magnitude and phase image in SPM12. These images were then realigned to correct for head movement, leading to exclusion of 3 participants with head movement over 2mm (1 voxel). With all functional images now spatially aligned with each other, images were slice-time corrected based on the middle slice in each volume. The MP2RAGE structural images were then warped to MNI space, and then co-registered to the functional images. This ensured the functional images were normalised to MNI space. No smoothing was performed on the images from the RSA experimental runs. Functional images from the localiser runs were spatially smoothed with a Guassian kernel of 9mm full-width at half-maximum.

Functional localiser analysis

A univariate General Linear Model (GLM) was implemented to examine the BOLD response associated with face and body stimuli in the functional localiser data. Faces > Houses contrast was used to localise cortical regions involved in face processing, and Body > Objects contrast was used to localise cortical regions involved in body processing. A second-level random effects analysis was carried out to identify regions of interest (ROIs) involved in face processing (OFA, FFA, STS, ATL) and body processing (EBA, FBA). To define ROIs in these areas, images were thresholded at an uncorrected threshold of $p<0.001$ and the peak coordinates in these areas were used to create a

ROI sphere of radius 9mm for the Faces > Houses (for face-selective areas) and the Bodies > Objects (for body-selective areas). MNI coordinates for the functional ROIs are found in Table 5.1 (right hemisphere) and Table 5.2 (left hemisphere). No peak coordinates could be identified for FBA in the left hemisphere. There was a degree of overlap between the right FFA and right FBA ROI spheres.

The face and body areas identified in the functional localiser analysis served solely as reference points in the correlation map figures presented in my main analysis. It's important to note that these areas were not subjected to further region of interest (ROI) analysis.

TABLE 5.1: Right hemisphere ROI coordinates from functional localiser task

Region	x	y	z
OFA	47	-78	-2
FFA	44	-49	-19
STS	51	-45	13
EBA	49	-74	7
FBA	44	-44	-16
ATL	48	7	-31

TABLE 5.2: Left hemisphere ROI coordinates from functional localiser task

Region	x	y	z
OFA	-52	-76	8
FFA	-44	-48	-22
STS	-46	-50	10
EBA	-50	-78	12
ATL	-48	0	-20

5.2.6 RSA Searchlight Analysis

Construction of models

Two basic categorical models were created to provide simple perceptual models for each of the basic stimulus categories: face and body. These two models were only concerned with whether a face was shown or not (Face-only model; Fig 5.1(a)) or a body was shown or not (Body-only model; Fig 5.1(b)). For example, in the face-only model RDM (Fig 5.1(a)), comparisons of face stimuli (i.e. isolated faces, faces with angry body posture, and faces with disgusted body posture) and isolated body stimuli were set to 1 (most dissimilar), because this model is only concerned with whether a face is present. Similarly for the body-only model RDM (Fig 5.1(b)), comparisons between body stimuli (isolated body stimuli and whole-person stimuli) and isolated face stimuli were set to be most dissimilar.

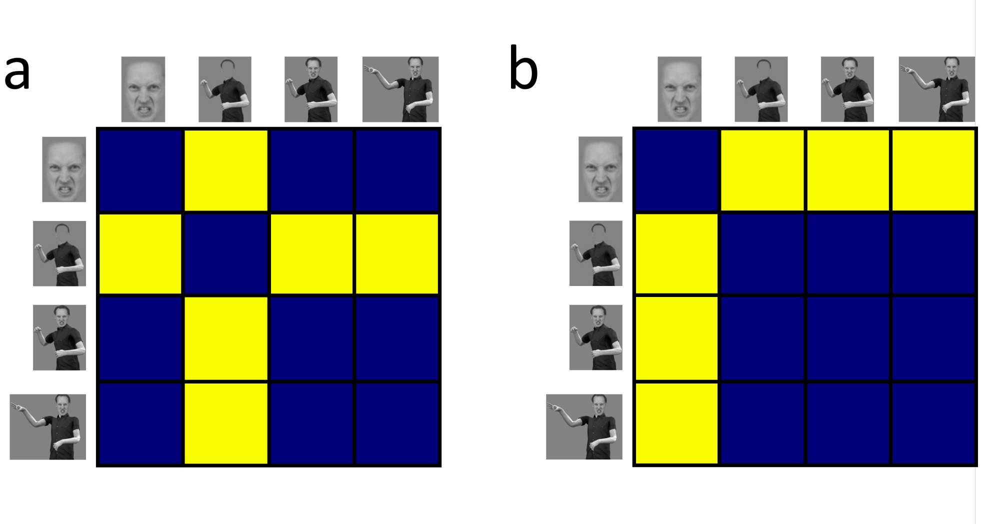


FIGURE 5.1: RDMs of the Face-only model (a) and Body-only model (b). Yellow = most dissimilar. Blue = most similar.

Two distinct emotion perception models were created to investigate how the brain integrates emotion information from face and body cues. The isolated emotion cue model is concerned with the perceptual discrimination dissimilarity of isolated emotion stimuli without the integration of body posture. By contrast, the integrated emotion cue model represents perceptual discrimination dissimilarity of emotion stimuli when integration has occurred. Perceptual discrimination data to create these models was derived from the psychophysical tasks. To construct an RDM based on participants' perceptual discrimination, their perceptual discrimination for a given stimulus morph level from the relevant psychometric function was used. To obtain dissimilarity measures for pairs of stimuli, the Euclidean distance between their respective perceptual discrimination was computed (Fig 5.2).

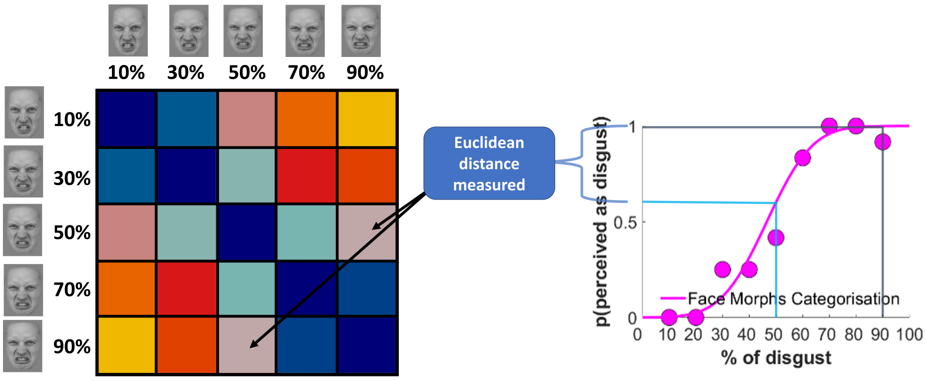
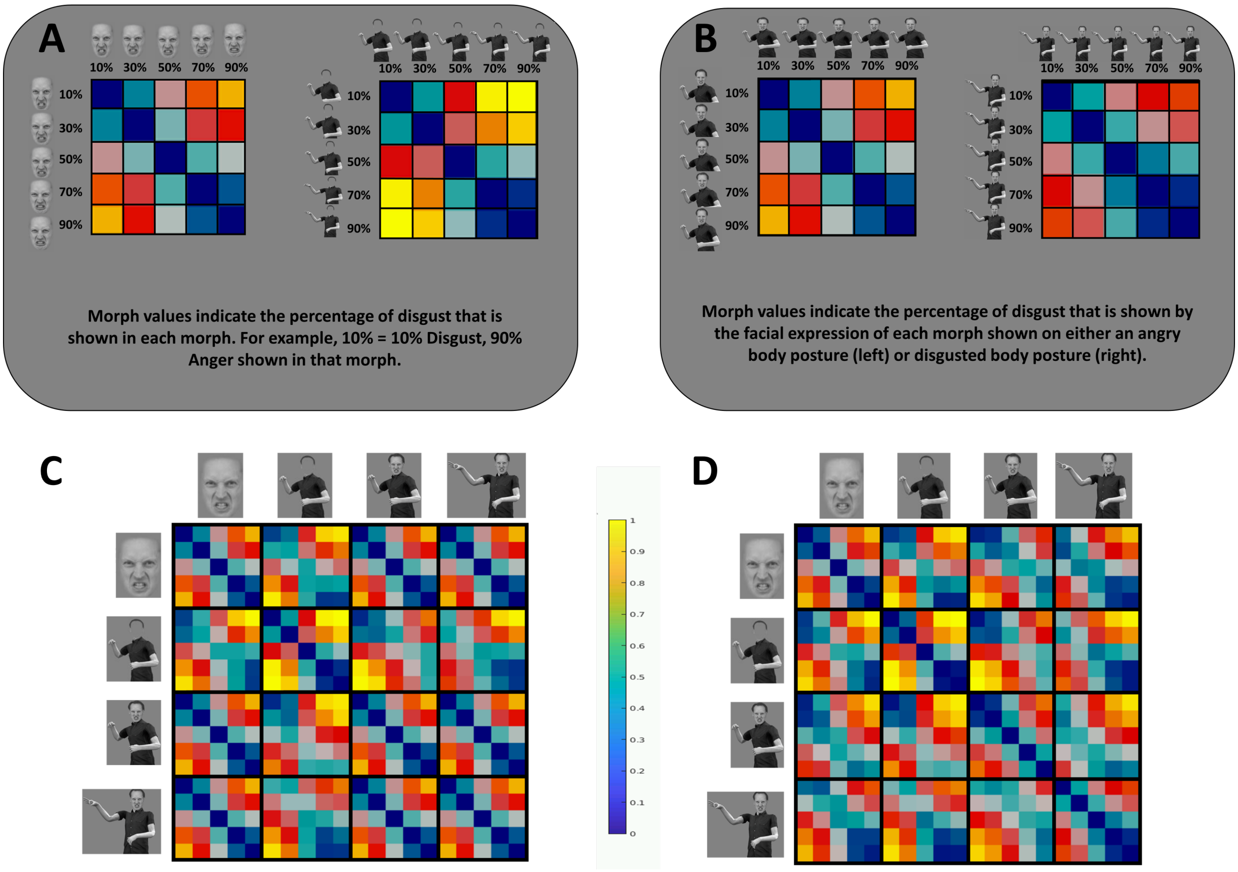


FIGURE 5.2: The individual perceptual discrimination RDMs were created using the psychophysical data collected in the online behavioural task. The Euclidean distance between the perceptual discrimination for each morph level pair represents the dissimilarity between stimulus pairs. Smaller numbers represent greater perceptual discrimination similarity, whereas larger numbers represent greater perceptual discrimination dissimilarity. % morph level represents the amount of disgust in the stimulus e.g. 90% = 90% disgusted and 10% anger in the stimulus.

The integrated emotion cue model was then created by averaging the perceptual discrimination RDMs for all participants (Fig 5.3(D)). For the isolated emotion cue model Fig 5.3(C), the perceptual discrimination dissimilarity for stimulus pairs was calculated as described above for the integrated emotion cue model, with one exception: the whole-person stimuli were treated as isolated face stimuli and therefore perceptual discrimination for these stimuli was based on the discrimination of isolated face stimuli at a given morph level. Therefore, the only difference between the isolated and integrated emotion cue models lies in the perceptual discrimination of the whole-person stimuli. In the isolated emotion cue model Fig 5.3(C), face and body information is not integrated and perceptual discrimination occurs in the absence of any influence of body posture on facial expression perception. Conversely, in the integrated emotion cue model Fig 5.3(D), face and body information has been integrated and body context has an influence on facial expression perception (as reflected in the shift in the psychometric functions for the whole-person stimuli).



Morph values indicate the percentage of disgust that is shown in each morph. For example, 10% = 10% Disgust, 90% Anger shown in that morph.

Morph values indicate the percentage of disgust that is shown by the facial expression of each morph shown on either an angry body posture (left) or disgusted body posture (right).

FIGURE 5.3: Top Panel: (A) Depicts a subset of the RDMs in (C) and (D) to highlight the morph levels for each stimulus in the RDM for isolated facial expressions and body postures. The morphs range from angry to disgusted, with percentage indicating the level of disgust displayed in the morph (e.g. 10% disgust and 90% anger). (B) Similar to (A), illustrates the morph levels for each stimulus, but here represent the percentage of disgust shown in a facial expression displayed with either an angry (left) or disgusted (right) body posture. Bottom Panel: (C) Isolated emotion cue model. (D) integrated emotion cue model. Yellow = most dissimilar. Blue = most similar. The models differ in their representations of face-whole person stimulus comparisons, as well as the whole person-whole person stimulus comparisons to reflect the change in representation when body posture is being integrated into facial expression perception in the integrated emotion cue model (D) compared with the isolated emotion cue model (C).

Mask

A searchlight with a radius of 9mm was carried out within a mask of the ventral visual pathway to evaluate the areas in which the neural activity pattern correlated with each model described above. For each subject, an RDM was calculated for each searchlight voxel within the mask. A schematic of the mask used is shown in Figure 5.4.

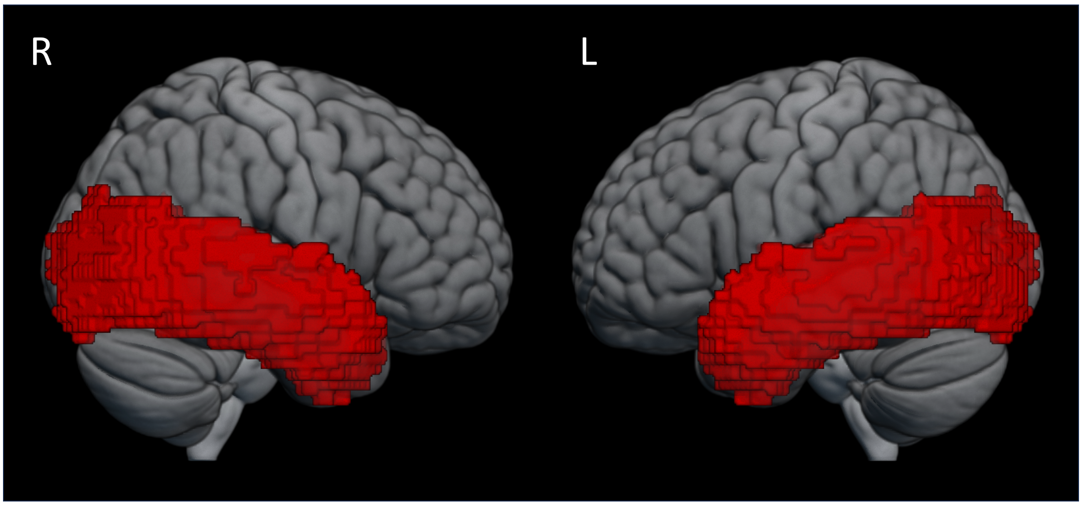


FIGURE 5.4: The searchlight mask which included the occipitotemporal lobe.

Statistical Analyses

To reveal which brain regions' activity patterns were most similar to each model, I performed a searchlight analysis (Kriegeskorte et al., 2006) in the RSA toolbox based in Matlab (Nili et al., 2014). Correlation maps within the mask were generated by calculating the correlation between the model RDM and the searchlight RDM (representing patterns of brain activity) centred at each voxel in each participant. Neural RDMs for each searchlight were Spearman correlated with each of the categorical models (Fig 5.1, the isolated emotion cue model (Fig 5.3(C)), and the integrated emotion cue model (Fig 5.3(D)). The given correlation value was then assigned to the centre voxel of each searchlight, which produced a 3D map of correlation values within the specified mask.

To conduct group-level statistical analyses, the Spearman's correlation values were Fisher-transformed. For the categorical models, I tested the null hypothesis that there was no significant difference between the correlation value and zero using a one-sided t-test. To compare the isolated emotion cue model with the integrated emotion cue model, I used paired t-tests to examine the null hypothesis of no difference between these two models. These tests were applied to assess the significance of the correlations and model differences in my analysis.

5.3 Results

5.3.1 Behavioural Results

Influence of body posture on facial expression perception

As in previous chapters of this thesis, the PSE change was used as a measure of the influence of body posture in each participant. The PSE for facial expressions displayed on an angry body (Mdn = 0.6237) was significantly higher than the PSE for facial expressions displayed on a disgusted body (Mdn = 0.3726) in my sample (Fig 5.5; Wilcoxon signed rank test. W = 454, $p < 0.001$), suggesting that body posture has a significant influence on facial expression perception. As in previous chapters, there is large variability in the extent to which individuals are influenced by body posture.

FIGURE 5.5: The influence of body posture on facial expression perception. Raincloud plot showing the difference in PSE of categorisation of facial expressions on angry body postures (green) and disgusted body postures (blue). Each data point represents an observer, with lines linking the same observer in each condition.

5.3.2 Categorical Model Results

A searchlight analysis within the mask (detailed above) identified significant correlations with the face-only model (Fig 5.1(a)) ($p<0.05$, FWE-corrected, Table 5.3; Fig 5.6) in left and right FFA and ATL, left STS, right middle temporal gyrus, and in right precuneus, which indicates the involvement of these brain areas in encoding the presence of a face.

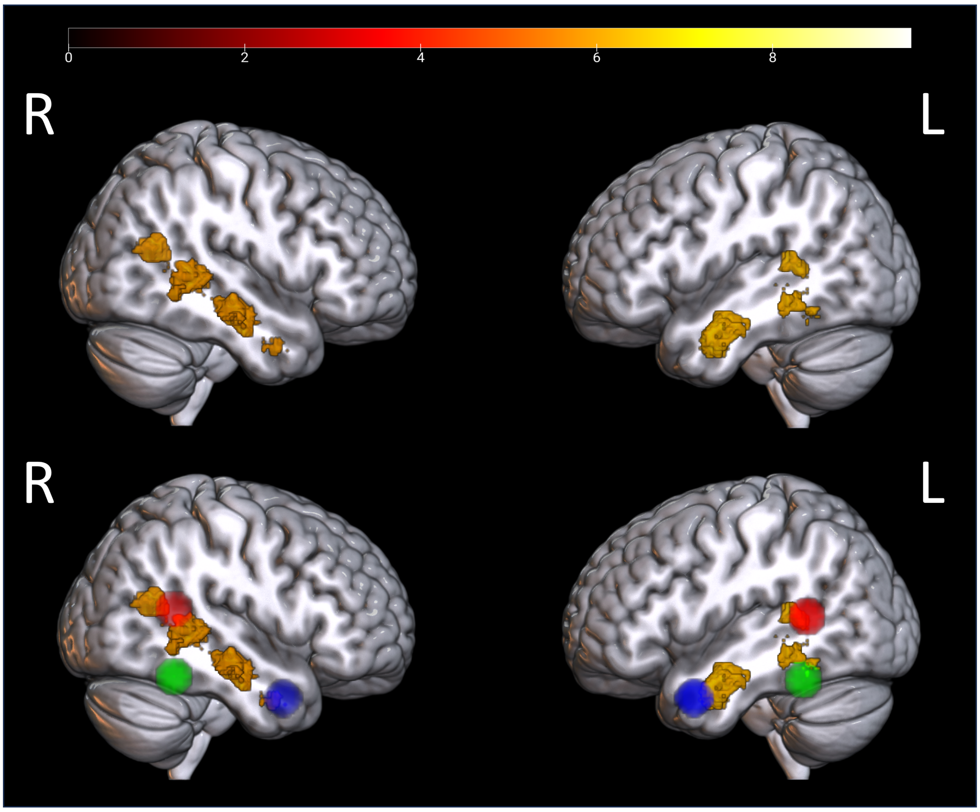


FIGURE 5.6: Brain regions showing significant correlation with the face-only model. Top panel: shows the areas that were significantly ($p<0.05$ FWE-corrected) correlated with the face-only model. Bottom panel: shows the same clusters but with the functional ROIs derived from the functional localiser data overlayed for reference. Shown is FFA (green), STS (red), and ATL (blue). The colour bar indicates the t-value associated with the cluster colours.

TABLE 5.3: The table displays the cortical area where the cluster is located, the hemisphere it was found in, the MNI coordinates of the voxel with the highest t-value, the t-value associated with the voxel, and the source of location information used to label the cortical area.

Cortical Area	**Hemisphere**	**x**	**y**	**z**	**Cluster Size**	**t-value**	**Source**
Fusiform Gyrus	L	-46	-54	-14	107	7.56	Neurosynth: *fusiform gyrus*
STS	L	-34	-48	8	99	8.28	Neurosynth: *sts*
ATL	L	-42	-10	-24	426	9.17	Neurosynth: *anterior temporal*
Fusiform Gyrus	R	36	-34	2	320	9.34	Harvard Oxford
Middle Temporal Gyrus	R	52	-16	-24	323	10.35	Harvard Oxford
ATL	R	36	2	-34	32	6.83	Neurosynth: *anterior temporal*
Precuneus Cortex	R	26	-62	14	188	8.84	Harvard Oxford

Another searchlight analysis within the mask (detailed above) identified significant correlations with the body-only model (Fig 5.1(b)). Regions with activity patterns that significantly correlated with the body-only model ($p<0.05$, FWE-corrected, Table 5.4, Fig 5.7) were found in the left and right EBA, as well as in the left lateral occipital cortex, which indicates the involvement of these brain areas in encoding the presence of a body.

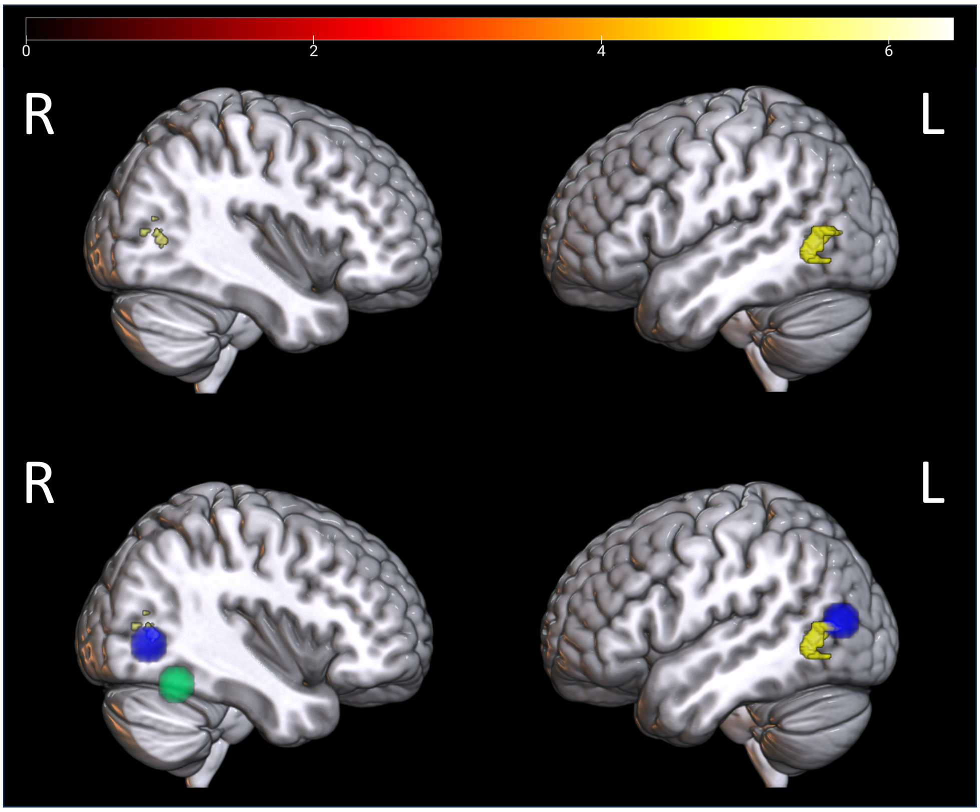


FIGURE 5.7: Brain regions showing significant correlation with the body-only model. Top panel: shows the areas that were significantly ($p<0.05$ FWE-corrected) correlated with the body-only model. Bottom panel: shows the same clusters but with the functional ROIs derived from the functional localiser data overlayed for reference. Shown is EBA (blue), and right FBA (teal). The colour bar indicates the t-value associated with the cluster colours.

TABLE 5.4: The table displays the cortical area where the cluster is located, the hemisphere it was found in, the MNI coordinates of the voxel with the highest t-value, the t-value associated with the voxel, and the source of location information used to label the cortical area.

Cortical Area	Hemisphere	x	y	z	Cluster Size	t-value	Source
Lateral Occipital Cortex	L	-52	-62	-2	207	7.64	Harvard Oxford
EBA	L	-48	-68	4	22	7.42	Neurosynth: *extrastriate*
EBA	R	42	-78	10	5	6.63	Neurosynth: *extrastriate*

5.3.3 Isolated emotion cue and integrated emotion cue model results

A paired t-test identified significantly ($p<0.05$, FWE-corrected, Table 5.5, Fig 5.8) greater correlation with the integrated emotion cue model compared to the isolated emotion cue model bilaterally in the FFA and ATL, the left STS, and right lingual gyrus. This demonstrates a higher correlation of brain patterns in these areas with the integrated emotion cue model than the isolated emotion cue model. No brain areas showed a significantly higher correlation with the isolated emotion cue model compared to the integrated emotion cue model. One-sided t-tests ($p<0.05$, FWE-corrected) were conducted for each model and indicated that both the integrated and isolated emotion cue models were significantly correlated with brain representations in the same areas. However, the results of the paired t-test provide strong evidence that the integrated emotion cue model is more prominently represented in these areas.

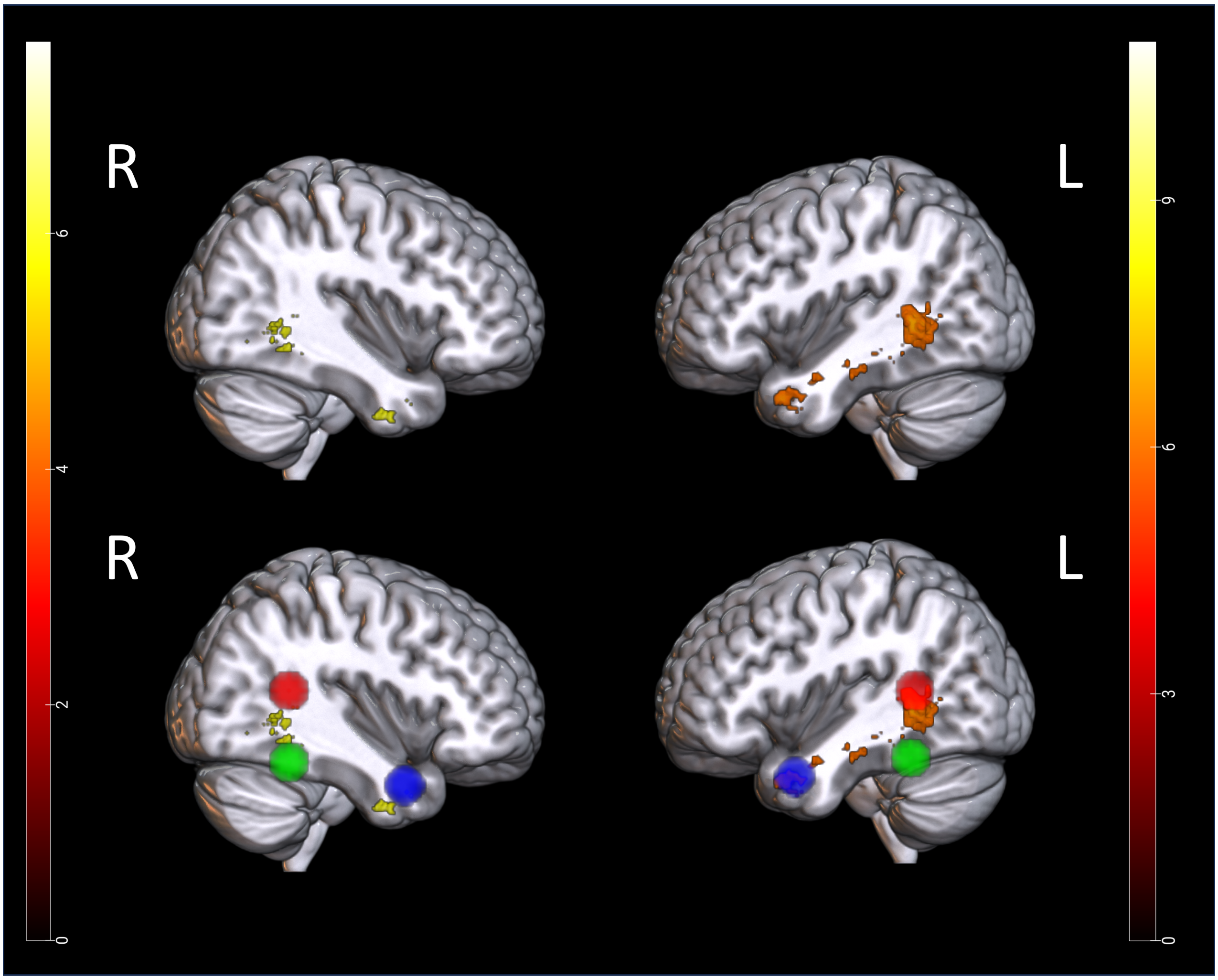


FIGURE 5.8: Brain regions showing significantly higher correlation with the integrated emotion cue model compared to the isolated emotion cue model. Top panel: shows the areas with significantly ($p<0.05$ FWE-corrected) higher correlation with the integrated emotion cue model compared to the isolated emotion cue model. Bottom panel: shows the same clusters but with the functional ROIs derived from the functional localiser data overlayed for reference. Shown is FFA (green), STS (red), and ATL (blue). The colour bar indicates the t-value associated with the cluster colours.

TABLE 5.5: The table displays the cortical area where the cluster is located, the hemisphere it was found in, the MNI coordinates of the voxel with the highest t-value, the t-value associated with the voxel, and the source of location information used to label the cortical area.

Cortical Area	**Hemisphere**	**x**	**y**	**z**	**Cluster Size**	**t-value**	**Source**
Fusiform Gyrus	L	-40	-38	-14	7	6.5	Harvard Oxford
Fusiform Gyrus	L	-44	-32	-12	2	6.15	Harvard Oxford
STS	L	-38	-50	2	245	11.59	Neurosynth: *sts*
ATL	L	-40	14	-34	41	7.6	Neurosynth: *anterior temporal*
ATL	L	-48	-20	-22	14	7.37	Neurosynth: *anterior temporal*
Fusiform Gyrus	R	36	-52	-10	10	7.57	Harvard Oxford
FFA	R	38	-56	-6	3	6.5	Neurosynth: *face ffa*
Fusiform Gyrus	R	32	-54	-6	1	5.9	Neurosynth: *fusiform*
ATL	R	40	-2	-42	19	8.52	Neurosynth: *anterior temporal*
Lingual Gyrus	R	32	-52	2	23	7.65	Harvard Oxford

5.4 Discussion

This study investigated the integration of emotion information from face and body along the visual processing hierarchy and found a higher correlation between brain patterns and the integrated emotion cue model compared to the isolated emotion cue model bilaterally in the FFA, and ATL, as well as in left STS. This finding suggests that integrated representations of face and body emotion are apparent at various stages along the visual processing hierarchy. My results conflict with accounts that suggest the integration of face and body cues occurs at either an early (Aviezer et al., 2008; Foster et al., 2021, 2022; Meeren et al., 2005; Pitcher et al., 2012) or late (Fisher and Freiwald, 2015; Harry et al., 2016; Hu et al., 2020; Song et al., 2013; Teufel et al., 2019) stage along the visual processing pathway. While my results don't show evidence for very early integration as proposed by, for example, Meeren et al., 2005 (e.g. visual cortex/occipital cortex), they do provide evidence for some integration of emotion information as early as FFA, conflicting with research suggesting ATL as a locus for integration (Harry et al., 2016).

The specific areas identified here as containing representations of integrated face and body emotion cues are aligned with previous research (Harry et al., 2016; Peelen et al., 2010; Song et al., 2013). There has been evidence provided for integrated, whole-person representations in the ATL (Harry et al., 2016), and an increased neural response to face-body stimuli in the FFA compared with isolated face or body stimuli (Song et al., 2013). My finding of integration in the STS is also in line with a previous study (Peelen et al., 2010), which found that the STS represents emotional information regardless of the modality of the cue (e.g. encodes the representation of anger regardless of whether expressed through a face or body). When considering these studies from an early vs. late integration perspective, it’s worth noting that the work of Harry et al., 2016 and Song et al., 2013 present conflicting insights into face and body integration. Harry et al., 2016 found no evidence for whole-person representations in the fusiform gyrus, but Song et al., 2013 did observe whole-person representation in this area. However, it is essential to recognise that these studies primarily focussed on the holistic representation of entire agents along the visual pathway. They did not investigate the integration of specific stimulus characteristics, such as emotion, identity, or viewpoint. This difference in focus makes it challenging to directly compare their results with the results presented here.

A more nuanced perspective for face and body integration was proposed by Foster, 2022, building upon research that found evidence for face and body integration at multiple points in the visual processing pathway (Foster et al., 2021, 2022; Peelen et al., 2010). For example, Foster et al., 2021 investigated how one recognises a person’s identity and can maintain this recognition across different viewpoints. They found evidence for the recognition of body identity across different viewpoints in the FBA and right ATL, implicating these areas as contributors in the extraction of high-level identity information from bodies (Foster et al., 2021). Furthermore, they found that identity information was abstractly encoded across both faces and bodies in the early visual cortex and the right inferior occipital cortex. This suggests a common coding of identity across face and body cues in the initial stages of the visual processing pathway (Foster et al., 2021). In a later study, Foster et al., 2022 explored how the brain processes orientation cues in faces and bodies. They found common coding for orientation recognition across face and body cues bilaterally at the intersection of OFA and

EBA, which indicates that this region can differentiate between orientation signals, regardless of whether they originate from a face or a body (Foster et al., 2022). In light of these findings, Foster, 2022 suggested a distributed model of face and body integration, wherein integration of different properties of face and body information (e.g. identity, expression, orientation) occur at different stages of the processing hierarchy. My results complement these findings and suggest that integrated representations of emotion from face and body are found along the visual processing pathway in the FFA, STS, and ATL.

In a recent review by Taubert et al., 2022, various hypotheses were presented regarding the integration of face and body information. These hypotheses span from entirely separate networks for face and body to networks exhibiting increasing integration and overlap between face and body regions. The findings of my study incorporate elements from both the weakly and strongly integrated network models (Taubert et al., 2022). The weakly integrated network model suggests that regions specialised for processing face and body cues maintain separate but loosely connected networks, with no functional overlap between key regions like OFA/EBA or FFA/FBA. Instead, functional overlap is observed in more anterior regions such as ATL. In my data, I observe alignment with this model, as there is no evidence of integrated representations of emotions from the face and body in early occipital regions such as OFA or EBA. This finding supports the idea that these early nodes preserve separate networks dedicated to processing cues from the face and body. However, it is important to highlight that I did not find a significant correlation between the isolated emotion model and the OFA in my analysis. This limits my interpretation regarding the lack of a correlation between the OFA and the integrated emotion cue model because the absence of a correlation here could reflect a lack of OFA activity identification overall in my results. On the other hand, the strongly integrated network model suggests that face- and body-selective brain regions mostly form integrated networks, with functional overlap occurring as early as OFA/EBA. My findings align with this model through evidence for integrated representations as early as FFA. However, my data deviates from this network model due to no evidence for integrated representations in the OFA, which is a central component of the strongly integrated model's concept of extensive overlap between face and body regions in early occipital areas. My findings lie at the intersection of these two network models, incorporating elements from both the weakly and strongly integrated models, emphasising the nuanced interplay of face and body processing networks. A notable strength of my results, and a difference to previous research on face and body integration, is my use of perceptual discrimination data to explore integration of emotion information. This approach offered a representation of perceptual integration between emotional cues from both the face and body – an approach that, to my knowledge, has not been used previously. Consequently, my results are able to demonstrate the points at which information from the face and body converge to form a representation that accurately reflects our perceptual integration process.

The findings from the face-only model and the body-only model allowed me to highlight areas involved in face processing and body processing more generally, using conceptual models and RSA. Conceptual models are useful when testing a presumed relationship between pairs of stimuli throughout the brain (Kriegeskorte et al., 2008) by displaying the difference between stimuli along a feature of interest (in my case, faces and bodies). For the face-only model, I identified areas bilaterally in the FFA and ATL, as well as in the left STS involved in face processing. This is in line with previous research, which has consistently shown areas in the FFA and anterior temporal lobes to be more active during face viewing than object viewing (Sergent et al., 1992), when viewing intact faces compared with scrambled faces (Aina Puce et al., 1996; Clark et al., 1996; Puce et al., 1995), as well as during face matching compared with location matching (Courtney et al., 1997; Haxby et al., 1991; Haxby et al., 1994). Puce et al., 1995 was also able to show increased activation in the STS when viewing intact faces compared with scrambled faces, with a later study (Aina Puce et al., 1996) also showing increased STS activation for faces compared with letter strings or textures. The anterior portion of the STS was also shown to be activated more by face stimuli than hand or feet stimuli (Pinsk et al., 2009). A more recent study was also able to show a stronger response to face stimuli compared with 19 other non-face stimulus categories in the temporal lobes (Harry et al., 2016). These previous findings support the results derived from my face-only model, with all 3 areas being shown to correlate significantly with this model in my study. Interestingly, no significant correlation was found between the face-only model and the OFA. The OFA is thought to process finer details of a face, such as facial features and their configuration (A. Calder and Young, 2005; Haxby et al., 2000; Pitcher et al., 2011), whereas the face-only model in this study is primarily concerned with differentiating between holistic faces and body posture, focussing on the overall presence of a face rather than its detailed characteristics. This could be the reason for the observed associations with the FFA, STS, and ATL, but not with the OFA. The face-only model aligns better with regions involved in the holistic representation of face stimuli, whereas the OFA specialises in processing facial details, making it less sensitive to the model's presence/absence differentiation.

For the body-only model, EBA in both the left and right hemisphere was found to correlate significantly with this model. This is in line with previous studies showing this area to be crucial in body processing, and that this area responds strongly to isolated bodies and not isolated faces (Downing et al., 2001). A later study (Peelen and Downing, 2005) was also able to show that body stimuli, but not face stimuli, activated a response in the EBA. Intriguingly, the FBA, a region associated with body processing (De Gelder et al., 2015; Downing et al., 2001), did not show a significant correlation with the body-only model. Previous research has shown that the FBA responds to headless and faceless bodies (Peelen and Downing, 2005), a distinction that is not represented in the body-only model. The body-only model treats both isolated body posture and whole-person stimuli (which include both body posture and a face) as the same, which could account for the observed absence of correlation between the FBA and the body-only model.

There were some methodological limitations within the scanning portion of this study. The first relates to the functional localiser, where different control contrasts were used to identify face-specific and body-specific areas along the visual processing pathway (Faces>Houses, Bodies>Objects). This approach aimed to capitalise on the stronger activations observed in the face and body areas when using these control contrasts. However, it introduces potential confounds to my analysis. For instance, if the control condition for face localisers (e.g., houses) elicits stronger neural responses than the control condition used for body localisers (e.g., objects), it may lead to false interpretations of the data. Employing different control conditions for face and body localisers may introduce complexity in interpreting the results, necessitating the need to account for any differences in baseline neural activity or response magnitudes between the control conditions to accurately interpret the observed activations. Furthermore, this methodological choice may have contributed to the lack of STS activity seen in the body localiser analysis. This finding is unexpected, as overlap in the STS between face and body representations has been well-documented previously (e.g., Peelen et al., 2010). Additionally, the observed accuracy rate in the functional localiser (1-back) task was lower than expected (83.1%). This deviation may be attributed to several factors, including the absence of practice trials and reliance on verbal confirmation for task comprehension. Future studies could benefit from incorporating practice trials before the scan to enhance participants' understanding of task instructions and potentially improve task performance. To mitigate participant fatigue during the RSA scanning sessions, I employed a low-level attentional probe detection task. Given the total duration of 45 minutes for the RSA scanning, employing a task demanding higher cognitive effort could have strained participant focus. However, the use of a low-level task might have impacted my results, as the nature of the behavioural and scanning tasks did not align. For instance, had the scanning task mirrored the behavioural task (e.g., categorising the emotion of a stimulus), the comparison of the data could have been more congruent, potentially offering deeper insights into my research question. Another limitation pertains to the use of a jittered interstimulus interval (ISI) in the main experimental scans. It has previously been argued that a jittered ISI might not be ideal for RSA because it is crucial to model each trial in isolation to maximise separation from other trials (Dimsdale-Zucker and Ranganath, 2018). With a jittered ISI, certain trials may be closer in timing, potentially leading to more accurate modelling of some trial activity patterns compared to others. However, this limitation was necessary due to time constraints, to fit as many trials as possible into a limited scanning session duration. Opting for a jittered ISI allowed me to achieve this without subjecting participants to excessively long scanning sessions. Another important aspect to consider is that my searchlight analysis focused solely on the visual processing pathway rather than encompassing the entire brain. This decision was deliberate, aimed at conducting a more targeted investigation into the integration of visual cues from the face and body. It was guided by prior literature on this phenomenon, aligning with the primary aim of my study. Additionally, by narrowing the analysis to the visual processing stream, I aimed to reduce the computational demands associated with whole-brain analyses, thus facilitating a more focused examination of the data. The choice to not compare my searchlight results to an ROI approach was primarily influenced by the exploratory nature of the study and the aim to capture distributed patterns of neural activity across the visual processing stream to address conflicting accounts in the literature. However, future analyses could benefit from adopting a combined ROI and searchlight approach, offering several advantages and insights. Firstly, utilising ROIs would allow future research to concentrate on specific brain regions known to be involved in face and body processing, enhancing specificity and sensitivity in detecting neural activations related to face-body integration within these regions. The searchlight approach could then complement this by enabling a comprehensive exploration of distributed patterns of neural activity across the brain, capturing both localised effects within specific ROIs and more widespread effects across the entire brain. This combined approach facilitates validation and cross-validation of results. By examining whether findings within specific ROIs align with broader patterns of activation identified through the searchlight approach, researchers can validate results within specific brain regions and vice versa. Furthermore, integrating both approaches enables a deeper understanding of network dynamics underlying face-body integration, exploring interactions between specific ROIs and their surrounding cortical areas and investigating how these interactions contribute to the integration of emotional cues.

There are also a few more general methodological limitations worth discussing. Notably, I did not explore the neural integration of cues in the opposite direction (i.e., the influence of facial expressions on body posture perception) in this study, even though I investigated it behaviourally in Chapter 3, Experiment 2. This omission was again primarily due to time limitations. Extending this study to examine the impact of facial expressions on body posture perception would require additional trials in both the behavioural and neuroimaging components, significantly increasing the time commitment for participants and increasing the likelihood of movement artefacts and inattention in the scanner. Considering how my current results can be framed between the weakly and strongly integrated networks presented in Taubert et al., 2022, one could expect the involvement of similar brain regions if the opposite direction of contextual influence was tested. Whether examining the impact of body posture on facial expression perception or the reverse, both situations entail integrating face and body emotion cues to process a whole-person stimulus. There were also a limited range of facial expressions and body postures employed to convey emotions, specifically due to time constraints and the number of repeats required per stimulus category for RSA, I looked at emotion morphs between anger and disgust only. Consequently, the findings may not be readily generalisable to the full spectrum of emotional expressions we encounter in our daily lives. However, the methods used in this study are extendable to a wider range of emotional expressions, to facilitate in the generalisability of these findings. Another limitation is the predominance of female participants in this study, which raises concerns about potential gender bias in the results. It is well-documented that females outperform males in emotion perception tasks (for meta-analysis, see: Thompson and Voyer, 2014), a trend that diminishes with age (Olderbak et al., 2019). This discrepancy could introduce bias, affecting the generalisability of the models developed using the behavioural data. Additionally, prior research has demonstrated gender differences in neural responses to facial expressions, with males showing heightened activation to angry faces and females to disgusted faces (Aleman and Swart, 2008).

These results challenge prevailing theories positing either early or late integration of face and body cues, suggesting instead a more distributed and nuanced pattern of integration. The identified brain regions align with previous research, underscoring the robustness of my findings. By incorporating perceptual discrimination data into the analysis, I provided a novel perspective on the integration process, shedding light on the points at which face and body cues converge to form cohesive emotional representations. While methodological limitations warrant consideration, such as the restricted range of emotional expressions and the predominance of female participants, this study offers valuable insights into the intricate interplay of face and body cues in emotion processing. Ultimately, these findings deepen our understanding of how emotional information is integrated within the brain's visual processing pathway, paving the way for future research to elucidate the underlying mechanisms and implications for social cognition and emotional perception.

5.5 Chapter Summary

This chapter explored the integration of emotional cues from faces and bodies within the visual processing pathway. The results reveal integrated representations of face and body emotion located at various points along the visual processing hierarchy, specifically in FFA, STS, and ATL. Activity patterns in these regions all exhibited higher correlation with the integrated emotion cue model compared to the isolated emotion cue model. These results challenge the current accounts that face and body integration occurs at either an early (Aviezer et al., 2008; Foster et al., 2021, 2022; Meeren et al., 2005; Pitcher et al., 2012) or late (Fisher and Freiwald, 2015; Harry et al., 2016; Hu et al., 2020; Song et al., 2013; Teufel et al., 2019) stage along the visual processing pathway. Instead, my results provide support for integrated representations across multiple brain regions along the processing pathway and as early as FFA.

Chapter 6

General Discussion

This thesis explored the integration of emotional facial expressions and body posture in the human brain. Chapter 3 addressed whether an individual's capacity to discriminate isolated facial expressions and body postures can account for the variations observed in the influence of body posture on facial expression perception (Experiment 1) or facial expression on body posture perception (Experiment 2) across the adult lifespan. I showed a bidirectional relationship between face and body cues; body posture has a significant influence on the facial expression it is presented with, and vice versa. In Experiment 1, I demonstrated that body posture's influence on facial expression categorisation increases across the adult lifespan, and that this increase was linked to the decline in facial expression recognition abilities seen across the adult lifespan. In Experiment 2, a reciprocal relationship was observed, with facial expressions influencing the perception of body posture, although to a lesser extent. Notably, this influence of facial expression on body posture perception remains stable across the adult lifespan. While the relationship between body posture discrimination and facial expression's influence on body posture did not reach statistical significance, it exhibits a clear trend: as body posture discrimination ability increases, the influence of facial expression on body posture decreases. These findings from Experiment 1 and 2 highlight the role of discrimination ability in shaping how one cue affects another within the perception of the whole person. Therefore, the constancy of the influence of facial expression on body posture perception could be attributed to the constancy of body posture discrimination ability also seen across the adult lifespan in Experiment 2. Chapter 5 then addressed the hierarchy of integration of these facial expression and body posture cues in the brain, revealing evidence for integrated face-body representations of emotion along the visual processing pathway, suggesting integrated representations appear as early as FFA and STS, but are also found in ATL.

Chapter 4 looked at the influence of body posture on facial expression perception in autistic individuals. The core question was whether the reduced facial expression recognition in autistic individuals leads to a more pronounced contextual influence, akin to non-autistic individuals. The findings revealed that autistic individuals displayed reduced discrimination abilities for facial expressions compared to the non-autistic comparison group. Notably, this decreased recognition ability was linked to an increased influence of body posture on facial expression perception in autistic individuals. This finding suggests that, despite the differences in social perception in autism, the mechanisms underpinning the integration of face and body emotion signals appear to be similar to those seen in non-autistic individuals.

6.1 Integration of face and body throughout the lifespan

The ability to recognise facial expressions and body postures changes across a person's lifetime. Previous studies have shown that older children exhibit improved ability to discriminate between facial expressions with high sensitivity to subtle changes in expression (Dalrymple et al., 2017; Thomas et al., 2007; Ward et al., 2023). A similar trend has been observed for body posture discrimination, with improvements in recognition ability in older children compared to younger children (Boone and Cunningham, 1998; Lagerlöf and Djerf, 2009; Ross et al., 2012; Ward et al., 2023).

In everyday life, facial expressions and body postures are rarely encountered in isolation; they are usually experienced together. Therefore, studying these cues in tandem is crucial for accurately reflecting our daily experiences. The influence of body posture on facial expression perception has also been demonstrated during childhood (Mondloch, 2012; Ward et al., 2023), with the degree of influence shown to decrease as children age (Ward et al., 2023). A recent study (Ward, I. et al. *in prep*) was able to show a significant link between facial expression discrimination ability and influence of body posture in adults, with lower facial expression discrimination ability being linked to a larger influence of body posture. Together, these results suggest a potential mechanism underpinning the influence of body posture on facial expression perception across childhood and adolescence, with discrimination abilities for facial expressions modulating the degree of influence that body posture has on facial expression perception.

I was able to extend this investigation by looking at the influence of body posture on facial expression perception across the adult lifespan (Chapter 3, Experiment 1). My results showed that facial expression discrimination ability decreases across the adult lifespan and that this decline is linked to an increased influence of body posture on facial expression perception with age. Importantly, body posture discrimination abilities remained stable across the adult lifespan, which suggests that the decline in facial expression discrimination ability seen was not due to a general perceptual or cognitive decline in older adults. My results suggest that similar mechanisms modulate the degree of influence of body posture through to old age, where the precision of facial expression representations determines the influence of body posture.

In a further experiment (Chapter 3, Experiment 2), I looked at the influence of facial expression on body posture perception across the lifespan. The findings of this study are in line with a previous study (Lecker et al., 2020) that showed a bidirectionality of influence between face and body, with facial expression being more susceptible to the contextual influence than vice versa. Unlike the influence of body posture on facial expression, however, the influence of facial expression on body posture perception remained stable across the adult lifespan. Considering the link found between facial expression recognition ability and the influence of body posture in Experiment 1, it's possible that the consistent stability in body posture discrimination ability across the adult lifespan in Experiment 2 could account for this pattern. A future study could investigate the influence of facial expressions on body posture perception in children, making use of their increasing discrimination ability throughout childhood and adolescence. This approach would help explore whether a similar underlying mechanism is responsible for the extent to which facial expressions influence body posture, much like how body posture influences the perception of facial expressions. If a reduction in the influence of facial expressions on body posture is linked to the improved ability to discriminate body postures in children and adolescents, it would provide evidence for a shared mechanism governing both aspects of this contextual influence. This investigation could further strengthen the proposition that a common mechanism drives the extent of influence across the entire lifespan, with the reliability of isolated emotional cues influencing the contribution of these representations to the perception of a whole person.

These findings challenge the social expertise model proposed by Hess and colleagues (2006) as an explanation for the increased influence of body posture in older adults (Abo Foul et al., 2018). The social expertise perspective posits that increasing age correlates with heightened sensitivity to relevant social cues, facilitating appropriate social functioning. According to a perspective put forward by Abo Foul et al. (2018), the increased influence of body posture observed in older adults stems from accumulated social experience. However, my findings challenge this explanation. Instead, the heightened influence of body posture in older adults appears to be modulated by their decreased ability to recognise facial expressions in isolation. This suggests a compensatory mechanism in older adults, wherein they increasingly rely on surrounding context to enhance their accurate recognition of facial expressions, rather than as a result of their accumulated social experience.

The research outlined in Chapter 1 suggested that the degree of impairment seen in older adults varies for different emotions (A. J. Calder et al., 2003). Older adults have been shown to struggle more in recognising negative emotions, such as anger and sadness, but seem to maintain their ability to recognise disgusted emotional expressions (D. M. Isaacowitz et al., 2007). A potential reason for this discrepancy could be an attention bias in older adults towards positive emotions. Some studies have indicated that older adults may initially avoid negative information in their attention processing (Mather and Carstensen, 2003). However, this explanation fails to account for the maintenance in recognition of disgusted emotions, which would also be regarded as negative. Another potential contributor to these previous results is gaze patterns in older and younger adults. The accurate identification of certain emotions from facial expressions relies on information in specific regions of the face. For example, fear, anger, and sadness are best identified from the eye region, while happiness and surprise can be recognised from both the eye and mouth regions, and disgust is primarily identified from the mouth region (A. J. Calder et al., 2000). Previous research has shown that older adults tend to fixate more on the mouth rather than the eye region when viewing angry, fearful, and sad faces compared with younger adults (B. Wong et al., 2005). This tendency was correlated with worse recognition accuracy for anger, fear, and sadness in older adults. Moreover, accompanying body posture can also alter the scanning patterns of the face. When an angry face is shown with a neutral or angry body posture, initial fixations are more focused on the eye region than the mouth region. Conversely, when the face is displayed with a disgusted body posture, the scanning pattern is reversed (Noh and Isaacowitz, 2013). Similar patterns are observed for disgusted faces displayed in different body postures. Older adults also tend to fixate more on the context region than the eye region compared with younger adults across all whole-person conditions (Noh and Isaacowitz, 2013), suggesting age-related differences in the processing of whole-person stimuli. These differences in scanning patterns between older and younger adults for different facial expressions and whole-person stimuli suggest a potential mechanism for the emotion-specific deficits seen in previous research on facial expression recognition.

6.2 Bayesian accounts of integration in Autism

Autism is associated with difficulties in social interactions, repetitive behaviours, and difficulties in dealing with change (Baron-Cohen, 1989; Chevallier et al., 2012). Previous research has suggested that Autism may be a primarily perceptual disorder in which social deficits manifest as a secondary symptom (F. Happé and Frith, 2006; Mottron et al., 2006). Bayesian models of perception have been proposed as potential frameworks for understanding the social and communication difficulties commonly observed in Autism (Haker et al., 2016; Lawson et al., 2014; Pellicano and Burr, 2012; Van De Cruys et al., 2014). At the core of Bayesian perceptual models is the concept that perception involves integration of current sensory information with pre-existing beliefs (known as priors), constituting a process of inference guided by prediction errors that are weighted by their precision (Griffiths et al., 2008). In the context of Autism, it has been proposed that there are alterations in perception due to incoming sensory signals being given greater weight relative to prior information (Brock, 2012; Friston et al., 2013; Haker et al., 2016; Van De Cruys et al., 2014). This shift would then lead to a heightened sensitivity to prediction errors, which is thought to be a potential cause of the reduction of contextual effects previously seen in autistic individuals (F. Happé and Frith, 2006; F. G. Happé, 1996; Iarocci and McDonald, 2006). This heightened sensitivity to prediction errors was termed HIPPEA (High, Inflexible Precision of Prediction Errors in Autism) (Van De Cruys et al., 2014). Within this theoretical framework, autistic individuals exhibit a higher sensitivity to prediction errors, which could lead to a strong focus on specific details and a difficulty integrating information into a coherent whole (Van De Cruys et al., 2014).

In a recent study (Randeniya et al., 2021), another two potential models through which predictive coding could influence sensory processes and perception in autistic individuals were examined. The first model, known as the “hypo-priors” model (Pellicano and Burr, 2012), suggests that the shift towards heightened sensory observation is due to noisier or less precise priors. This imprecise prior information would lead to a less robust model of the environment, subsequently assigning less weight to this weakened model. This perspective aligns with the WCC theory discussed in Chapter 4 of this thesis, by postulating that broader, less precise priors result in perception that is not biased by top-down processing or prior knowledge (Van De Cruys et al., 2014). The second model tested, proposed by Brock, 2012, posits that perceptual input is sharper in autistic individuals, leading to a lower uncertainty and higher precision when compared with the “hypo-prior” model. The consequence of this sharper likelihood would be a sensory representation that is more narrowly tuned and less susceptible to contextual influence (Brock, 2012). Randeniya et al., 2021 found no difference in how perceptual input was weighted between the autistic and non-autistic groups, which indicates that both the “hypo-priors” model (Pellicano and Burr, 2012) and Brock’s (2012) proposed model may not explain the sensory processes and perception in autistic individuals (Randeniya et al., 2021). This result suggests that the relationship between predictive coding, sensory processing, and Autism might be more complex than initially proposed, requiring further investigation to fully account for the observed patterns in Autism.

In this thesis, I provide evidence for a common mechanism for face and body integration between autistic and non-autistic individuals. The findings from Chapter 4, which demonstrated that reduced discrimination abilities for facial expressions in autistic individuals were linked to a higher influence of body posture, challenge Bayesian accounts for perceptual differences in Autism. These accounts suggest that autistic individuals are less influenced by surrounding context due to heightened sensitivity to prediction errors (Haker et al., 2016; Van de Cruys et al., 2017), which is not supported by my findings. My results show no evidence for different weighting being given to priors. Instead, similar to non-autistic individuals across the lifespan, what matters is how precisely an isolated cue is perceived and that this precision determines its impact on the final perception. However, it is worth noting that while my study did not reveal a direct relationship between contextual influence and body posture precision, future research should explicitly address this aspect through computational modelling to further elucidate the role of body posture representations in the context of Autism.

6.3 How cues, other than body posture, influence facial expression perception

The investigation of contextual cues, containing emotional content, affecting the interpretation of facial expressions extends beyond body posture. It encompasses a range of other cues that play a role in our understanding of the emotions conveyed by facial expressions. Specifically, affective prosody (De Gelder and Vroomen, 2000; Müller et al., 2011), visual scenes (Pourtois et al., 2000; Righart and De Gelder, 2008), and vocalisations (Pell et al., 2022; Young et al., 2020) have been shown to influence the perception of facial expressions.

These previous studies offer valuable insights into how these contextual cues can bias our judgements of emotion from the face. For instance, previous research has demonstrated that the ability to identify emotions in a person's facial expression is influenced by the simultaneous tone of voice when reading a sentence delivered in either a sad or happy tone (De Gelder and Vroomen, 2000). This is consistent with prior findings where body posture was found to bias judgements of facial expressions (Aviezer et al., 2008; Meeren et al., 2005). In line with my own findings, which indicated an influence of body posture on facial expression judgements despite explicit instructions to focus solely on the face (Chapter 3, Experiment 1; Chapter 4), this study also found that emotional judgements of the face were biased by the tone of voice, even when participants were asked to base their judgements on the face only (De Gelder and Vroomen, 2000). They were also able to show that this is bidirectional in nature, with emotion from the face being shown to bias emotional judgements of tone of voice, mirroring my finding of a bidirectional influence of facial expression and body posture, with facial expression also being shown to influence how body posture is perceived (Chapter 3, Experiment 2). Similarly, when subjects encounter faces paired with sounds of human screams rather than neutral sounds, they tend to rate fearful and neutral faces as more fearful, further highlighting the impact of vocalisation on the perception of facial emotion (Müller et al., 2011). In a recent study by Pell et al., 2022, the interaction between emotions conveyed through both voice and facial expression was explored. Participants were asked to assess the emotional states conveyed by facial expressions following voice stimuli that expressed anger, sadness, or happiness, while concurrent EEG was recorded. Their results showed that judgements regarding the emotional content of facial expressions were made more rapidly and accurately when the face-voice pairs were congruent compared to incongruent. Additionally, they observed an increase in P200 amplitudes for incongruent pairings. This suggests that the brain registers emotional congruency between facial expressions and vocalisations early during the processing of sensory information. The findings from these studies, which explore the impact of vocalisations on the perception of facial expressions, closely align with my own findings through the indication that emotional vocalisations bias the perception of facial expressions in the direction of the emotion depicted by the vocalisation. Further mirroring my findings, this influence was shown to operate bidirectionally; facial expressions also significantly influence the perception of emotional vocalisations (De Gelder and Vroomen, 2000). Additionally, in line with the early integration hypothesis of face and body emotion signals (Meeren et al., 2005), it was found that congruency between facial expressions and voice is apparent early in sensory processing (Pell et al., 2022).

The visual scene in which a facial expression is presented also influences how that facial expression is perceived. Akin to congruency between vocalisations and faces (Pell et al., 2022), the categorisation of facial expressions is faster when presented in a congruent visual scene (e.g. fearful face shown with a crashed car) than in an incongruent one (e.g. neutral face shown with a crashed car) (Righart and De Gelder, 2008). Interestingly, this effect remains unchanged even with an increased task load, mirroring previous research on the impact of body posture on facial expression categorisation (Aviezer et al., 2011). This suggests that the integration of visual scenes and facial expressions is an automatic and rapid process, much like has been hypothesised for face and body integration (Aviezer et al., 2011; Meeren et al., 2005). Further evidence for congruency of visual scenes and facial expressions being recognised early in processing can be seen through the increase in N170 amplitude with congruent pairings of faces and scenes (De Gelder, 2006; Pourtois et al., 2000). In a study that paired identical faces with either neutral or emotionally charged clips, it was revealed that judgements of facial expressions were biased in a positive or negative direction by positive and negative visual scenes respectively, compared to neutral ones (Mobbs et al., 2006). This effect was mirrored in the fMRI data, which showed increased activation in various brain regions, including the temporal lobe, STS, anterior cingulate cortices, and the amygdala when faces were paired with emotionally charged clips (Mobbs et al., 2006). The representation of emotion in paired visual scenes and facial expressions at various locations can be related to my own findings in this thesis. I found evidence of integrated representations of facial and bodily emotions at multiple points along the visual processing pathway, including as early as the FFA. The increased activations reported in Mobbs et al., 2006, especially in the STS and temporal lobe, align with my findings, indicating that integrated emotional content within facial expressions is represented along the visual processing pathway, rather than solely in higher-level visual processing areas.

There are notable parallels between findings regarding the influence of body posture on facial expressions and those concerning vocalisations and visual scenes. For instance, all three forms of context have been shown to bias facial expression perception, and similar bidirectional influence is observed in vocalisations, akin to body posture. Studies utilising EEG have demonstrated that congruency and incongruency in vocalisation and facial expressions are detected early during processing (Meeren et al., 2005; Pell et al., 2022). Likewise, results concerning visual scenes and facial expression integration mirror my own findings, with integrated representations observed along the visual processing pathway. These observed similarities between the integration of visual scenes and vocalisations with facial expressions and the integration of body postures with facial expressions suggest that the findings contribute to a broader model for contextualised emotion perception. It is conceivable that similar mechanisms underlie the degree of influence exerted by surrounding context across these various forms.

While, based on the discussion above, body posture can be conceptualised as another form of context in a broad sense, it is important to acknowledge its unique relationship with facial expressions. Unlike vocalisations, facial expressions are almost always encountered alongside an accompanying body posture, rarely existing without each other in real-world social situations. This unique characteristic places body posture in its own category when it comes to the surrounding context. Consequently, the relationship between facial expressions and body posture in whole-person perception may exhibit unique characteristics not observed with other forms of context. However, further research is necessary to draw definitive conclusions. Investigating whether other forms of context exhibit similar mechanisms of modulations over facial expressions will clarify whether body postures are treated as a unique form of context in facial expression perception.

6.4 Multimodal integration

Expanding on the discussion of how other cues, such as vocalisations and visual scenes, influence facial expression perception, it is interesting to consider how these signals are integrated at a neural level. While my thesis focussed on the integration of emotion signals from face and body, similar principles may govern the integration of emotion signals arising from other cues as well. The neural underpinnings of multimodal integration will now be discussed, to shed light on how distinct sensory modalities converge to provide a holistic representation of emotion.

A study by Peelen et al., 2010 demonstrated, using MVPA, the successful categorisation of emotions across facial, vocal, and body cues in the STS and medial PFC (mPFC). These findings provide evidence for modality-independent but emotion-specific representations in these regions (Peelen et al., 2010). A behavioural observation linked to multimodal integration is that, when compared to unimodal presentations (e.g., face-only stimuli), multimodal representations (e.g., combining both face and voice) result in more accurate and quicker emotional judgments (Klasen et al., 2012). This response to multimodal versus unimodal representations is also mirrored in fMRI contrasts, revealing increased activation in response to multimodal expressions as opposed to unimodal ones in several brain regions, including the thalamus, superior temporal sulcus (STS), fusiform face area (FFA), insula, amygdala, and the prefrontal cortex (PFC) (Klasen et al., 2012). These findings underscore the presence of integrated representations in multiple brain regions, and notably, the FFA and STS align with the findings from my own research, indicating integrated emotion representations in these specific areas. Schirmer and Adolphs, 2017 later proposed a comprehensive model for the integration of emotion cues across sensory modalities. They propose that this process is two-fold: first, regions like the FFA (vision), medial STS (audition), and posterior insula (proprioception) may support modality-specific representations. At this stage, emotional cues are mapped onto a stored emotional template or “emotional gestalt” (Schirmer and Kotz, 2006). Second, at a later stage of processing, regions like the pSTS may support supramodal representations of emotion. My findings are consistent with this model, in which I found evidence for integrated emotional representations from face and body cues in the FFA, STS, and ATL. My results speak to the proposed notion that multimodal emotion integration does not occur exclusively in later stages of processing, and that the STS is a likely convergence zone for supramodal emotional representations (Schirmer and Adolphs, 2017). Future research could apply the psychophysical and multivariate imaging methodologies used in this thesis to investigate the influence of other sensory cues on facial expression perception. This would involve exploring the modulatory mechanisms in the integration of these cues and identifying potential sites for integrating multimodal emotional cues.

Based on these results, it appears that emotional representations in the brain may develop similarly across different sensory modalities, suggesting the presence of supramodal emotional representations, as early as FFA. However, the specific mechanisms underlying these processes of multimodal integration remain somewhat unclear. My thesis has demonstrated a mechanism where the impact of one cue (e.g. body posture) on another is determined by the precision of the other cue (e.g. facial expression), a concept supported by behavioural evidence throughout my research. One way to conceptualise these results, and multimodal integration more generally, is a framework proposed by Zaki, 2013, which hinges on the idea that inferences drawn from the convergence of multimodal social cues can be interpreted through a Bayesian brain perspective (Ernst and Bülthoff, 2004; Ma et al., 2009). The crux lies in the ability to assign appropriate weights to each sensory cue based on the reliability of the sensory information available. Across time and varied social contexts, individuals refine their perceptions, adapting their expectations in response to accumulating experiences and new information Zaki, 2013. The findings in this thesis align with Zaki's (2013) proposed framework through several key observations. Notably, my findings offer evidence for the influence of body posture on facial expression perception increasing as discrimination ability for facial expressions decreases, a pattern observed across the lifespan (Chapter 3, Experiment 1; Ward et al., 2023) and in autistic individuals (Chapter 4). According to the proposed Bayesian framework (Zaki, 2013), the decreased discrimination ability observed in older adults and autistic individuals can be regarded as a less reliable cue. In response to this, the influence of body posture gains prominence in shaping perception to provide a more accurate account of affect. These findings reflect the application of Bayesian logic in understanding how individuals incorporate multiple cues and adjust their cognitive frameworks to effectively navigate intricate social situations.

6.5 Future Directions

To critically assess the broader implications of my findings as a model for emotion perception, it's crucial to address a key limitation: the exclusive focus on anger and disgust expressions throughout the thesis. These emotions were selected due to their established high perceptual similarity, as evidenced in prior research (Aviezer et al., 2008; Susskind et al., 2007). Specifically, Susskind and colleagues (2007) demonstrated significant perceived similarity between anger and disgust, as well as between fear and surprise expressions. However, emotions such as sadness and happiness did not exhibit similar levels of perceptual similarity with any other emotion examined. This limitation raises questions regarding the extent to which the research findings can be extrapolated beyond the perception of anger and disgust. While concentrating on these emotions has provided valuable insights into specific aspects of emotion processing, it may not fully encapsulate the intricacies of emotion perception across diverse emotional states. Nevertheless, despite its limited generalisability, this research establishes a groundwork for understanding potential mechanisms that could influence the impact of body posture. By investigating the interaction between body posture and specific emotions like anger and disgust, this research offers valuable insights into how contextual factors shape emotion perception. However, to expand upon these findings and draw broader conclusions about emotion perception across different populations, such as autistic individuals, future studies should consider integrating fear and surprise stimuli. Leveraging their perceptual similarity (Susskind et al., 2007) could provide a more comprehensive understanding of the emotion perception process across a wider range of emotions.

Another way to broaden the applicability of my findings would be to explore the influence of body context on facial expressions using displays of emotion from both males and females. This addition would be particularly interesting because male body postures are often perceived as more stereotypically angry than female body postures (Kret et al., 2013), with similar perceptions found for facial expressions of anger (D. A. Harris et al., 2016). Understanding the differences in how male and female faces and body postures are perceived is essential for generalising these findings across the general population.

It's also important to consider that facial expressions and body postures in real-world scenarios are dynamic, not static. Previous research has shown an increased influence of body posture when dynamic incongruent whole-person stimuli are used in both children and adults (Nelson and Mondloch, 2017). Therefore, future studies should address the research questions in this thesis using dynamic facial expressions and body postures to mirror the complexity of real-life social perception within a research setting.

A question that arises from this thesis is how to determine whether integration occurs at a genuinely ′late′ or ′early′ point in the visual processing pathway. Defining this solely based on brain area is challenging due to recurrent connections between areas, making it difficult to ascertain whether a particular region is involved at an early or late stage in the processing hierarchy (Atkinson and Adolphs, 2011). To address this issue, future research should conduct a multi-modal study investigating the spatio-temporal dynamics of face and body integration. This approach could involve combining fMRI with electrophysiological techniques such as magnetoencephalography (MEG). By integrating these methods, researchers can simultaneously examine both the spatial and temporal dynamics of an integrated stimulus. This comprehensive approach would offer insights into whether integration occurs as a late, early, or distributed process along the visual processing hierarchy, crucial for understanding how the brain processes complex social cues and perceives whole-person representations.

6.6 Conclusion

In conclusion, this thesis provides valuable insights into the integration of emotional facial expressions and body postures in the human brain. I found that the influence of body posture on facial expression perception increases with age and is linked to decreased facial expression discrimination abilities. This relationship between the precision of facial expression representations and the influence of body posture on facial expression perception was also observed in an autistic population, where autistic individuals showed an increased influence of body posture on facial expression perception relative to non-autistic individuals, due to their reduced facial expression representation precision. These findings suggest a common mechanism for face and body integration, whereby autistic individuals exhibit similar mechanisms modulating the degree of influence of body posture on facial expression perception. I also found evidence for integrated emotional cue representations, across the visual processing hierarchy, as early as FFA, and extending into STS and ATL. This is consistent with accounts that multimodal emotion integration does not occur exclusively at later sites of processing, and that the STS may be a convergence zone for supramodal emotional representations across different modalities. The specific mechanisms underlying these integration processes remain somewhat unclear, but the integration mechanism suggested within my findings, where the influence of one cue is determined by the precision of another cue, can be conceptualised within a Bayesian brain perspective. Individuals fine-tune their perceptions by adapting their expectations about probabilities in diverse social situations. In sum, this thesis provides initial mechanistic understanding of how body posture influences facial expression perception and lays the foundation for further investigations into the mechanisms of integration across various sensory cues, contributing to a better understanding of social perception more broadly.

Appendix A

Appendix

A.0.1 Regions identified in participants

TABLE A.1: Right Hemisphere: Number ROIs for OFA, FFA, STS, EBA, FBA, ATL

Region	Number
OFA	22
FFA	22
STS	21
EBA	21
FBA	21
ATL	19

TABLE A.2: Left Hemisphere: Number ROIs for OFA, FFA, STS, EBA, FBA, ATL

Region	Number
OFA	20
FFA	22
STS	18
EBA	22
FBA	20
ATL	17

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