Title of PhD Thesis

The Effect of Normal Aging on Social Perception of Faces

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I, Tao Yang, confirm that the work presented in this thesis is my own.
Where information has been derived from other sources, I confirm that this has been indicated in the thesis.

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ABSTRACT

Typical aging is associated with declined cognitive functions and neural deterioration. This thesis investigates the effect of normal aging on social perception of facial emotion and facial identity. Firstly, this thesis examines older adults' ability to perceive facial emotions and facial identities with subtle changes using behavioural investigations. It is revealed that normal aging is linked with declined ability to make fine-grained judgements in the perception of facial emotion (anger and happiness) and facial identity (upright- and inverted-), but not for facial traits judgement. In addition, the relationship between age and each face perceptual performance were explored using regression model fitting. Additionally, this thesis further examines whether typical aging is associated with the perception of subtle changes in facial emotion and facial identity with older adult faces, and whether the age-related facial identity perceptual decline is a face-specific decline or it extends to non-social perception. I developed novel tasks that permitted the ability to assess facial emotion (happiness perception), facial identity, and non-social perception (object perception) across similar task parameters. It is observed that older adults have decreased ability to make fine-grained judgements in the perception of happiness and facial identity (from older adult faces), but not for non-social object perception. These behavioural findings are discussed with theories within the current literature. This thesis also explored the neural mechanisms underlying social perception in older adults using non-invasive high-frequency transcranial random-noise stimulation (tRNS) and electroencephalogram (EEG). The results revealed that stimulating inferior frontal cortex facilitates older adults' anger perception, especially low-performing older adults. The event-related potentials (ERPs) results have shown that older participants exhibited neural overactivation in the left frontal and centromedial region (100-200ms stimuli onset) and frontal region (250-850ms stimuli onset) during emotion perception.

These findings are discussed in the context of existing literature on normal aging and social perception.

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PUBLICATIONS ARISING FROM THESIS

Invited Book Chapter:

Yang, T., and Banissy, M.J. (2016). Empathy and aging: Mechanisms of empathy throughout adulthood. In *Psychology and Neurobiology of Empathy*, Edited by D.F. Watt and J. Panksepp. Nova.

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CHAPTER 1: INTRODUCTION

Our ability to correctly perceive and interpret social cues (social perception) is a critical component of human life. One important source of social signals is the face. For instance, from a face we are able to judge if someone we meet is a friend or a stranger (i.e. their identity), whether that person is pleased or upset to see us (e.g. if they are happy, angry, or sad), and make trait judgments about that person's character (e.g. judging if they look trustworthy or aggressive). While these processes are relatively rapid, they can have profound effects on our behaviour.

Two main aspects of social perception of faces are perception of facial identity and facial emotional expressions, which corresponding to the abilities to identify facial features, perceive and understand the emotional content and cues present in the environment. This chapter introduces the background of the research and presents the motivation to investigate the effect of normal aging on social perception. An overview of recent psychological and neurobiological studies is provided which reveals insights into the neurocognitive mechanisms of social perception in normal aged brain.

Cognitive and neural mechanisms involved in face perception

1.1.1 Face identity and face emotion perception

We live in a complex world where we see countless items at one time. The brain must evaluate these external visual signals and devote more cognitive resources to process important external items. Faces are the most "biologically and socially significant" visual stimuli in the human environment, therefore people devote enhanced cognitive resources for processing human faces (Palermo and Rhodes, 2007). Faces contain a lot of information, which require us to categorise faces in order to identify individuals (face identity perception) and to encode different types of facial expressions (face emotion perception).

The face-specificity and expertise views

Extensive evidence ranging from behavioural, brain lesion and brain imaging studies suggest that domain-specific cognitive and neural mechanisms are involved in face processing (e.g. Bentin et al., 1996; Kanwisher, 2000; Moscovitch et al., 1997), which is dissociable from the processing of non-face objects. The 'face-specificity' view was first suggested by the observation of brain lesion patients who were selectively impaired to discriminate faces, but retained relatively intact abilities to recognise other objects (McNeil and Warrington, 1993; Hecaen and Angelergues, 1962). This condition has been referred as 'prosopagnosia', or 'face blindness'. This face-specific disorder is associated with selective brain damage to ventral occipito-temporal cortex, involving the lingual and fusiform gyri (Schiltz, Sorger, & Caldara et al., 2006; Haxby et al, 2000). Brain imaging studies have found a specialised brain area called 'face fusiform area' in the ventral visual cortex which exhibits increased activity to faces but not non-face stimuli (Kanwisher, McDermott, & Chun, 1997, Haxby et al., 1999). Furthermore, the face-specific event-related potential (ERP) N170 component was first proposed by Bentin et al. in 1996, who measured ERPs from participants during presentation of faces and other objects, and found that human faces elicited robust negative ERP amplitudes between 160 and 180ms at occipito-temporal sites compared to other object categories (Bentin et al., 1996; George, Evans, Fiori, Davidoff, & Renault, 1996). Behavioural studies have shown that the facial identity perception relies on more holistic processing that encodes individual features in a global manner, as it has been found that the perception of faces is more impaired when faces are presented inverted, as compared to other non-face stimuli ('face inversion effect', Yin 1969; Diamond and Carey 1986; Bruce & Humphreys, 1994; Farah, Wilson, Drain, & Tanaka, 1998).

However, the view of domain-specificity for faces has been challenged by the expertise view, which proposed that the identification of fine-detailed, subordinate objects shares the same mechanism as facial identity perception. They found people with expertise with objects showed large activations in the face fusiform areas during such subordination object perception (Gauthier et al., 1999; Bukach, Gauthier, & Tarr, 2006).

Functional specialization in the face perception system

Current literature on face perception propose that the processing of faces starts with an initial stage of encoding, followed by independent processing of changeable aspects of faces (i.e facial emotion and gaze) and processing of invariant aspects of faces (facial identity and gender) (Bruce & Young, 1986; Haxby, Hoffman, & Gobbini, 2000, 2002; Fisher, Towler & Eimer, 2016). Neurologically, this model is divided into a core system for the visual analysis of faces, which comprises three occipital/temporal regions (fusiform face area – FFA, occipital face area – OFA, superior temporal sulcus - STS); and an extended system that includes neural systems that are involved in other cognitive functions. It has been proposed that the processing of face-invariant information is associated with a neural pathway linking OFA to FFA, whereas processing of changeable face information (e.g. facial expression, eye gaze) is associated with the neural pathway linking OFA and STS. This view has been confirmed by numerous behavioural studies (Young & Bruce, 1991), neuropsychological studies (e.g., Bruyer et al., 1983; Schweich & Bruyer, 1993), and brain imaging studies (e.g., Sergent, Ohta, MacDonald, & Zuck, 1994; Vuilleumier, Armony, Driver, and Dolan, 2003). For example, the distinction between the neural processing of invariant aspect of faces and changeable aspect of faces were found in a functional brain imaging study (Winston, Henson, Fine-Goulden, & Dolan, 2004). It was found that viewing or matching of invariant aspect of faces (identity, gender) elicited responses in the FFA region; however, attending to a changeable aspect of the face (eye gaze, facial emotion) reduced the magnitude of the response in the FFA region. This finding suggests that the FFA region plays a role in processing invariant features of faces, but not changeable aspect of faces. Neuropsychological studies of patients with brain lesions and nonhuman primates indicate that the perception of face identity is anatomically dissociated from the perception of facial expression and eye gaze (Fox, Hanif, Iraria, & Duchaine et al., 2011; Campbell et al., 1990; Young, et al., 1995). Fox et al. (2011) used structural and functional MRI to correlate four patients' face perceptual deficits with damage to the core regions of the face-processing network using morphed face identity and face emotion discrimination tests. They found patients who were selectively impaired at recognising face identity were associated with damage to fusiform and occipital face areas, and medial occipitotemporal structures; whereas the patients with impaired expression perception were associated with damage to posterior superior temporal sulcus. Using single-cell recording approach (Hasselmo, Rolls and Baylis, 1989), researchers found that neurons in the superior temporal sulcus (STS) were responsive to facial expressions, while neurons in the inferior temporal gyrus were responsive to facial identity. It should be noted that, additional neural regions also contribute to the accurate recognition of the signals gathered from faces. For instance, the perception of facial emotion activates limbic regions that are associated with processing emotion (Morris et al., 1996; Phillips et al., 1997, 1998), and the perception of eye gaze direction activates parietal regions that are associated with spatial attention (Hoffman and Haxby, 2000).

As stated above, there is good evidence to suggest that the perception of face identity and face emotion are neurologically dissociable from each other. Chapter one of this thesis will summarise and review studies in current literature investigating the effect of typical aging on face emotion perception and face identity perception in different sections.

Spatial frequencies in face processing

Images we see from external world consist in complex luminance arrays. These variation of luminance intensities were filtered by human early visual cortex and decoded into different neural signals representing "luminance over spatial regions of different size" (Goffaux and Rossion, 2006). High spatial frequencies (HSFs) correspond to small-scale variations of luminance - features such as sharp edges and fine details; whereas low spatial frequencies (LSFs) correspond to large-scale variations of luminance - features such as global shape and coarse visual information. Human faces are complex stimuli, which contain multiple internal (e.g. eyes, nose, mouth) and external (e.g. hair, moustache) facial features. Researchers have explored the roles of different types of spatial frequencies play in face perception.

Goffaux, Hault, Michel, & Vuongô (2005) explored the respective roles of low and high spatial frequencies in supporting encoding of faces. The encoding of faces involves extracting and processing both "first-order relations" and "second-order relations" of faces (Chaby, Naeme & George, 2011). The first-order relation of faces refers to the overall configural information of faces, or the spatial relations between facial components (i.e. two eyes above a nose and a mouth). The second-order relation of faces refers to the distance between features, such as the distance between two eyes, or the distance between mouth and nose. In Goffaux et al.'s study, it was found that low spatial frequencies (LSFs, below 8 cycles per face width) played a dominant role in configural processing of faces, whereas high spatial frequencies (HSFs, above 32 cycles per face width) were more important for featural processing of faces. In the study, participants were presented with triplets of faces that were filtered to preserve either LSFs, HSFs, or the full frequency spectrum and they were required to match one of two testing faces to a target face. The distractor testing face differed from the target either configurally, featurally, or both featurally and configurally. They found participants' performance were better with LSF faces than with HSF faces when the difference was at the configural level, whereas their performance were better with HSF faces than with LSF when the difference was at the featural level. These results support the dominant role that LSFs play in the configural processing of faces, whereas featural processing is largely dependent on HSFs.

Recently, some researchers proposed that the processing of face identity and face emotion may rely on different spatial frequencies. Using event-related functional magnetic resonance imaging (fMRI), Vuilleumier, Armony, Driver, & Dolan (2003) found repeating the same face identity with high spatial frequency elicited greater neural responses in fusiform cortex than face stimuli with low spatial frequency, regardless of emotion expression. In contrast, amygdala, pulvinar and superior colliculus exhibited greater neural responses for fearful faces with low-frequency than for fearful faces with high-frequency. This finding suggests that recognising facial identities might rely on high frequencies of information, whereas the recognition of facial emotion (fear) relies on low spatial frequencies of information. This finding has been confirmed by Bar and colleagues (Bar, Neta, & Linz, 2006). They found that people's perception of threat from faces was fast (within the first 39ms of exposure), and the detection of threat from faces mainly rely on low spatial frequencies. However, these studies only used the facial stimuli of fear and ignored other types of facial emotions (e.g. happiness, anger). It is not certain whether LSFs play a more important role than HSFs in processing other facial emotions.

1.1.2 Proposal of face trait model

According to the face trait model proposed by Oosterhof and Todorov (2008), faces can be sufficiently evaluated on two primary dimensions: trustworthiness and dominance. They also tested whether the dimensions of trustworthiness and dominance are sensitive to different types of facial information by exaggerating the features specific to an evaluative dimension. For example, it was found that moving from the negative to the positive extreme of the trustworthiness dimension, faces seemed to change from expressing anger to expressing happiness. Whereas moving from the negative to the positive extreme of the dominance dimension, faces seemed to change from feminine and baby-faced to masculine and mature-faced. In other words, the judgement of trustworthiness seems associated with facial emotional expressions whereas judgement of dominance correlates more with certain facial features.

Some neural findings also seem to support this model where the perception of trustworthiness shares or partially shares the neural regions of emotion processing. Functional brain imaging studies showed that the subcortical brain region amygdala is not only critical for decoding emotions of fear and consolidating emotional memories, but also plays a key role in the judgement of face trustworthiness (Engell, Haxby, & Todorov, 2007; Winston, Strange, O'Doherty, & Dolan, 2002). Furthermore, Adolphs, Tranel, and Damasio (1998) found that patients with bilateral amygdala damage perceived untrustworthy-looking faces as trustworthy. The neural mechanism for perception of trustworthiness dissociate from the neural route of facial identity processing. Developmental prosopagnosics who are severely impaired in processing facial identity can still make normal trustworthiness judgements from faces (Todorov and Duchaine, 2008).

Collectively these studies indicate that the judgement of trustworthiness is more sensitive to information of facial expressions rather than identity or certain features of faces, and the key mechanism underlying the judgement of trustworthiness involves the amygdala which is also involved in decoding the facial expressions (Engell, Haxby & Todorov, 2007; Todorov and

Engell, 2008; Todorov, Said, Engell & Oosterhof, 2008). It seems that the judgement of trustworthiness from faces is both neurologically and behaviourally closely related to the perception of facial expressions. Prior facial trait studies found that older and younger adults' perceptual ratings on trustworthy faces were similar, but older adults perceived untrustworthy faces to be more trustworthy than younger adults (Castle, Eisenberger, & Seeman et al. 2012; Bailey, Szczap, McLennan et al. 2015). The pattern of results was discussed with older people's 'positivity bias' - they are less sensitive to cues that are related to negative experience (Castle, Eisenberger, & Seeman et al. 2012, Bailey, Szczap, McLennan et al. 2015). In addition, the neural imaging results found that younger adults showed greater anterior insula activation to untrustworthy versus trustworthy faces, older adults showed little activation of the anterior insula to untrustworthy faces (Castle, Eisenberger, & Seeman et al. 2012). Previous aging studies on facial trait perception have explored the older adults' perception of facial trait of trustworthiness, but few studies have studies older adults' perception of facial trait of dominance/aggressiveness, and whether the impairment of facial emotion or identity perception in older adults extends to such trait judgements remains unknown. Therefore, I would like to examine whether deficits in recognising emotions could extend to facial trait perceptual abilities (trustworthiness and aggressiveness).

Normal aging on facial expression perception

1.2.1 Background

Over the recent decades, population aging has become a global phenomenon. The proportion of older people (population aged 60+ years) has been increasing in both developing and developed countries (Shrestha, 2000). The number of people aged 60 years and above have tripled from its number in 1950 to 600 million in 2000, this number has surpassed 700 million in 2006, and the current projection suggests that the aged population will reach around the 2 billion by 2050 (Chuks, 2010). Therefore, this change of social structure requires more research to focus on aged population to aid this increasing population areas of life quality and health, both physically and psychologically.

Emotional facial expression perception plays an important role in interpersonal communication, with emotions often expressed through changes in facial expression, eye contact, body posture and movement (Ruffmana, Henryb, & Livingstonec et al., 2008; Ryan, Murray & Ruffman, 2009). Emotional expression can alter the meaning of speech and the ability to accurately identify emotional content is particularly important in social interaction (Ryan, Murray & Ruffman, 2009). Difficulties with emotion perception are associated with specific types of social impairment, including poor interpersonal interaction, reduced social competence and interest and inappropriate social behaviour (e.g., Spell and Frank, 2000). It is therefore unsurprising that considerable research interest has focused on establishing how capacity for emotion perception is affected as a function of normal adult aging, as well as the extent and implications of any observed difficulties.

1.2.2 Behavioural investigations

The effect of aging on social perception has received considerable interest in recent years, particularly the effect of age on perceiving emotions in faces. The general pattern that emerges from literature is that older adults appear to have declined perception of some negative facial expressions of emotions such as anger, sadness, fear and surprise (e.g. McDowell et al., 1994; Phillips et al., 2002; Calder et al., 2003; Sullivan & Ruffman, 2004). In contrast, age related differences in the perception of happiness are less consistent, but this may reflect that in several studies happiness perception performance was at ceiling for at least one age group tested (e.g. Moreno et al., 1993; Orgeta & Phillips, 2007; McDowell et al., 1994; Brosgole & Weisman, 1995; Isaacowitz et al., 2007). Figure 1.1 summarises the relevant studies from recent years. Previous research on age differences on the perception of facial emotions has focused on perception of posed facial expressions with mid- and high-emotion intensities (Ekman & Friesen, 1976; Matsumoto & Ekman, 1988). MacPherson, Phillips, and Della Sala (2002) compared younger, middle-aged and older groups' perceptual performance on Matsumoto & Ekman's (1988) Japanese and Caucasian Facial Expression of Emotion (JACFEE) and found the older group only performed significantly worse than the younger group on the recognition of sadness. In the study, participants were presented with colour photographs of facial expressions and they were required to choose one emotion type that they perceived from what they saw from a series of emotion type labels: happy, sad, angry, disgusted, frightened, surprised, and contempt. Memory demands were minimal as each photograph remained on the computer screen until the participants replied. It should be noted here, the participants of the study were Caucasians, and the face stimuli of the original JACFEE task (Matsumoto & Ekman) contains both Japanese and Caucasion faces. Therefore the results of the study might be biased as some previous research have found 'own-race bias' in face processing and perceptual accuracy - people are better able to identify and recognise faces of their own race than faces of another race (e.g. Brigham and Malpass, 1985; Stahl, Johanna, & Wiese, 2008).

The facial expression stimuli of Ekman and Friesen's set (1976) have been used extensively in prior studies. The stimuli set contains six basic facial expressions (happiness, sad, fear, anger, surprise, and disgust) and a neutral facial expression, which are posed by young and middle-age Caucasian females and males. All the stimuli images are in grayscale. Phillips et al. (2002) compared thirty young and thirty older participants' facial emotion perceptual performance using the Ekman and Friesen's set (1976). In the study, they presented participants with a sequence of twenty-four photographs from Ekman and Friesen (1976) set of faces. For each face image, participants had to choose which of the six emotion labels (anger, happiness, fear, disgust, sadness, and surprise) best matched the face. They found age-related perceptual decline on sadness and anger in the older group, and these age-related declined perceptual performance was not mediated by fluid and crystallised intelligence after including these variables in the multivariate analysis. These results were consistent with other prior studies suggesting that older people are associated with deficits in recognising negative emotions such as sadness and anger (McDowell et al., 1994; Moreno et al., 1993).

In Isaacowitz et al. (2007)'s study, age differences on emotion perception were examined in a cross-sectional sample of adults aged between eighteen to eighty-five years. In the study, a total of thirty-five Ekman and Friesen's set (1976) images were used, participants were asked to match the facial emotion exhibited by the facial stimuli they saw in each trial to one of the emotion labels (anger, disgust, fear, happiness, sadness, surprise, and neutral) and their responses were recorded. Before comparing the two groups' performance difference, researchers measured age-related response bias in emotion recognition task and they found older people were more likely to incorrectly label facial stimuli as disgust and fear. After controlling for these biases, the results showed that older group performed significantly worse than younger group in perceiving facial expressions of anger, disgust, fear, and happiness.

One factor that contributes to age differences in emotion perception is age-related changes in the perceived intensity of emotional expressions (Phillips and Allen, 2004). Some researchers were not entirely happy with the original Ekman and Friesen's set (1976) that only contained images of relatively high emotion intensities. They improved the facial expression stimuli by using morphing/blending techniques that generated new stimuli with different emotional intensities. For instance, Calder et al. (2003) examined young and older adults' perceptual ability of six basic emotions using photographs of Ekman and Friesen (1976) set and the morphed continua of those facial emotions. In experiment 1, twenty-four young participants and twenty-four older participants were assessed on Ekman and Friesen's (1976) multiple-choice facial emotion labeling task. Consistent with most previous studies claiming that increasing age are associated with poorer perception of negative emotions (Phillips et al., 2002, McDowell et al., 1994; Moreno et al., 1993), their results indicated that older participants showed significantly worse recognition of fear and sadness, however, their recognition of disgust was significantly better than younger participants. Calder et al. (2003) further investigated the effect of aging on the perception of emotion in a larger sample of participants (one hundred and twenty-five participants) whose ages spanned between 20 and 75 years on the same task (experiment 2a) and another Emotion Hexagon task (experiment 2b). The Emotion Hexagon task (experiment 2b) comprises "morphed continuum" ranging between the following six expression pairs (happiness–surprise, surprise–fear, fear–sadness, sadness–disgust, disgust–anger, anger–happiness) and each continuum contains five morphed images in the same proportions (Calder, 2013). For example, happy–surprised continuum contains images of 90% happy–10% surprise, and then 70–30%, 50–50%, 30–70%, and 10–90% of the same two expressions. A total of thirty morphed images were presented individually and randomly on a computer screen, and participants were asked to choose which of the six emotion labels (anger, happiness, fear, disgust, sadness, and surprise) best matched the face. Experiments 2a and 2b showed a linear reduction on the perception of fear with increasing age, which began at around 40 years of age; and the perception of disgust was preserved with increasing age rather than a improvement. Calder et al. (2003) proposed that the different patterns of effect of aging on perception of fear and disgust might be due to these two emotions being related with different neural regions and normal aging affects these emotion-related regions differently.

Unlike Calder et al. (2003)'s study (experiment 2b) that used still images of morphed stimuli of expressions, Sullivan and Ruffman (2004a, study 1) used moving morphed emotional images that could change from one emotion to another (e.g. anger-happy) to investigate age differences in perceiving the changes of emotions. In the study, participants were told that they would be presented with a face expressing an emotion, then the emotion would change to another emotion. They were asked to press a key as soon as they detected the new emotion. They found that older adults were worse than younger adults in perceiving facial expressions of sadness and anger, whereas no differences were found between the two age groups in perceiving fear or happiness, or in a task requiring recognising non-emotion shapes (control task). In the study 2, older and young groups were shown two still images of those morphed expressions (from study 1) on each trial, and they were asked to match an image to a specific emotion label (e.g. anger). The results showed that older group were associated with declined performance on judging which of two faces showed a greater amount of anger, sadness, or fear. Older group showed similar performance as the younger group when judging other emotions or when judging which of two containers had more fluid in it (control task). In study 2, Sullivan and Ruffman (2014) also included a gender matching task which used the similar experimental paradigm as the still morphed emotion perception task. The results showed that older people had no problem in matching gender from faces, which suggested that older adults' deficits in recognizing some emotions (anger, sadness) did not extend to general facial processing skills.

Orgeta et al. (2008) assessed the thresholds for accurately identifying emotions in young and older adults. The facial images used in the study were taken from the Facial Expressions of Emotion: Stimuli and Tests (FEEST) (Young, Perrett, Calder, Sprengelmeyer, & Ekman, 2002). These grey-scale images comprise six basic emotions (happiness, surprise, disgust, fear, anger, and sadness) which were portrayed by three male and three female actors (each portraying the six emotions). Differing from the morphed images used previous studies (blending two different facial emotions with varying proportions), the facial stimuli used in Orgeta et al.'s (2008) study were generated by morphing only one emotion with neutral emotion with different proportions (25%, 50%, 75%, and 100%). The benefits of doing so is to reduce the ambiguity of the morphed facial expressions that where generated from two different emotions - which can be very difficult to categorise to one specific emotion. In Orgeta et al.'s (2008) task, participants were asked to identify 1) whether an emotion was present, 2) and label the facial emotion they saw from provided verbal labels. The accuracy of emotion perception at each of the four levels of intensity (25%, 50%, 75%, and 100%) for each emotion was calculated. Older people had difficulties in labeling fear, anger, and sadness from 50% to 100% intensity of emotions. The performance gap between younger and older groups were smaller at 25% emotion intensities. No age-difference was found for perception of happiness, surprise and disgust, even in the lowest emotion intensity (25%), which might be due to ceiling performance by both age groups.

All the face stimuli used in previous studies described above only contain young faces or middle-aged faces. Ebner et al. (2010) created a new face database which included older face stimuli (60 years +) with different types of emotions. These face stimuli have been validated and used in their studies (Eber and Johnson, 2009; Ebner et al., 2010). In Ebner et al's (2010) study, they used one hundred and seventy-one colour naturalistic faces of young, middle-aged, and older women and men. Each face is represented with six facial expressions (neutrality, sadness, disgust, fear, anger, and happiness). They asked young, middle-aged, and older male and female participants to label these faces in terms of perceived facial expression and perceived age. The two age groups did not differ on perception of fearful, happy, or neutral faces. However, the older group showed significantly more errors in correctly identifying angry, disgusted and sad faces. On the perception of age task, older participants made more errors on their perceptions of the age of young faces; however, they were more accurate in judging the age of older faces than young and middle-aged participants, which might reflect the 'own-age' bias in face perception.

Study	N	Age ranges by group	Stimuli	Answer format	A	D	F	H	Sa	Su	N
MacPherson et al. (2002)	90	20–38, 40–59, 61–80	Still posed expressions (Matsumoto & Ekman, 1988)	MC, verbal labels	=	=	=	=[c]	↓	=	NT
Phillips et al. (2002)	60	20–40, 60–80	Still posed expressions (Ekman & Friesen, 1976)	MC, verbal labels	↓	=	=	=[c]	↓	=	NT
Calder et al. (2003, Study 1)	48	18–30, 58–70	Still posed expressions (Ekman & Friesen, 1976)	MC, verbal labels	=	↑	↓	=[c]	↓	=	NT
Calder et al. (2003, Study 2a)	227	17–30, 31–40, 41–50, 51–60, 61–70	Still posed expressions (Ekman & Friesen, 1976)	MC, verbal labels	↓	↑	↓	=[c]	=	=	NT
Calder et al. (2003, Study 2b)	125	18–30, 31–40, 41–50, 51–60, 61–75	Morphs of posed expressions (based on Ekman & Friesen, 1976)	MC, verbal labels	↓	↑	↓	=[c]	=	=	NT
Sullivan & Ruffman (2004, Study 1)	61	20–38, 60–84	Moving morphs of posed expressions (based on Ekman & Friesen, 1976)	MC, verbal labels	↓	NT	=	=	↓	NT	NT
Sullivan & Ruffman (2004, Study 2a)	56	18–29, 63–79	Still posed expressions (based on Ekman & Friesen, 1976)	MC, two images to match target emotion	↓	=	↓	=	↓	=	NT
Isaacowitz et al. (2007)	357	18-39, 40-59, 60-85	Still posed expressions (Ekman & Friesen, 1976)	MC, verbal labels	↓	↓	↓	↓	=	=	=
Orgeta et al. (2008)	80	17-37, 61-81	Still posed expressions (FEEST, Young, Perrett, Calder, Sprengelmeyer, & Ekman, 2002)	MC, verbal labels	↓	=	↓	=	↓	=	NT
Eber and Johnson (2009)	56	18-22, 65-84	Still posed expressions of young, middle-aged, and older faces (Ebner et al., 2010)	MC, verbal labels	↓	NT	NT	=	NT	NT	↓
Ebner et al. (2010)	154	20–31, 44–55, 70-81	Still posed expressions of young, middle-aged, and older faces (Ebner et al., 2010)	MC, verbal labels	↓	↓	=	↓	↓	NT	↓

Figure 1.1. Previous research on young-old behavioural performance on facial emotion perception. In the first row, *A* represents anger; *D* represents disgust; *F* represents fear; *H* represents happiness; *Sa* represents sadness; *Su* represents surprise; *N* represents neutral.
In the findings cells, *NT* refers to not tested, = represents no significant differences, ↓ signifies that older adults performed worse, and ↑ signifies that older adults performed better. In *answer format*, *MC* represents multiple choice. [c]Ceiling effect in perception scores. (The format and partial contents of this table is adapted from Isaacowitz et al., 2007).

Limitations within previous behavioural investigations

Emotional intensity

A general limitation involved in most previous research is that only high-intensity prototypes of facial expression images have been used. This is problematic for two reasons. Firstly, it is known that the ability to correctly perceive facial emotional expressions can vary across different prototypical emotions (i.e. they are not matched for difficulty; e.g. see Calder et al., 2003), thus comparisons in performance differences across emotion types can be difficult.

Secondly, although the study of high intensity emotion has proved useful, more subtle facial expression that have lower intensities are common in daily social interactions (Orgeta and Phillips, 2007). For example, Pictures of Facial Affect (Ekman & Friesen, 1976) is a widely used emotion perception task (e.g. Moreno et al., 1993; Calder et al., 2003) consisting of photographs of six basic facial expressions happiness, sadness, anger, fear, disgust, and surprise and a neutral expression. Although this database has proved to be an invaluable resource, use of the database is limited to considerably high intensity of emotions.

Face stimuli age

The age of facial stimuli has been found to affect people's emotion perception. There might be an 'own-age' bias involved in facial emotion perception. In an emotion perception study using fMRI, Ebner, Johnson, and Rieckmann et al. (2013) found older participants showed greater activations in medial prefrontal cortex, insula, and amygdala to own-age faces in neutral and happiness trials. However, the emotion perception of older faces was reported to be harder than young faces, as the wrinkles and folds of older faces can reduce the signal clarity of facial expressions (Hess, Adams Jr., Simard, Kleck, 2012; Courgeon et al., 2009). In a behavioural study, Ebner, He, & Johnson (2011) investigated both younger and older people's emotion perception of young and old faces, and revealed that both age groups had better performance for young faces.

In light of this, it is therefore possible that the facial identity perception results of most previous research suggesting that younger participants have superior face performance compared with older participants might be biased by the age of facial stimuli, as most previous face processing studies investigating young-old differences only used young faces (Verdichevski & Steeves, 2013).

Experimental paradigm

Most face emotion perceptual tasks used in previous studies experimental paradigm might theoretically tap additional processes alongside perceptually driven performance factors. For example, labelling based measures of emotion processing require additional demands of assigning a verbal label to an emotion, thus placing additional constraints on performance related to variation in emotional vocabulary (Barrett, Lindquist, & Gendron, 2007). Further, labelling and same-different judgment tasks often require increased working memory demands, thus placing additional constraints on performance related to cognitive load (Phillips, Channon, Tunstall, Hedenstrom, & Lyons, 2008).

1.2.3 Explanations of the age-related decline in facial expression perception

Socio-emotional selectivity theory (SST; Carstensen, Isaacowitz, Charles, 1999) has been used to interpret the older people's decline in negative emotion perception. According to SST, older people perceive time as increasingly limited and thus become selective in investing resources to emotionally meaningful goals and activities. Therefore, aging is associated with a motivational shift towards positive information and avoidance of negative information, which was referred to 'positivity effect'. Based on this theory, older people's poorer performance in negative perception might be due to their avoidance to negative emotions (Ruffman et al., 2008).

However, neuropsychologists have argued that the young-old difference in emotion perception observed was largely due to structural, neurochemical and physiological changes in brain regions in aged people (D'Esposito, 1999; Esposito et al., 1999; Grady, 2000; Calder et al., 2003; Isaacowitz et al., 2007; Ruffman et al., 2008; Philllips et al., 2002; Sullivan and Ruffman, 2004). In particular, normal aging is associated with thinning of the cerebral cortex, volumetric reductions of most subcortical structures, and decrease in dendritic synapses or loss of synaptic plasticity (Fjell, Walhovd, & Fennema-Notestine et al., 2009; Rosenzweig and Barnes, 2003). Frontal and parietal show greater decline compared to temporal and occipital lobes. Loss of dendritic synapses and volume appear to be serious in the prefrontal cortex, the striatum and the hippocampus (Raz, 2004, 2005). Gray matter loss is most pronounced for orbital and inferior frontal, cingulate, insular, inferior parietal (Resnick, Pham, & Kraut, 2003). The cerebrum loses 1–2% of its mass each year as well as white matter structural integrity (Raz et al., 1997; Fjell et al., 2009). The cerebrum weight starts decline at the age of 40, and the decline rate significantly increase over the age of 70 (Scahill et al., 2003).

This neural change has affected the facial emotion processing neural networks. For example, this network includes temporal regions such as amygdala and fusiform cortex, which were considered to play a general role in responding to all facial expressions (Adolphs et al., 1999; Davis and Whalen, 2001); the ventral striatum that responds to anger (Calder, Keane, Lawrence, & Manes, 2004). The linear reductions in amygdala volume with age (Tisserand et al., 2000; Grieve et al., 2005) may lead older adults to have difficulty recognising facial expressions of fear. Similarly, the volume reduction and metabolic decline in the anterior cingulate cortex could lead to older people's reduced ability in recognising facial expression of sadness (e.g. Garraux et al., 1999; Pardo et al., 2007). In contrast, the relative sparing of some structures within the basal ganglia with age may result in preserved ability at identifying disgusted expressions in older adults (Calder et al., 2003; Williams et al., 2006).

1.2.4 Neuroimaging investigations

Electroencephalography (EEG) has better temporal resolution than hemodynamic-dependent brain imaging techniques (such as fMRI) and enables inference about the time course of emotional facial expression processing in human brain. This is because event-related potentials (ERPs) originate as postsynaptic potentials (PSPs), which provide a "direct, instantaneous, millisecond-resolution" measure of neural activity, which contrasts with "delayed, secondary consequence" of the blood oxygen level-dependent (BOLD) signal in fMRI (Luck, 2014). Up to date, few studies have investigated that whether the emotion-related ERPs are affected by advancing age.

Previous studies have explored the ERP components during facial emotion processing in younger adults (e.g. Eimer and Holmes, 2002; Eimer, Holmes, and McGlone, 2003; Balconi, Pozzoli, and Pozzoli, 2003; Kissler, Herbert, and Winkler et al., 2009). During passive viewing of displays of facial expressions, younger adults showed three major ERP components: firstly, an enhanced early frontocentral positivity was elicited in response to emotional as opposed to neutral faces within 120ms after stimulus presentation (Eimer and Holmes, 2002; Eimer, Holmes, and McGlone, 2003), followed by a broadly distributed sustained positivity beyond 250ms post-stimulus (Eimer and Holmes, 2002; Eimer, Holmes, and McGlone, 2003), and then followed by an enhanced negativity at lateral posterior sites (EPN) (Eimer, Holmes, and McGlone, 2003; Balconi, Pozzoli, and Possoli, 2003; Kisslerm Herbert, and Winkler et al., 2009).

The early frontocentral positivity (within 120ms post-stimulus) and later broadly distributed positivity (beyond 250ms post-stimulus) were found very similar across different types of basic emotional expressions; in other words, these ERP positivities are not modulated by emotion type (Eimer et al., 2003, 2007). In addition, these emotional positivities are modulated by attention, as it was found that these positivities disappeared when attention was directed away from the faces (Eimer et al., 2003). These early and late emotion-related cortical positivities reflect non-automatic and attentive processing of facial emotions, which is in contrast to the automatic and inattentive subcortical emotion processing (e.g. amygdala) (Eimer et al., 2003, 2007). Prior studies on negativity at lateral posterior sites (EPN) suggested that the amplitudes of the EPN were enhanced by emotional faces, as viewing threatening (Holmes et al., 2003; Schupp, Ohman, et al., 2004) and happy (Schacht & Sommer, 2009) faces elicited an enhanced EPN compared to neutral faces. However, the amplitudes of EPN did not vary between pleasant and unpleasant stimuli (Schupp et al., 2003). In addition, the EPN component was not modulated by different levels of attentional demands, as EPN amplitudes remained consistent across a verity of viewing paradigms (e.g. passiving viewing, target detection). EPN only increases when the emotional intensity of facial stimuli increases (Schupp et al., 2003).

Up to now, few studies have investigated the whether the emotion-related ERPs are affected by advancing age. A recent ERP study (Wieser, Mühlberger, Kenntner-Mabiala, & Pauli, 2006) compared older and younger adults' ERPs elicited by facial expressions (neutral, positive and negative) and revealed that early EPN (168–232ms) was reduced in older adults compared to younger adults, but the late EPN (232–296ms) was not affected. However, some questions remain to be answered, such as whether other ERP components are affected by normal aging (e.g. early and late emotion-related positivities); and what are the effects of task difficulty and stimuli age in modulating these emotion-related components.

Functional neuroimaging techniques, such as positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) have a spatial resolution in the millimeter range, and this cannot be matched by scalp electrical recordings. These methods enable researchers to explore the precise neural activation patterns during emotion processing tasks. The processing of facial emotion is a complex psychological process, and it activates a broad range of neural networks. A recent meta-analysis review of fMRI studies (Fusar-Poli, Placentino and Carletti et al., 2009) on neural activations of basic facial emotions (i.e., fear, disgust, anger, happiness, sadness) revealed that the processings of facial emotions were associated with increased neural activations in "visual areas (fusiform gyrus, inferior and middle occipital gyri, lingual gyrus), limbic areas (amygdala and parahippocampal gyrus, posterior cingulate), temporal areas (middle/superior temporal gyrus), temporoparietal areas (parietal lobule, middle temporal gyrus, insula), prefrontal areas (medial frontal gyrus), subcortical areas (putamen) and the cerebellum (declive)". The role played by the amygdala in processing facial emotion appears to be greatest for processing fear or potential threat (Adolphs, 2002; Calder et al., 2001; Haxby, Hoffman, & Gobbini, 2002). The amygdala, along with the STS, also plays a more general role in processing information that is critical for social cognition, such as judging the state of mind based on perception of the eye region (Baron-Cohen et al., 1999; Kawashima et al., 1999). The basal ganglia and insula are associated with processing expressions related to disgust (e.g., Haxby et al., 2002; Phan, Wager, Taylor, & Liberzon, 2002), the ventral striatum is associated with processing expressions related to anger (Calder, Keane, Lawrence, & Manes, 2004) (figure 1.2). Most neuroimaging research on the neurobiological basis of facial emotion processing have investigated young participants in their studies. Normal aging affects emotion processing related brain regions (Mu, Xie, & Wen, 1999; Chételat, G., Landeau, B., Salmon, 2013), however, few research have studied the neural processing patterns in aged population.

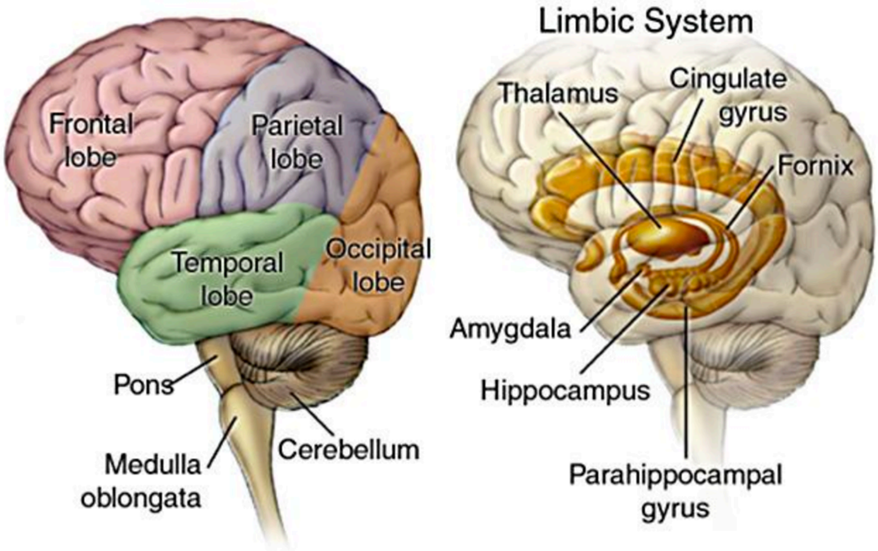


Figure 1.2. Anatomy of brain. The cerebrum is divided into four lobes: frontal, parietal, temporal, and occipital (left graph). Location of major limbic system structures (right graph)

Evidence for two models of age-related hemispheric asymmetry in the emotion processing context have been summarised and reviewed. The two models are 'right hemisphere aging' model and 'hemispheric asymmetry reduction in old adults (HAROLD)' model. The right hemisphere aging model proposes that normal aging is associated with significant decline in right hemisphere, whereas the HAROLD model supports that older people tend to recruit more frontal cortical regions to compensate their less subcortical neural activations compared to younger people during emotion processing, especially for negative facial expressions. The right hemisphere aging model is supported by a mix of behavioural, neuropsychological and neuroimaging studies which utilised different approaches, and few results were replicated. In contrast, the HAROLD model is mainly evidenced by neuroimaging studies that used fMRI to record younger and older adults' neural activation during presentation of emotional facial displays, and the results were quite consistent across a few studies (e.g. Iidaka, Okada, and Murata, 2002; Gunning-Dixon, Gur, & Perkins, 2003; Fischer, Sandblom, and Gavazzeni, 2005). Some researchers suggested that it is possible that the two models are compatible with each other (Dolcos, Rice, and Cabeza, 2002).

Right hemisphere aging model

Human lesion and neuropsychological studies have investigated the roles of right and left hemispheres played in emotion processing. A number of researchers agreed on the 'right hemisphere dominance' view, which postulated that the right hemisphere is dominant for emotion processing (Blonder et al., 1991; Adolphs et al., 1996; Borod et al., 1997). Another valence hypothesis suggested that right and left hemispheres play different roles in processing emotions – left hemisphere is in charge for processing positive emotions, whereas right hemisphere is responsible in processing negative emotions (Davidson, 1992; Derryberry and Tucker, 1992).

A collection of of evidence suggested that the right cerebral hemisphere declines faster than the left cerebral hemisphere in normal aging processing (Prodan, Orbelo, & Ross, 2007; Goldstein and Shelly, 1981; Paradiso, Vaidya, & McCormick, 2008; McDowell et al., 1994). For example, Goldstein et al (1981) tested 1247 participants with age range from 20-70 years using a Halstead-Reitan battery, and the test scores were analysed with Russell, Neuringer, and Goldstein localisation key which has proven to be highly reliable in predicting neurological deteriorations for both normal and clinical population. The results provided neuropsychological evidence directly showing that normal aging leads to significant increase in right hemisphere deterioration, but a less pronounced effect for left hemisphere.

Further studies have shown that the age-related right hemisphere deterioration is linked with declined perception of facial affective information. McDowell et al. (1994) compared younger and older adults' facial emotion perception and age-related hemisphere asymmetry. In the study 1, participants were asked to identify stimuli of facial emotional expressions from five emotion labels – happy, neutral, angry and fearful. Older people showed significantly more errors in recognising negative and neutral expression, but their perception of happiness was consistent with the younger group. In the study 2, the researchers investigated the effects of different visual field presentation and valence of the stimuli on participants' response time for the recognition of the emotional stimuli. In each trial, participants were asked to look at a fixation cross (mid-line of the screen), and a happy or angry emotion stimuli selected from Ekman and Friesen's (1978) was presented in either the right visual field (RVF) or the left visual field (LVF). Participants were asked to label the stimuli as 'happy' or 'angry' as soon as it was presented. Older people showed increased hemisphere asymmetry in processing of facial emotions. Specifically, the older adults responded faster to angry stimuli when they were presented to their right hemisphere (left visual field) than when they were presented to their left hemisphere (right visual field). In contrast, the visual field of presentation did not affect younger adults in processing facial emotions, as the younger group responded to the different facial emotions with similar speed, regardless of visual field. McDowell et al. thought older adults' faster response time to angry stimuli presented to the right hemisphere does not support the right hemisphere aging hypothesis. However, the findings of study 1 favored the right hemisphere aging hypothesis since older adults showed similar performance as younger adults in recognising happiness whereas they showed greater difficulty with negative affect, which would suggest that right hemisphere mediated skills (processing negative emotion) are affected more than left hemisphere mediated skills (processing positive emotion) in the older adults. McDowell et al. concluded that their finding served as a partial support (study 1) to the right hemisphere aging hypothesis. Some researchers argued that if the results were interpreted in the context of the valence hypothesis of emotion processing which claims right hemisphere is responsible for processing negative emotions, then the results could fully support the right hemisphere aging hypothesis (Dolcos et al., 2002). Later, in Prodan, Orbelo, and Ross's (2007) study, both younger and older participants were tested by flashing randomised facial displays of emotion to the right and left visual fields. Older people showed significant decline in processing eye region information by the right hemisphere compared to the younger group.

In addition, Paradiso, Vaidya, & McCormick (2008) found that normal aging is positively correlated with high overall alexithymia score and reduced bilateral rostral and right dorsal anterior cingulate cortex (ACC) grey matter volume, and higher alexithymia scores correlated with reduced right rostral ACC volume. Alexithymia score is an indication of ‘emotion blindness’- difficulty to perceive and describe emotions of others and themselves. Therefore, this result suggested that the age-related decline in emotion awareness and perception was associated with right hemisphere neural deterioration.

The above summarised behavioural, neuroimaging and neuropsychological studies which supports the right hemisphere aging model in emotion processing. However, the right hemisphere aging hypothesis still lacks direct neuroimaging evidence to confirm the proposal. Secondly, these studies used quite different approaches and their findings have not been replicated by other studies. Future research should further confirm these findings by combining brain imaging methods.

Hemispheric asymmetry reduction in old adults (HAROLD)

In 2002, Iidaka and colleagues investigated age-related differences in the neural substrates of facial emotion perception by comparing younger and older people’s neural activation patterns during presentation of positive, negative and neutral facial expressions. During the task, participants were asked to judge the gender of presented faces and their brain activations were recorded using fMRI. The findings showed that compared to younger participants, older participants showed significantly reduced activity in left amygdala during presentation of negative facial expressions (anger and disgust); whereas during presentation of positive facial expression, older participants showed significantly reduced neural activation in the right parahippocampal gyrus. They also found the overall activity in the right hippocampus during the task correlated negatively with age in older participants. This study revealed that normal aging is associated with decreased activity in temporo-limbic neural areas, including amygdala (processing negative emotion) and hippocampus and parahippocampal gyrus (processing positive emotions). However, no neural regions were found to have greater activations than younger participants during emotion processing tasks.

The previous study only required participants to discriminate gender of facial displays but not facial expressions. Later studies revealed more interesting results by requiring participants to recognise type of emotions from displays of facial expressions. Concurrent with relative lower limbic regions responses, later studies found recruitment of additional cortical areas in older people during facial emotion processing. Gunning-Dixon, Gur, & Perkins (2003) examined age-related neural activations in cortical and limbic regions using fMRI by presenting facial displays of a mixture of mostly negative emotions (happiness, sadness, anger, fear, disgust) to both young and older adults. In emotion-discrimination task, relative to baseline neutral condition, younger adults activated the amygdala and surrounding temporo-limbic regions, whereas older adults activated left frontal regions. This results firstly suggested that normal aging might be associated with less amygdala activity but increased frontal activations during facial emotion processing.

Later, some studies have further explored older people's neural processing of negative emotions using fMRI and their results showed similar patterns. Fischer, Sandblom, and

Gavazzeni (2005) explored perception of anger in older people by using paradigm of 'passive viewing of facial perception', which reduced the mental effect of discrimination tasks. They presented facial displays of anger and participants' ratings of emotional valence were collected. They compared the fMRI neural activation patterns and subjective ratings of emotional valence between younger and older participants. There was no significant age difference in the subjective ratings of degree of anger. Regarding the neural responses, in line with previous findings, the results confirmed that aging is associated with significantly lower subcortical activation but higher cortical activations. Specifically, they found that older participants showed significantly higher neural activations in right agranular insula cortex and lower activations in amygdala and hippocampus. In their later study (Fischer, Nyberg, & Backman, 2010), similar age-related neural activation patterns have been replicated by displaying facial images of fear.

In Tessitore, Hariri, and Fera et al.'s (2005) study, they compared older and younger participants' neural processing of fearful and threatening stimuli using fMRI. Direct group comparisons revealed that aged participants showed increased prefrontal cortical neural responses, including Broca's area and left medial prefrontal cortex; and significantly lower neural responses in the amygdala and posterior fusiform gyrus. It should be noted that, different from other experiments, the control/baseline condition used in this experiment was a geometric shape matching task instead of a neutral emotion perception task. Therefore, after subtracting the baseline condition neural activation from emotion discrimination task, it still contains face-related processing neural regions. The fusiform gyrus has been extensively reported as a specialised area for processing facial features or high-class delicate object features (Kanwisher et al., 1997, 2000; Gauthier et al., 1997, 1999). The finding of additional decreased posterior fusiform gyri neural activation might reflect a decline in processing facial shapes and features.

These studies consistently showed a general age-related pattern in processing negative emotions, suggesting age-related higher frontal cortical activation might reflect ‘functional compensation’ in older adults due to their less efficient processing of emotional facial expressions in subcortical limbic regions, such as amygdala and hippocampus. Fischer et al. (2010) proposed that older and younger people might rely on different neural networks for processing emotions. Young people rely more on amygdala processing, which is an automatic, unconscious and effortless way of emotion processing; whereas older people rely more on neocortical processing, which relates to an attentional, conscious, effortful way of affect processing (e.g., Ochsner et al., 2004; Eimer and Holmes, 2007). Furthermore, this unique age-related neural activation pattern for negative emotion processing in older people seemed only restricted in facial expressions, and it does not extend to non-social objects. Kensinger and Schacter (2008) found both younger and older participants recruited right amygdala and orbito-frontal, and parietal cortices during encoding of both negative and positive objects, suggesting there is no age-related difference in processing emotional objects.

Unlike other studies that only investigate negative emotion processing, Keightley et al. (2007) studied behavioural responses and neural activities of recognising different basic facial expressions (happiness, surprise, anger, disgust, fear, sad, neutral) in both younger and older adults. The behavioural results showed that older participants had significantly lower accuracy than younger participants in recognising negative emotions, whereas their perception of happiness did not differ from younger participants. They also found that the neural activity pattern for processing different emotions were age-specific. Consistent with previous findings (e.g. Gunning-Dixon et al., 2003, Tessitore et al., 2005), older adults showed more widely and increased cortical responses for processing negative emotions, including bilateral frontal and temporal regions, and somatosensory cortex. Furthermore, this age-specific pattern was also exhibited during neutral emotion perception. For happiness perception, young adults additionally activated the amygdala, lateral PFC, posterior cingulate, temporal and parietal regions than older adults. The lack of reliable amygdala activity in happiness perception in older adults seemed in line with previous studies using negative emotions, which was explained as age-related reduced limbic neural activity. However, young adults surprisingly activated more cortical regions in happiness perception, this result is novel as none of other studies has compared happiness perception in both young and older groups. This result needs to be confirmed by more studies and the underlying mechanism needs to be explained.

Implications

Perception of facial emotion may contain two important mechanisms: 1) "construction of a simulation of the observed emotion in the perceiver" via the connection from the amygdala to motor structures, hypothalamus, and brainstem nuclei; and 2) "the modulation of sensory cortices via top-down influences", where the amygdala can modulate perceptual attention via feedback. The second mechanism mostly contributes to fine-tuning the categorization of the facial expression (Adolphs, 2002). Thus, decline in the ability in perceiving facial expressions and decrease in activation in emotion processing areas in older adults might be directly related to the decrease in perceiving the observed emotion and physiological responding in various social situations that contain different emotional information, which would lead to poor interpersonal functioning and communication, reduced quality of life and inappropriate behaviours (Spell and France, 2002, Carton et al., 1999). Previous behavioural and neuroimaging studies have attempted to understand the underlying reasons for older people's poor perception of facial expressions and revealed some age-related changes within the emotion perception neurocognitive mechanisms. This would also help to boost current knowledge in general emotion processing.

Previous findings suggest that older adults show impairments in the social perception of faces, including the perception of emotion and facial identity. The majority of this work has tended to examine performance on tasks involving young adult faces and prototypical emotions. While useful, this can influence performance differences between groups due to perceptual biases and limitations on task performance. Here I sought to examine how typical aging is associated with the perception of subtle changes in facial emotional and facial identity in older adult faces. I developed novel tasks that permitted the ability to assess facial emotion (happiness perception), facial identity, and non-social perception (object perception) across similar task parameters. This research would help to constrain our understanding of age-related changes in social perception. Further, by introducing novel tests using older facial stimuli and non-face stimuli that assess performance under equivalent conditions I hope to provide the field with important measures that can be used in future research: our new tasks adapt the current gold standard measures (Cambridge Face Perception Tests; Duchaine et al. 2007) that are used in young adults to identify face processing difficulties (e.g. prosopagnosia) to include older adult target stimuli and non-face stimuli. The development of these novel measures therefore has the potential for use in face perception studies examining a range of groups that extend beyond typical older / younger adults that are tested in our current study.

A caveat is that most neuroimaging studies only used facial displays of negative emotions in their studies (i.e. Tessitore, Hariri, and Fera et al., 2005; Fischer et al., 2010). However, some neural regions such as amygdala and hippocampus are related with general emotion processing, which were well established in previous emotion studies using young participants (Phan, Wager, & Taylor et al., 2002). Therefore, it is not entirely clear if the age-related compensation pattern reflects older people's general emotion processing, or processing of negative emotions only (Fischer et al., 2005). Furthermore, in previous studies the facial emotion displays only contained high-intensity of anger, which cannot reflect real life social signals which contain both subtle and obvious facial emotions. Most previous brain imaging studies which recorded behavioural discrimination of emotion (Gunning-Dixon, Gur, & Perkins, 2003; Tessitore, Hariri, and Fera et al., 2005) or subjective rating of emotion valence (Fischer, Sandblom, and Gavazzeni et al., 2005) have shown that older people can achieve similar performance as younger people, but using significantly higher reaction times. In other words, older people's compensation strategy enabled older people to recognise high-intensity negative emotions, but the processing takes significantly longer than young people. It is unknown if older people's compensation strategy can efficiently process subtle/low-intensity facial expressions. Can they still achieve similar behavioural performance as younger people? Do older people exhibit the similar neural patterns to process low-intensity facial emotions? If not, what other neural areas might older people recruit additionally to process subtle facial expressions?

1.2.5 Summary

This section has summarised and reviewed the recent behavioural and neuroimaging studies that investigate facial emotion processing in normal aged population, and discussed two popular brain asymmetry aging models. The behavioural studies suggested that healthy older population show declined facial expression perception of anger, sadness and fear, while the perception of happiness showed inconsistent results which requires further investigations. Neuroimaging studies have proposed two age-related brain activation models during facial emotion processing, both of which have suggested that older adults exhibited different brain activation patterns from younger adults. The general limitations of behavioural and neuroimaging studies were 1) they only investigated only one (mostly high-) emotion intensity, and 2) only young face stimuli were used in those studies, which could cause other-age face perceptual bias. Furthermore, most neuroimaging studies only used facial displays of negative emotions, few studies have compared the young-old neural activations during perception of happiness. These limitations show that previous findings might not reflect a comprehensive account of older people's facial emotion perception. To fill these research gaps and give a fuller account of this area, one of my research aim was to investigate the age-related difference in recognising facial expressions of happiness and anger using images of low intensities ranges from 3%-40%. Another research aim is to clarify whether the observed age-related facial emotion perception decline was due to the use of young facial stimuli by using both young and old facial images in face emotion perception tasks.

Aging and facial identity perception

1.3.1 Behavioural investigations

People perceive thousands of faces during the whole life. Face identity perception, however, does not stay steady during life course. Older people do not exhibit higher expertise in facial identity perception due to more exposure to faces and experiences in perceiving facial identities. In contrast, previous behavioural studies have established that normal aging is associated with a decline in perceiving familiar and unfamiliar faces relative to younger adults (e.g. Bowles et al., 2009; Megreya & Bindermann, 2015; Owsley, Sekuler, & Boldt, 1981; Searcy, Bartlett, & Memon, 1999; Habak, Wilkinson, & Wilson, 2008; Rousselet et al., 2009, 2010). Older adults show similar hit rates but more false alarms compared with young adults in face identity perception (Searcy et al., 1999). This age-related decline is independent of loss of visual acuity and contrast sensitivity (Schretlen, Pearlson, Anthony, & Yates, 2001), age-related memory load decline (Lamont et al., 2005), or general cognitive decline (Hildebrandt et al., 2011). Further, the relationship between facial identity memory ability and aging has been shown to reflect an inverted parabola, with performance increasing during young to middle adulthood, before declining into and throughout older adulthood (Germine, Duchaine, & Nakayama, 2011).

Face-matching is a popular approach for assessing people's facial identity perception (e.g. Habak, Wilkinson, & Wilson, 2008; Megreya & Bindermann, 2015). Searcy and Bartlett (1999) showed age-related increased difficulties in perceiving unfamiliar facial identities using the Benton Face Recognition Test (BFRT) (see Benton, 1980). In the task, participants were shown an unfamiliar target face and a line of six unfamiliar faces, and their task was to choose one face from the several to match the target face. The BFRT task comprised two conditions, the choice faces can either contain or not contain the target faces. Compared with the young adult participants, older adult participants exhibited lower accuracy and higher false choosing rates. Schretlen, Pearlson, Anthony, & Yates (2001) also used the BFRT test (Benton et al., 1983) to investigate the effect of normal aging on the perception of facial identities in one hundred and seventy-four healthy adults (age range 20 to 92 years). In each trial, a full frontal gray scale adult face image was presented, beneath each target face were six other choice faces, which were in full or partial light and in full frontal or three-quarter profile orientations. The results confirmed that the ability of discriminating unfamiliar faces under different light and exposure conditions declined with advancing age (Benton et al., 1983; Mittenberg et al., 1989; Searcy and Bartlett, 1999). Schretlen et al. (2001) also explored the effect of other factors on participants' face perceptual performance on the BFRT task, such as age, sex, education, perceptual comparison speed, and neuroanatomic variables [e.g. ventricle-to-brain ratio (VBR)] derived from magnetic resonance imaging. They found that the VBR and processing speed alone accounted for nearly 34% of the variance in facial perceptual performance. These findings suggest that both age-related neural changes and decreases in processing speed contribute to older people's declined facial identity perception.

Habak, Wilkinson, & Wilson (2008) further demonstrated older adults' ability in matching facial identities at same-view and different-view conditions. In the study, there were nineteen healthy younger adult participants (age range 20–30 years) and twenty-one older adult participants (age range 58–72 years). In each trail, participants were shown a target face briefly, followed by a mask screen for 200ms, and two choice faces shown side-by-side. Participants were asked to match one of the two shown faces to the target face. The screen would not change until participants made a decision. They found that older adults' ability in matching same-view (front-front or side-side) facial identities were preserved, however, older adults showed deficits in matching facial identities that were shown in different views (e.g. front and turned 20° to the side). This results indicate that the mechanisms underlying same-view facial identity discrimination were maintained with age. In contrast, the processing of facial identity across views was degraded. Megreya & Bindermann (2015) explored the development of face identity perception from childhood to late adulthood using the 1-in-10 matching task for unfamiliar faces (Bruce et al., 1999). A total of 330 Egyptian participated in this experiment, which included children, adolescents, young, middle-aged, and older adults. In each trial of 1-in-10 matching task (Bruce et al., 1999), participants were shown a target face and a line of ten choice faces, in which the target face could be present or absent. Participants were asked to decide whether the target is present, then participants needed to choose which face matched the target face. There were fifty trials in total for each participant (twenty-five target present and twenty-five target absent), which were presented in a random order. The task was self-paced so the perceptual performance was not affected by motor or perceptual speed. It should be noted that, all face stimuli used in the task were young adult faces, which could potentially bias children, adolescents and older participants' performance due to 'own-age' bias. The accuracy was calculated for each participant. The results suggest that that face identity matching accuracy increases between 7 and 10 years and also between 13 and 16 years of age, and then remains steady during middle-age, and declines in 65 years.

Most face identity task were face matching which required participants to choose a face from several to match the target face. Recent studies have adopted a new approach that requires participants to sort or arrange several randomly located morphed faces from most likeness to least likeness to the target face, which is more sensitive in measuring people's ability in detecting facial identity differences (e.g. Cambridge Face Perception Task: Duchaine, Germine, & Nakayama, 2007a; Duchaine, Yovel, & Nakayama, 2007b).

1.3.2 Neuroimaging investigations

In event-related potentials (ERPs), N170 refers to a component of the ERP that reflects the neural processing of faces. The face-specific N170 component was first proposed by Bentin et al. in 1996, who measured ERPs from participants during presentation of faces and other objects, and they found that human faces elicited robust negative deflection between 160 and 180ms at occipito-temporal sites compared to other object categories (Bentin et al., 1996; George, Evans, Fiori, Davidoff, & Renault, 1996). The occipito-temporal sites are consistent with a source located at the fusiform and interior-temporal gyri (Allison, Puce, & Spencer et al., 1999; Ghuman, Brunet, & Li et al., 2014). A small collection of ERP studies have demonstrated the effect of normal aging on the N170. Previous studies have found older people also displayed N170 when seeing faces, but its amplitude was significantly higher than younger participants (Chaby, George, Renault, & Fiori, 2003). In addition, younger people showed a right-hemisphere dominant N170 distribution, whereas older people did not show the right-lateralised N170 pattern but exhibited a more symmetric distribution (Pfutze, Sommer, & Schweinberger, 2002; Chaby, George, Renault, & Fiori, 2003; Gao et al., 2009; Daniel and Bentin, 2012). Daniel and Bentin (2012) explained that older people's additional recruitment of the left hemisphere compared to younger people lead to a reduction of hemispheric asymmetry in face identity perception. The additional recruitment of the left hemisphere might be due to age-related right hemisphere aging. In addition, they also found increased activation of frontal regions in older people.

Grady, Maisog, and Horwitz et al. (1994) firstly investigated age-related neural changes associated with face identity perception using positron emission tomography (PET). Participants carried out face and spatial location matching tasks, in which the target and choice stimuli were presented simultaneously to eliminate any memory component. The task difficulty is relatively low as each trial only require participants to choose one stimuli from two to match the target. In both tasks, older people exhibited significantly longer response time than younger people, but the accuracy of the two age groups did not significantly differ. The PET results showed that younger and older participants exhibited similar regional cerebral blood flow (rCBT) activation in ventral occipital and occipitotemporal area during face matching and dorsal occipital and parietal activation during location matching trials. However, older participants utilised more prefrontal and temporal cortex and showed less medial occipital activation in both tasks.

Lee et al. (2011) used an fMRI adaptation paradigm to identify the age-related neural changes in face identity processing. This technique is based on the assumption that neuronal populations show reduced responses (neural adaptation) when specific stimuli to which they are sensitive are repeated (Grill-Spector & Malach, 2001). In the study, both younger and older participants were presented with successive face images that varied in identity and view points and participants were required to perform a head size detection task. It was found that older people did not show neural adaptation in right fusiform face area (FFA) when the same face was repeatedly presented in the same view, whereas the same stimuli condition elicited the most adaptation in young participants. The researchers also examined the correlation between whole-brain activation and participants' behavioural performance. They found that high-performing older participants activated the same face-processing network as high-performing younger participants across almost all conditions, whereas low-performing older adults used this network significantly less. However, higher-performing older adults recruited more neural regions such as left inferior occipital gyrus, frontal, and parietal regions additionally to aid better performance in all conditions. Based on these findings, Lee, Grady, Habak et al. (2011) suggested that core face-processing neural regions become less efficient with aging and the recruitment of extra neural network was used to compensate for the deficiencies in the core face processing regions.

A limitation of this study described above is lack of non-face stimuli in the testing to demonstrate if the age-related neural changes is face-specific. Burianová et al. (2013) compared younger and older people's whole-brain neural activity and neural connections using fMRI during same-different matching tasks of faces, houses and objects. In behavioural tasks, there was no significant difference in either accuracy or RT between younger and older adults. They proposed that age-related neural changes involve two critical phenomena: dedifferentiation and compensation. The proposal of age-related neural 'dedifferentiation' was supported by their whole-brain analysis. It showed that young adults recruit a network of neural regions that were specific for face processing during face discrimination task, including bilateral occipitotemporal gyrus, fusiform gyrus, inferior frontal gyrus, middle occipital gyrus, medial frontal gyrus, and precuneus (Haxby et al., 2000). In contrast, older people recruited face-specific neural regions not only in face discrimination task, but also in house and object discrimination tasks; suggesting a lack of specificity to different stimulus categories. This result is in line with other studies showing that older people's ventral and dorsal visual pathways for faces and objects are less functionally segregated (i.e. Park et al., 2004; Goh, Suzuki, & Park, 2010). Burianová et al.'s (2013) finding of age-related compensatory recruitment was seen in their functional connectivity analysis. Young adults showed functional connectivity between the right fusiform gyrus and its surrounding region during face processing, whereas older adults showed a functional connection between the right fusiform gyrus and left orbitofrontal cortex. In addition, the frontotemporal functional connection activity was found to positively correlated with face-matching behavioural performance, suggesting increased involvement of this functional link for successful facial identity perception with increasing age (compensation).

To sum up, recent neuroimaging studies have found age-related neural changes for perception of facial identities. Older people seem to have similar or reduced neural activation in the core face processing regions compared to younger adults, but their additional neural activation in prefrontal regions and reduction of hemispheric asymmetry activation patterns during facial identity perception reflect a compensation strategy (i.e. Grady, 1994; Lee, Grady, Habak et al., 2011; Burianová et al., 2013). In addition, older people's use of face-specific neural regions for processing objects reflects their age-related neural dedifferentiation underlying their perception mechanism (Park et al., 2004; Goh, Suzuki, & Park, 2010; Burianová et al., 2013). However, it is still not clear if the additional neural activations are functionally specialised for perception of faces, or whether they play a role in general cognitive execution. Secondly, in a few of the neuroimaging studies the facial identity perception tasks were relatively easy and older people showed similar or equivalent accuracy compared to younger participants. It is critical to clarify if older people can still achieve equivalent behavioural performance in harder situations (i.e. match the target face from several face stimuli instead of only two), and how does this affect their neural processing? Does their compensation strategy survive in such situations?

1.3.3 Mechanism underlying the age-related decline in facial identity perception

Age-related holistic- or feature- processing deficits

The encoding of faces involves extracting and processing both "first-order relations" and "second-order relations" of faces (Chaby, Naeme & George, 2011). The first-order relation of faces refers to the overall configural information of faces, or the spatial relations between facial components (i.e. two eyes above a nose and a mouth). The second-order relation of faces refers to the distance between features, such as the distance between two eyes, or the distance between mouth and nose. A number of previous studies have been carried out to explore possible age-related changes in the encoding of different types of facial information. Some researchers argued that these changes might be due to older people having difficulty in encoding facial features in a global manner (also referred to as 'holistic processing'), which plays a critical role in facial identity perception (Murray, Halberstadt, Ruffman, 2010; Daniel & Bentin, 2012). Murray, Halberstadt, Ruffman (2010) found older people were less sensitive to configurally distorted faces than younger people, whereas there was no group difference in judging featurally distorted faces. They suggested that older people might have deficits in encoding configural information while their basic feature processing remains intact. Consistent with this finding, ERP face perceptual studies (Gao, Xu, Zhang & Zhao et al., 2009; Daniel & Bentin, 2012) found an absence of the typical face-inversion effect on N170 amplitude in older participants, which suggested their reduced sensitivity in integrating face features into global structures (holistic processing). This perceptual change might be the cause for poorer identification for facial identity perception.

However, several other studies claimed that the age-related decline in facial identity perception might not be due to reduced holistic processing (Boutet and Faubert, 2006; Konar, Bennett, and Sekuler, 2010; Meinhardt-Injac, Persike & Meinhardt, 2014). Using a composite face effect measure – an index of configural processing ability, Konar et al. (2010) did not find a significant group difference in the composite face effect measure. However, the older group still exhibited a decline in facial identity perception. Boutet and Faubert (2006) compared both younger and older adults' performance for upright-, inverted- faces and objects, and they found a significant group difference for perception with upright faces but not upright objects. In addition, it was found that facial identity perception was more significantly affected by inversion than object perception in both young and older adults. This finding suggests that the mechanism involved in the face inversion effect is not influenced by age differences; in other words, holistic processing is not impaired in older adults.

Spatial frequency hypothesis in face and object perception

Recently, Meinhardt-Injac, Persike & Meinhardt (2014) proposed that older people did not show decline in processing faces holistically, but they have difficulty in handling precise internal facial features. In the study, they found the age-related perception decline in both face and object (watch) perception, while the decline in facial identity perception was stronger than object perception. Both groups showed inversion effect for faces but not objects. They compared both old and young participants' performance in matching external and internal faces/watches. The results showed that older people only had poorer performance than younger participants in matching internal face features (e.g. eyes, nose), but not in external facial features (e.g. hairstyle, moustache), nor internal/external object features.

They proposed that the main differences between faces and objects (watches) are the individual features and fine spatial relationships between these features. Different spatial frequencies encode different aspects of faces and objects, and visual cues used for face and object discrimination might be associated with distinct spatial frequencies (Morrison and Schyns, 2001). Gaspar et al. (2008) measured face identification thresholds for upright and inverted faces embedded in different types of noise and concluded that people use information conveyed by similar narrow bands of spatial frequencies to identify upright and inverted faces, which is roughly 1.5 octaves wide and centred on 7 cpf. Previous studies also found that older adults showed problems in discriminating internal facial features or judging the fine spatial distances between eyes (Chaby et al., 2011; Slessor et al., 2012), whereas judging the broader spatial distance along the vertical axis (i.e. from eyes to mouth) was found to be maintained in older adults (Chaby et al., 2011). This dissociation pattern might reflect aging is associated with deficit in discriminating short-range spatial cues but intact at discriminating long-range spatial cues (Meinhardt-Injac, Persike & Meinhardt, 2014).

1.3.4 Limitations in previous research

Face stimuli age

People are better at recognising faces of their own age (Bäckman, 1991; Anastasi & Rhodes, 2005; Wright & Stroud, 2002; Wiese, Komes, & Schweinberger, 2012); in other words, people seems to have superior facial perception ability when face stimuli are congruent with their own age. This phenomenon has been referred to as ‘own age bias. For example, Bäckman (1991) found that young adults (*Mean age* = 23.8 years) showed better perception for young faces than for old faces, whereas older adults (*Mean age* = 68.5 years) showed better perception for old faces than for young faces. Although there are some inconsistent findings (e.g., Wallis et al., 2012; Wiese, Schweinberger, & Hansen, 2008), a recent meta-analysis of facial identity perception studies has revealed that all age groups exhibited superior facial identity perception ability for same-age compared with other-age faces (Rhodes & Anastasi, 2012). Thus, the own age bias appears to be a robust effect that influences the accuracy of facial identity perception. The authors suggested that the ‘own age bias’ might be due to more exposure with one’s own age group relative to other-age groups. Furthermore, people tend to spend longer time looking at own age faces during facial identity perception tasks (He, Ebner, and Johnson, 2011), which might suggest an own-age preference during face processing.

In light of this, it is therefore possible that the facial identity perception results of previous research suggesting that younger participants have superior face performance compared with older participants might be biased by the age of facial stimuli, as most previous face perception studies investigating between younger and older participants' differences only used young faces (Verdichevski & Steeves, 2013). Few studies have investigated how the effect of age interacts with the other variables of the stimuli faces. Therefore, it is very important to clarify whether age-related facial identity perception decline might be due to face stimuli age bias.

Does the age-related facial identity perception decline extend to object perception

Numerous studies have shown that normal aging is associated with declined facial identity perception. However, not many studies have investigated whether the age-related facial identity perception decline is specific or whether it also extends to object perception. For these reasons, it is important to include control conditions to examine whether deterioration in facial emotion perception would be independent of object perception. The results might also contribute to the knowledge of the face-specificity/expertise controversy and the underlying mechanisms.

1.3.5 Summary

Most behavioural investigations of aging and facial identity perception have agreed that older people have declined ability in perceiving face identities. Inconsistent with findings of behavioural studies, a few neuroimaging studies found that older people showed similar or equivalent accuracy compared to younger participants, which might be due to lower levels of task complexity. Neuroimaging studies suggested that older people have similar or reduced neural activation in the core face processing regions compared to younger people, however, they adopt a wider spread of neural regions such as prefrontal cortex and bilateral hemisphere during facial identity perception tasks. However, it is still not certain what role the additional activated neural regions play during facial identity perception tasks. Do they compensate for the inefficacy of the core face processing neural regions? Or they just boost the general cognitive execution to let older people attend to facial identity perception tasks better? Furthermore, most neuroimaging studies only compared young-old behavioural performance on a single task that only comprises one level of task complexity and most of these complexity levels were relatively low. It is not clear if older people still show the same neural activation patterns in a different task complexity, and if older people can still show similar behavioural performance as younger adults.

Some behavioural and ERP studies suggested that older people have difficulty in holistic processing of faces, but some evidence against this view. In recent years, some researchers raised the spatial frequency hypothesis, which suggests that face and object perception might be associated with distinct spatial frequencies and this might lead to an age-related dissociation pattern in face and objects perception. In my PhD research I will try to explore what underlying mechanisms contribute to the facial identity perception decline in older people, and whether the age-related facial identity perception decline extends to object perception. I will also use both younger and older face stimuli in facial identity perception tasks to investigate the effect of 'own-age' bias in both younger and older adults.

Compensation-related utilization of neural circuits hypothesis (CRUNCH) model

1.4.1 Proposal of the CRUNCH model

Previous two sections have summarised the latest findings of age-related neural changes in facial emotion and facial identity perception, and older people's use of compensatory strategy in these facial perception tasks. Other studies have explored age-related declines in other mental abilities and the underling neural activations, which include attention (Johannsen, Jakobsen, & Bruhn, 1997; Madden, Turkington, & Provenzale, 1997; Anderson, Iidaka, & Cabeza, 2000), working memory (Hartley, Speer, & Jonides et al., 2001; Mitchell, Johnson, & Raye et al., 2000) and executive functioning (Smith, Geva, & Jonides, 2001). These studies have shown a general pattern that older people tend to recruit more cortical regions than younger people when performing an identical task, especially frontal regions when performing effortful tasks (Grady, 2000; Raz, 2000). Older people's increased recruitment of additional neural areas might reflect an attempt to compensate for inefficiency in cortical networks (Gunning-Dixon, Gur, & Perkins, 2003).

Reuter-Lorenz and Cappell (2008) reviewed neuroimaging studies of age-related functional brain organisation and proposed the compensation-related utilization of neural circuits hypothesis (CRUNCH) model. The model illustrates younger and older people's behavioural performance and neural activation patterns at low and high task demands and explained the possible underlying mechanisms. According to the CRUNCH model, at lower levels of task demand, older adults exhibit a region-specific neural overactivation pattern but they can achieve similar or equivalent behavioural performance as younger adults (successful neural compensation). However, beyond a certain level of task demand, the older people's brain falls short of sufficient neural activation and their behavioural performance declines compared to the young people (neural compensation failure). This model is based on the assumption that older people's processing inefficiencies cause the aging brain to recruit additional neural resources to achieve the similar output as younger brain. This compensatory strategy is effective at lower level of task demand. However, as task demand increases, older people's neural resourses ceiling is reached and this results in insufficient compensation and age-related behavioural performance decline. This aging compensation model has been well supported by studies of other cognitive functions, such as memory (Daselaar, Fleck, & Dobbins, 2006), language processing (Cappell, Gmeindl, & Reuter-Lorenz, 2006; Martin, Joanette, and Monchi, 2015) and executive functioning (Martin, Joanette, and Monchi, 2015). However, to date no one has demonstrated this model in the context of aging and face perception.

1.4.2 Aging and neural plasticity

The CRUNCH model suggests potential for neural plasticity that persists into the later years of the human lifespan. Normal aging, along with the neurological decline, gradually lower the neural resource ceiling which leads to inefficient compensation and worse behavioural performance. Reuter-Lorenz and Cappell (2008) further suggested that behavioural training, exercise, and other interventions applied in older adults might potentially increase their neural resources and compensatory potential. Using a non-invasive brain stimulation method, some studies supported this hypothesis and found older people's cognitive ability can be enhanced by boosting neural excitability.

Transcranial magnetic stimulation (TMS) is a non-invasive method that applies focally directed magnetic pulses to the scalp to stimulate the underlying neural tissue. It can temporarily excite or inhibit specific areas by applying an activating or deactivating mode.

Rossi et al. (2004) found that neural overactivation in older adults is essential for behavioural success. Older people normally exhibit bilateral prefrontal activation during perceptual memory. It was found that their perceptual memory was impaired when either side of hemisphere was temporarily inhibited by TMS, suggesting bilateral activation is necessary for their normal functioning of perception memory. In contrast, younger people normally show unilateral activation during perception memory, and their performance can only be affected by applying TMS deactivation to one side of hemisphere. Furthermore, using fMRI, Solé-Padullés et al. (2006) found repetitive transcranial magnetic stimulation (rTMS) can modulate low performing older adults' neural activation pattern from unilateral to bilateral neural activation, and this change lead to their significantly improved their memory performance.

1.4.3 Research aims

Aging-related facial identity perception compensation pattern

The CRUNCH model partially explains the inconsistent behavioural results in previous facial perception studies as almost all face identity and facial emotion perception studies only compared younger and older people's behavioural accuracy and neural activation patterns on one task demand. The task demand of individual studies varies, which can be lower or higher than older people's neural resource ceiling, and these variations lead to inconsistent results.

It is already proven that normal aging affects other cognitive functions such as language processing and executive functioning, which is in line with the CRUNCH model. But, do face identity and facial expression perception rely on the same compensatory mechanisms to maintain performance as one gets older? Surprisingly, few studies have tried to answer this question. Therefore, one of my research aims is to demonstrate if older people rely on the

CRUNCH compensatory model for their facial emotion perception. I will address this question in my EEG study.

Explanation of age-related overactivation

Most face identity and face emotion perception studies showed an age-related frontal over-activation neural pattern compared to younger people. The explanation for this additional neural recruitment also varies. Some researchers pointed out the additionally activated frontal neural areas played a role in the specific face-related processing, in other words, these additional neural regions were functionally adapted or reorganised into the specific facial perception tasks by normal aging (e.g. Gunning-Dixon et al., 2003; Keightley et al., 2007; Fischer et al., 2005). However, some researchers argued for an increased visual perceptual or executive functioning for these additional frontal activations (Tessitore et al., 2005). As it is well established that lateral and inferior prefrontal regions are critical regions for executive functions such as attention selection, inhibition and maintenance; in addition, prefrontal activation has been shown across different studies including working memory, language processing, and facial identity perception.

It it still not very clear what exact roles these frontal overactivations compensate for. I will try to explain this question using EEG to observe and compare older and younger people's brain activation pattern in response to facial perception tasks with different difficulty levels.

The effect of brain stimulation on older people's facial perception

The CRUNCH model provides a theoretical foundation for the age-related neural compensation and neural plasticity. Several non-invasive brain stimulation studies on memory have proved the effectiveness of brain stimulation in enhancing older people's behavioural performance by boosting their cortical activations. The evidence suggested that the older people's neural resource ceiling can be altered by boosting the cortical neural activation and recruiting additional neural regions. This type of study has not been done in facial perception studies in older population. Therefore one of my research aims is to use a non-invasive method to enhance older people's facial emotional perception. This can help to understand the age-related neural changes and neural networks related to facial emotion perception.

Aims of PhD research

My PhD research seeks to examine the effect of aging on social perception, and to further explore the changes in the underlying neural mechanisms using brain stimulation and brain imaging techniques. During the start of my PhD I conducted behavioural studies, which forms the foundation for brain stimulation and brain imaging studies. This thesis sought to address the following questions:

1. a) To investigate the age-related difference in perceiving low-intensity anger and happiness, b) whether the emotion perception deficits extend to facial traits judgement, and c) whether these face perception deficits observed with increasing age reflects an emotion-specific impairment rather than a general face perceptual decline. *(Chapter 2)*

2. To assess social perception of subtle changes in facial emotion and facial identity shown by older adult actors using same experimental paradigm and levels of difficulty. Additionally, in order to ensure that any differences in performance were specific to social perception I sought to examine the extent to which age related differences in the perception of subtle visual cues extended to the perception of non-social stimuli (object perception). *(Chapter 3)*

3. To investigate whether non-invasive brain stimulation (high-frequency tRNS) can modulate older adults' abilities to perceive facial emotion (anger and happiness perception) and facial identity? I also assessed the extent to which any changes in performance following stimulation would be influenced by pre-stimulation (i.e. baseline) perceptual abilities. *(Chapter 5)*

4. To investigate age-related neural activation patterns at neutral (baseline), easy and hard conditions for anger and happiness emotion perception in young and old adult participants. *(Chapter 6)*

CHAPTER 2: AGING AND PERCEPTION OF FACIAL EMOTIONAL EXPRESSIONS AND FACIAL IDENTITY

In recent decades a variety of behavioural studies have investigated age differences in facial emotion perception. Older adults appear to have declined perception of negative facial expressions of emotions, whereas age related differences in the perception of happiness are less consistent. A general limitation involved in most previous research is that only high-intensity prototypes of facial expression images have been used. In this chapter, I investigated the effect of normal aging on perception of lower-intensity facial emotional expressions and facial identity with subtle differences. Secondly, most face perception studies into the relationship between aging and social perception have only investigated one aspect of face processing at a time (i.e. emotion or identity in isolation) or used tasks that have paradigms involving different task complexities (e.g. working memory demands). In order to demonstrate whether there is a domain-specific deficit in emotion perception or a more domain-general shift in the ability to make fine-grained visual discrimination, I compared older and younger participants' perceptual performance of facial emotional expressions and facial identities using the same experimental paradigm. Thirdly, behavioural and neuroimaging evidence has shown that facial trait perceptual abilities are closely related to the perception of facial expressions and facial identities. However, whether the facial emotion perception decline in older adults extends to such trait judgements remains unknown. In this chapter, I also examined two age groups' perceptual performance on facial trait judgement and demonstrated the relationship between facial trait perceptual performance and two other facial perceptual performances (facial emotional expression and facial identity). The results have revealed that older people have a declined ability in facial identity perception, and facial expression perception of anger but a lesser extent in facial happiness *perception. No group difference was observed in the facial trait perception tasks. I also explored the pattern of change in different face perception abilities across the lifespan. These results are explained with prior studies and the potential underlying age-related face processing mechanisms are discussed.*

2.1 Introduction

Chapter one has summarised the recent findings of older people's perception of facial emotions and limitations involved in previous studies. The general pattern that has emerged is that older adults appear to have declined perception of negative facial expressions of emotions such as anger, sadness, fear and surprise (Phillips et al., 2002; Calder et al., 2003; MacPherson et al., 2006; Sullivan & Ruffman, 2004; Isaacowitz et al., 2007). However, a general limitation involved in most previous research is that only high-intensity prototypes of facial expression images have been used and low intensity emotion stimuli were largely ignored (Hess, Blairy, & Kleck, 1997, Orgeta and Phillips, 2007). A number of questions remain: e.g. a) are these differences a consequence of domain-specific deficits in subtle emotion perception or more domain-general shifts in the ability to make fine-grained visual discrimination, b) could the lack of age-related effects in certain emotions relate to task sensitivity (e.g. better performance on happiness perception relative to other emotion types).

In addition to facial expression perception, there is also prior work suggesting that facial identity perception abilities may decline with age (Bowles et al., 2009; Megreya & Bindermann, 2015). Further, the relationship between facial identity memory ability and aging has been shown to reflect an inverted parabola, with performance increasing during young to middle adulthood, before declining into and throughout older adulthood (Germine, Duchaine, & Nakayama, 2011). Despite evidence that both facial identity and facial emotion perception changes during typical adult aging, most face perception studies on the relationship between aging and social perception have only investigated one aspect of the face processing at a time (i.e. emotion or identity in isolation) or used tasks that have inconsistent paradigms involving different task complexities (e.g. working memory demands). In this regard, prior work struggles to give a clear picture about how normal aging is related to different aspects of face perception, meaning that the extent to which age influences face identity and face expression perception abilities in similar or different manner remains unclear. In addition, face inversion is commonly linked with reduced performance compared to upright facial perception. This is often thought to relate to configural processing being disrupted by facial inversion. By including inverted faces we were able to check whether differences in performance on the identity processing task were specific to perceptual processes associated with upright versus inverted face processing.

The CFPT format requires participants to discriminate between visual stimuli on the basis of visual properties alone (Duchaine et al., 2007a, b; Bowles et al., 2009). This offers benefits to assess perceptual differences over other task formats (e.g. labelling tasks, same-different judgment tasks) that might theoretically tap additional processes alongside perceptually driven performance factors (Adolphs, 2002; Palermo, O'Connor, Davis, Irons, & McKone, 2013). For example, labelling based measures of emotion processing require additional demands of assigning a verbal label to an emotion, thus placing additional constraints on performance related to variation in emotional vocabulary (Barrett, Lindquist, & Gendron, 2007). Further, labelling and same-different judgment tasks often require increased working memory demands, thus placing additional constraints on performance related to cognitive load (Phillips, Channon, Tunstall, Hedenstrom, & Lyons, 2008). The face perception tasks that have been used in this study were validated and used in other published studies (e.g.

Janik et al., 2015; Romanska et al.,2015; Rezlescu et al., 2014), which used the same way of measuring performance.

2.1.1 Exploration of aging and facial trait judgement

As discussed in chapter one, Oosterhof and Todorov (2008) proposed that the judgement of trustworthiness is associated with facial emotional expressions whereas judgement of dominance correlates more with certain facial features. In addition, numerous evidences have shown that the judgement of trustworthiness from faces is both neurologically and behaviourally closely related to the perception of facial expressions.

Prior facial trait studies found that older and younger adults' perceptual ratings on trustworthy faces were similar, but older adults perceived untrustworthy faces to be more trustworthy than younger adults (Castle, Eisenberger, & Seeman et al. 2012; Bailey, Szczap, McLennan et al. 2015). The pattern of results was discussed with older people's 'positivity bias' - they are less sensitive to cues that are related to negative experience (Castle, Eisenberger, & Seeman et al. 2012, Bailey, Szczap, McLennan et al. 2015). In addition, the neural imaging results found that younger adults showed greater anterior insula activation to untrustworthy versus trustworthy faces, older adults showed little activation of the anterior insula to untrustworthy faces (Castle, Eisenberger, & Seeman et al. 2012).

Previous aging studies on facial trait perception have explored the older adults' perception of facial trait of trustworthiness, but few studies have studies older adults' perception of facial trait of dominance/aggressiveness, and whether the impairment of facial emotion or identity perception in older adults extends to such trait judgements remains unknown. Therefore, I also examined whether deficits in recognising emotions could extend to facial trait perceptual abilities (trustworthiness and aggressiveness) in Experiment 1.

2.1.2 Summary of Experiment 1

The first aim of the experiment was to investigate the age-related difference in perceiving anger and happiness in low-intensity facial expression stimuli. Another important theoretical consideration relates to whether the emotion perception deficits observed with increasing age reflects an emotion-specific impairment rather than a more general face perceptual decline (face-identity task). Finally, according to Oosterhof and Todorov (2008)'s facial trait model, facial trait of trustworthiness correlates with facial information of emotional expressions whereas judgment of dominance correlates more with certain facial features. The third aim is to investigate if there is age-related difference in facial trait judgment.

2.2 Methods

Participants

Participants consisted of twenty-three younger adults (seventeen female and six male; age range 18 – 40 years, mean age = 23 years, SD = 5 years) and twenty-two older adults (sixteen female and six male; age range 57 – 75, mean age = 65 years, SD = 6 years). All participants were native-English Caucasians, with no known history of neurological problems, dyslexia or other language-related problems, and with normal or corrected- to-normal vision. Younger participants were recruited through the university's undergraduate participant pool, and older participants were recruited from local elderly community centres.

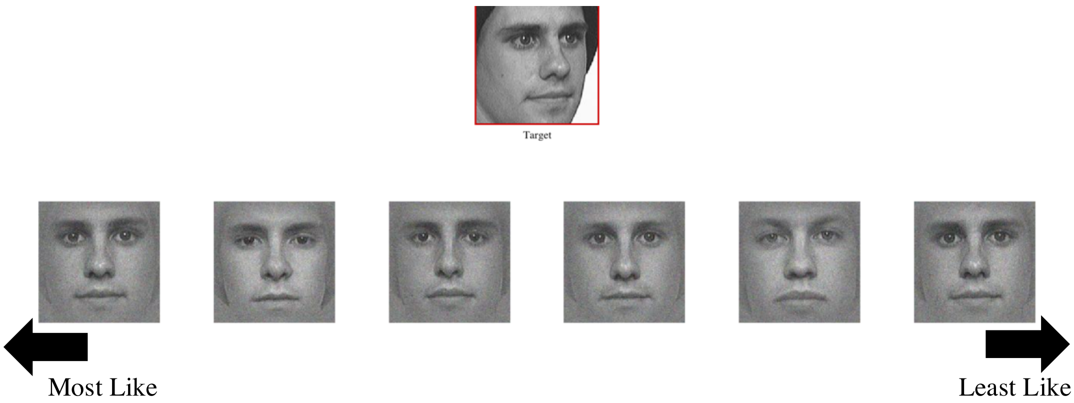
Level of education, premorbid intelligence (NART), and handedness were recorded at the beginning of experiments; the two groups did not significantly differ in these factors (details given in the Results section). The Mini-Mental State Examination (MMSE) was used as a screening evaluation to test older participants for possible dementia (Folstein, Folstein, & McHugh, 1975). The MMSE appears to be the most widely used measure to screen for cognitive status. A cut-off limit of < 24 was used, which has a good sensitivity for dementia in the older population (Chayer, 2002). No participants were excluded from the study on the basis of this criterion. All participants gave informed consent prior to beginning the experiment and were fully informed about the experimental procedure. The local ethics committee approved the study.

Materials and procedure

Three main tasks were carried out: *CFPT, CFPT-Facial Expression, CFPT-Facial Trait*. Participants completed all tasks in a counterbalanced order. These tasks are detailed below.

Test of facial identity perception (CFPT)

To investigate facial identity perception the Cambridge Face Perception test was used in the experiment (CFPT; Duchaine, Germine, & Nakayama, 2007a; Duchaine, Yovel, & Nakayama, 2007b). This test demonstrated participants' ability to perceive differences between facial identities. During the task, participants were presented a target face (from a 3⁄4 viewpoint) and six faces (from a frontal view) morphed between the target and distractor in varying proportions (88%, 76%, 64%, 52%, 40%, 28%) so that they vary systematically in their similarity to the target face [see Figure 2.1 (a) for examples]. In each trial, participants were asked to sort the six faces by similarity to the target face with a one-minute time limit. Participants sorted the faces by clicking on the face that they wished to move and then indicating where the face should be by clicking in the area between two faces. The desired face was then moved to the chosen location by the program. If participants completed the trial before the time limit expired they were able to click an option on screen to begin the next trial ial (i.e. the task was self-paced). Memory demands are minimal because faces are presented simultaneously. The task involved eight upright and eight inverted trials that alternated in a fixed pseudo-random order. This allowed investigation of the inversion effect for face perception. Performance of each subject was measured using percentage of correct responses. Change performance is 36%.



a.

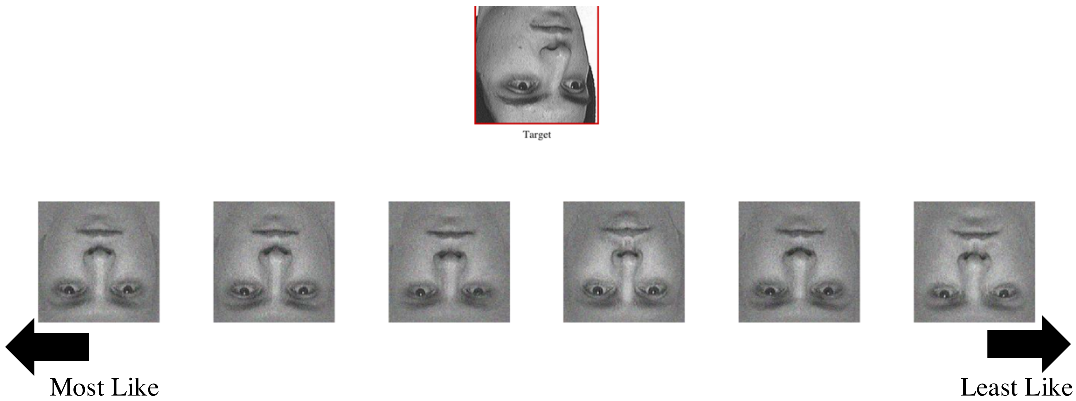


Figure 2.1. (a) Example trials of *CFPT* task. In *CFPT* trials, participants were displayed a target face and six faces (from a frontal view) morphed between the target and distractor in varying proportions (88%, 76%, 64%, 52%, 40%, 28%). Participants' task is to sort the six faces according to the degree of similarity to the target (shown at the top in three-quarter view). Half of the trials contain upright faces (upper graph) and half inverted faces (lower graph).

CFPT – Facial Expression

Two tasks were used to test perception of facial expression [happiness (Janik-McErlean et al. (Submitted) and anger (Janik et al., 2015)), which use the same experimental paradigm as the test of facial identity perception (Cambridge Face Perception Test), although no target face was presented. In this test, participants were asked to sort faces according to perceived happiness/anger. During the task, participants were presented six faces (from a frontal view) morphed between the expression of 'happiness'/'anger' and a 'neutral' expression in varying proportions (Happy: 15%, 12%, 9%, 6%, 3%, 0%; Anger: 40%, 32%, 24%, 16%, 8%, 0%) [figure 2.1 (b)]. These six faces were presented on the screen in random order. Participants were required to sort them according to how happy/angry they appeared, from the face that looks least happy/angry on the left to the face that looks most happy/angry on the right. The time limit for each trial was 60 seconds. Performance was measured by an error score, which was calculated by summing the deviations from the correct position for each face, with one error reflecting each position that a face must be moved to be in the correct location. Error scores on the trials were summed to determine the total number of errors.

b.

Figure 2.1. (b) Example trials of *CFPT-Facial Expression* task (upper graph: *CFPT-Happiness*; lower graph: *CFPT - Anger*). Six faces (from a frontal view) morphed between the expression of 'Happiness'/'Anger' and a 'neutral' expression in varying proportions (Happy: 15%, 12%, 9%, 6%, 3%, 0%; Anger: 40%, 32%, 24%, 16%, 8%, 0%;). These six

faces were presented on the screen in random order. Participants were required to sort them according to how happy/angry they appear from the face that looks least happy/angry to the face that looks most happy/angry.

CFPT – Facial Trait

Two tasks were used to test perception of personality traits from faces [trustworthiness (Rezlescu et al., 2014; Romanska et al., 2015) and aggressiveness], which use the same experimental paradigm as the test of facial identity perception (Cambridge Face Perception Test). I used 'aggressiveness' instead of 'dominance' as it represents a similar trait and people are more familiar with the trait 'aggressiveness'. In this test, participants were asked to sort faces according to perceived trustworthiness/aggressiveness [figure 2.1(c)]. During the task, participants were shown six faces (from a frontal view) with different levels of trustworthiness/aggressiveness. The 'correct' sorting orders for traits trustworthiness and aggressiveness were determined based on average ratings obtained from 338 online participants (each average score included at least 48 data points). These six faces were presented on the screen in a random order. Participants were required to sort them according to how trustworthy/aggressive they appear, from the face that looks least trustworthy/aggressive on the left to the face that looks most trustworthy/aggressive on the right. The time limit for each trial is 60 seconds. Performance was measured by an error score, which was calculated by summing the deviations from the correct position for each face, with one error reflecting each position that a face must be moved to be in the correct location. Error scores on the trials were summed to determine the total number of errors.

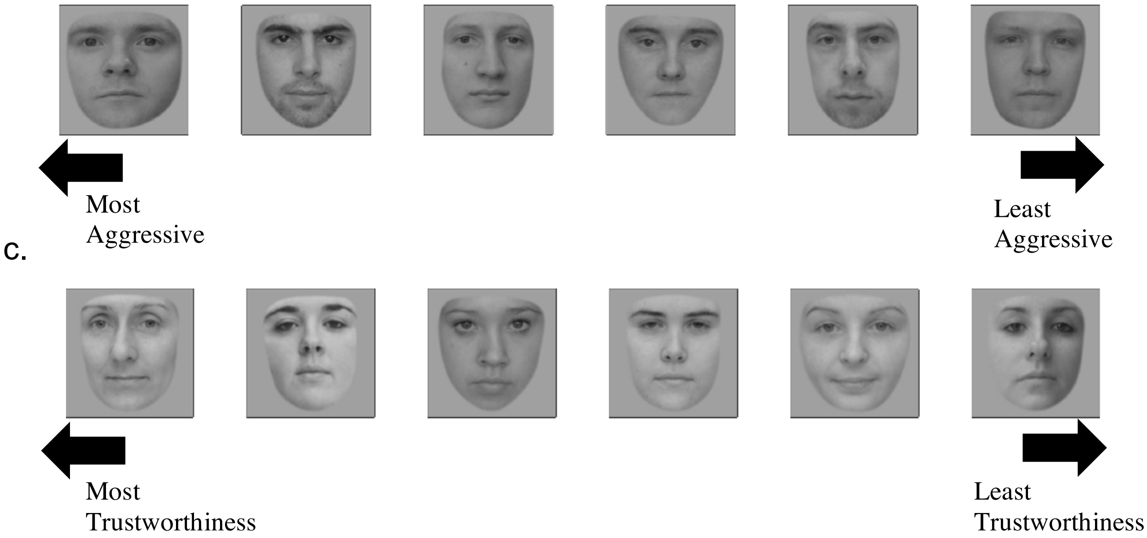


Figure 2.1. (c) Example trials of *CFPT-Facial Trait* task (upper graph: *CFPT-Aggressiveness*; lower graph: *CFPT - Trustworthiness*). Participants were shown six faces (from a frontal view) with different levels of aggressiveness/trustworthiness. These six faces were presented on the screen in random order. Participants were required to sort them according to how aggressive/trustworthy they appear from the face that looks least aggressive/trustworthy to the face that looks most aggressive/trustworthy.

2.3 Analysis and Results

Before further analysis, two younger and one older participants were withdrawn from the analysis due to them being identified as outliers in at least one task. More specifically, each participant that was withdrawn performed three standard deviations away from the group mean on either one or more tasks, and were verified as outliers using Grubb's Test.

Demographic differences

After excluding outliers, twenty-one young and twenty-one old participants' experimental data were used for further analysis. The mean age of the young group was 23 years (SD = 5 years) and the mean age of the old group was 65 years (SD = 6 years). The years of education (young group: mean = 16 years, SD = 2 years; old group: mean = 16 years, SD = 2 years) and NART scores (young group: mean = 115.89, SD = 7.38; old group: mean = 118.33, SD = 8.62) of two age groups were compared and they were not significantly different. The gender and handedness of two groups were matched. The younger group comprised of sixteen females and five males, with none left handed participants. The older group comprised of fifteen females and six males, with 1 left handed participant.

Social perception performance differences

Perceptual performance of two groups were analysed using 2 (group) × 6 (task type) mixed-ANOVA with the between-participants factor of group (young and old) and within-participants factor of task type (anger and happiness expression perception, upright and inverted identity perception, trustworthiness and dominance facial trait perception). Mauchly's test indicated that the assumption of sphericity had been violated so the Greenhouse-Geisser correction was employed. The results revealed a significant effect of task type [$F(3.833, 153.302) = 29.640, p < .001, \eta 2 = .426$]. Bonferroni corrected post-hoc comparisons revealed that this was because overall participants performed better on the facial expression (both happiness and anger conditions) and upright facial identity perception relative to inverted face perception and aggressiveness facial trait perception. There was also a significant main effect of group [$F(1, 40) = 22.704, p < .001, \eta 2 = .362$], which was due to older adult participants performing worse overall compared to young adult participants.

The results also revealed a significant interaction between group and task type [$F(3.833, 153.302) = 3.469, p = .011, \eta 2 = .080$]. Pairwise comparisons were performed between older and young group on the accuracies from the six face perception tasks (figure 2.2), with a significant difference found in anger ($p < 0.001, d = 1.194$, Bonferroni corrected), upright ($p < 0.001, d = 1.243$, Bonferroni corrected) and inverted ($p = 0.018, d = .985$, Bonferroni corrected) facial identity perception tasks. Although it is not significant, there is a trend showing age-related group difference in happiness facial expression task ($p = 0.096,$

Bonferroni corrected). No group differences were found in aggressiveness (*p = .186,* Bonferroni corrected) and trustworthiness (*p = .804,* Bonferroni uncorrected) facial trait perception tasks.

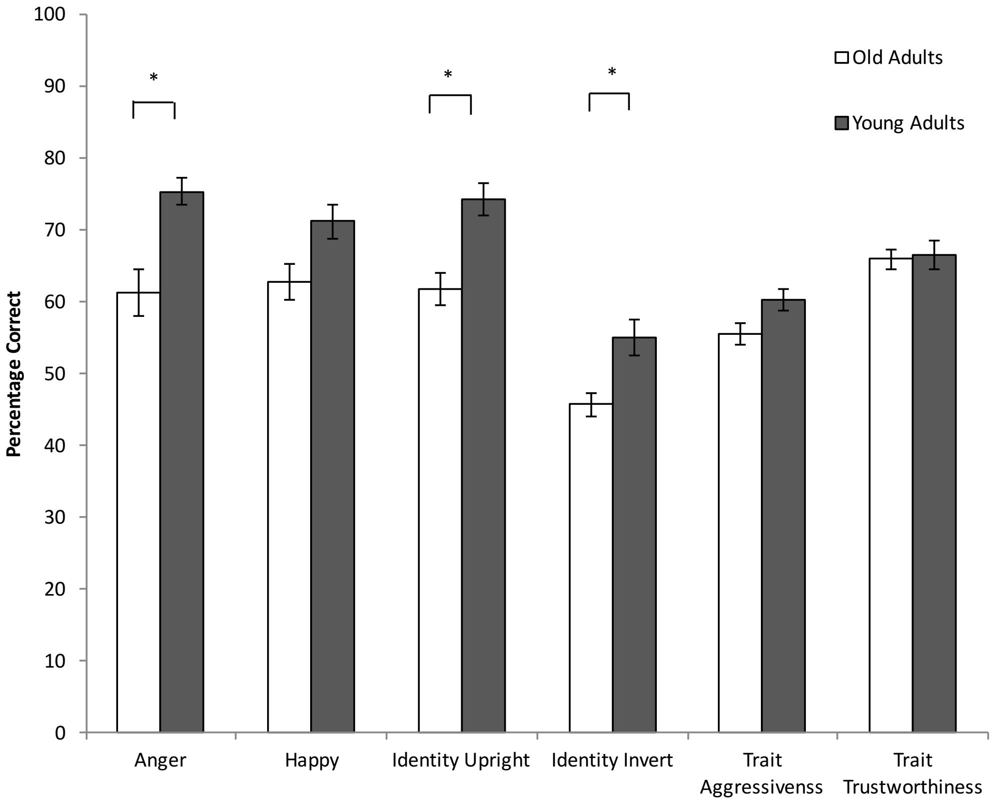


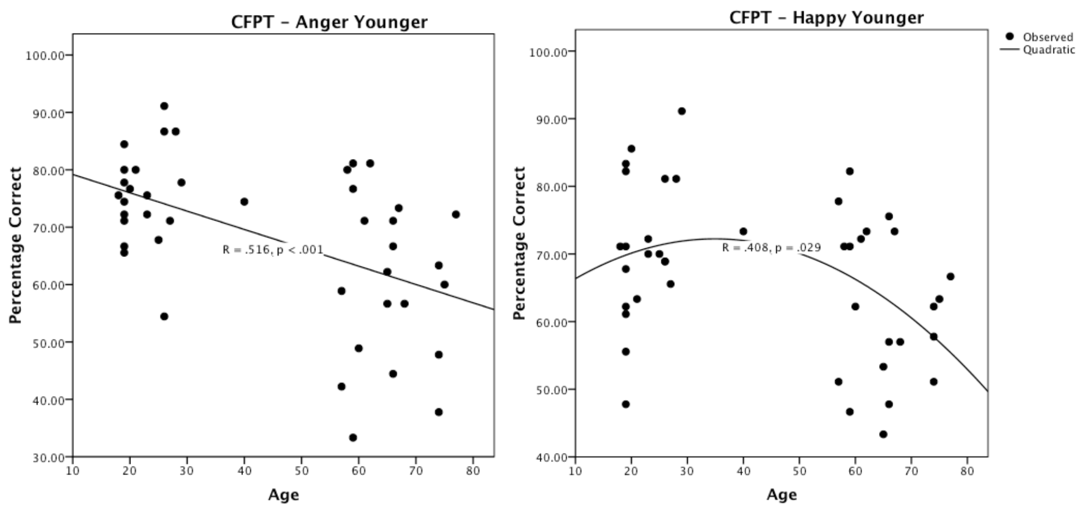
Figure 2.2. Mean perceptual accuracies (± one S.E.) of two age groups on (a) *Anger,* (b) *Happy, (c) Identity-Upright,* (d) *Identity-Invert,* (e) *Trait Aggressiveness and* (f) *Trait Trustworthiness*. Significant differences were found between the performance of young and old participants on anger perception [$p < 0.001$, $d = 1.194$], upright facial identity perception [$p < 0.001$, $d = 1.243$] and inverted face perception [$p = 0.018$, $d = .985$] (Figure 2.2a, 2.2c, 2.3d). Accuracy performance of happiness perception and facial trait perception did not differ significantly between the two age groups (Figure 2.2b, 2.2e, 2.2f).

The trajectory of age-related changes

In addition to comparing between groups, I also sought to examine the trajectory of age-related changes in social perception. To do this I examined the correlation between age and performance accuracy on each perceptual task. This revealed significant negative correlations between age and performance on the CFPT-Facial Emotion Younger Adult [both Anger ($r = -.516$, $p = <.001$) and Happiness Trials ($r = -.357$, $p = .020$)], and the CFPT-Facial Identity

Younger Adult [both Upright (*r = -.552, p = <.001*) and Inverted Trials (*r = -0.448, p = 0.003*)], and the Facial Trait Aggressiveness Trials (*r = -.367, p = .017*). There was no significant relationship between age and Facial Trait Trustworthiness Trials [*r = -.052, p = .746*]. With this in mind, then I next fitted the data to a quadratic function and examined this using polynominal regression. This revealed a significant quadratic relationship between age and performance on the CFPT-Happy task [$\beta = -1.64$, $t = 1.35$; $F(2, 41) = 3.89$, $p = .029$], with performance increasing in younger adult participants from 18 to 30 years but declining in older participants from 50 years and over (Figure 2.3a, right graph). In this regard, while aging does affect the perception of subtle facial cues related to happiness perception, it appears that performance continues to improve during young adulthood (potentially peaking in middle adulthood) before a decline during later life. In contrast, for anger expression perception and identity perception, age was a significant predictor of CFPT-Angry Younger trial performance [$\beta = -.516$, $t = 3.81$; $F(1, 41) = 14.51$, $p < .001$], CFPT-Identity (Older) Upright trial performance [$\beta = -.552$, $t = 4.19$; $F(1, 41) = 17.56$, $p < .001$] and Inverted trial performance [$\beta = -.448$, $t = 3.17$; $F(1, 41) = 10.07$, $p = .003$] and CFPT-Facial Trait Aggressiveness [$\beta = -.367$, $t = 2.50$; $F(1, 41) = 6.23$, $p = .017$] in a linear way (figure 2.3).

a.



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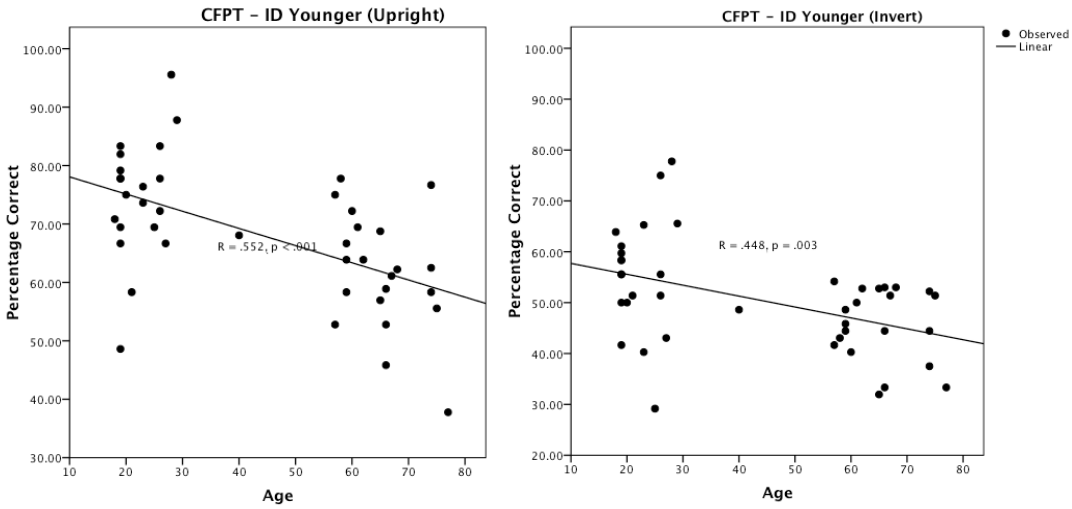


c.

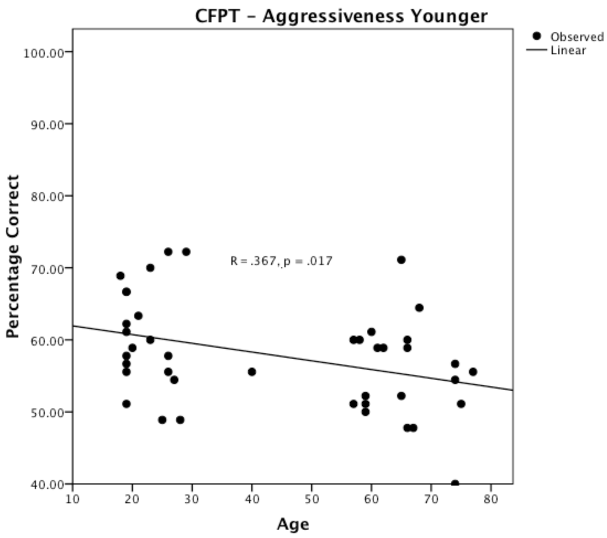


Figure 2.3. The trajectory of age-related changes on perception of (a) *anger and happy facial expressions*, (b) *upright- and inverted- facial identity*, (c) *facial trait of aggressiveness*. Results revealed a significant quadratic relationship between age and performance on the *CFPT-Happy* task ($p = .029$), with performance increasing in younger adult participants from 18 to 40 years but declining in older participants from 57 years and over (figure 2.3a, right graph). In contrast, for anger and identity perception, age was a significant predictor of *CFPT-Anger* ($p < .001$) (figure 2.3a, left graph*), CFPT-Identity Upright* trial performance ($p < .001$), *Inverted* trial performance ($p = .003$) and *CFPT–Facial Trait Aggressiveness* trial performance ($p = .017$) in a linear fashion (figure 2.3b, 2.3c)

2.4 Discussion

Social perception performance differences

The results revealed that older participants showed declined performance on the perception of subtle facial expressions of anger. Combining with previous literature, this finding adds strength in confirming that normal aging is associated with decay in perceiving anger, in both low- and high- emotional intensities. Older people's perceptual performance of happiness did not show a significant difference from younger people at a group level. This finding agrees with prior findings claiming that there is no significant age-related decline in perception of happiness (Moreno et al., 1993; Calder et al., 2003; Orgeta and Philips, 2008). However, it should be noted that there is a trend that older people might have age-related difference in perception of happiness from low-intensity facial expressions ($p = 0.096$). Therefore, this finding awaits further confirmation from further studies.

For facial identity perceptual performance, older people exhibited significantly lower accuracies in both upright- and inverted- facial identity tasks compared to younger adults. This result is in line with the prior finding (Boutet and Faubert, 2006; Meinhardt-Injac & Meinhardt, 2014) that there are reliable age-related differences for both upright- and inverted- face perception. With this in mind, there are at least two ways to interpret this pattern of results. First, it could be argued that my data fit with prior work suggesting that some common neurocognitive processes are recruited for upright and inverted face processing (e.g., Freiwald et al. 2009; Pitcher et al. 2011; Susilo et al. 2013), and normal aging affects this general face identity processing. The present pattern of results seems to challenge another prior view positing that the perception of upright and inverted face depend on qualitatively different neurocognitive processes (e.g. Tanaka and Farah, 1993; Moscovitch et al. 1997; Yovel and Kanwisher, 2004). Based on this proposal, it can also be argued that normal aging might affect processing of perception of both upright- and inverted- faces and thus these two different neurocognitive process. In order to explore this question further and if this is a face-specific perceptual deficit, or whether this deficit also extends to object perception, an object perception task will be carried out in experiment two.

For facial trait perception, no age-related group difference was found in either facial trait trustworthiness or aggressiveness perceptual performance. Given that this experiment has shown older adults' significant age-related decline in both anger and facial identity perception, these facial trait perception results do not fit the model proposed by Oosterhof and Todorov (2008), which claims that the encoding of trait trustworthiness is associated with the encoding of facial expression, and the perception of trait aggressiveness/dominance is associated with perception of facial identity. This finding suggests that the age-related decline in anger and facial identity perception did not extend to facial trait perception.

The trajectory of age-related differences in social perception

The regression results have shown that normal aging affects facial identity perception, anger perception, and facial trait aggressiveness perception in a linear decline from 18 years to 75 years. In contrast, the normal aging seems to affect perception of happiness in an inverted-U curve – younger adults' performance starts to increase from 18 to middle adulthood and reaches a peak performance in middle adulthood (from 30 years to 50 years), followed by gradual performance decline from approximately 50 years. However, this finding needs further confirmation as the current data lacks middle aged participants.

2.5 Summary

In experiment 1, older people have shown declined ability in perceiving subtle facial expression of anger but a lesser extent to subtle facial expression of happiness. Older people's perceptual performance on both upright- and inverted- facial identities were significantly lower than younger adults. No group difference was found in perception of facial trait trustworthiness or aggressiveness. Furthermore, polynominal regression revealed a significant quadratic relationship between age and performance on the CFPT-Happy task, suggesting that normal aging affects the perception of facial happiness in an inverted-U curve with a potential peak in middle age. In contrast, normal aging affects anger, facial identity and facial trait aggressiveness perception in a linear fashion.

CHAPTER 3: AGING AND FACE PERCEPTION (OLDER FACES) AND A FURTHER INVESTIGATION ON OBJECT PERCEPTION

Previous findings suggest that older adults show impairments in the social perception of faces, including the perception of emotion and facial identity. The majority of this work has tended to examine performance on tasks involving young adult faces and prototypical emotions. While useful, this can influence performance differences between groups due to perceptual biases and limitations on task performance. In this chapter I sought to examine how typical aging is associated with the perception of subtle changes in facial emotional and facial identity in older adult faces. I developed novel tasks that permitted the ability to assess facial emotion (happiness perception), facial identity, and non-social perception (object perception) across similar task parameters. I observe that aging is linked with declines in the ability to make fine-grained judgements in the perception of facial happiness and facial identity (from older adult faces), but not for non-social perception. Interestingly, the pattern of change in social perception abilities across the lifespan differed for facial happiness and facial identity. Facial happiness was associated with increases in performance in young adulthood, but declines in old adulthood. Facial identity was associated with linear declines from young to old adulthood. This pattern of results is discussed in relation to mechanisms that may contribute to declines in facial perceptual processing in older adulthood.

3.1 Introduction

In Chapter 2, it was shown that older adults have significantly declined performance in facial anger and facial identity perception compared to younger adults. It should be noted that all facial stimuli used in experiment 1 were depicting only younger faces. People are better at recognising faces of their own age (Anastasi & Rhodes, 2005; Mason, 1986; Wright & Stroud, 2002; Perfect & Harris, 2003; Wiese, Komes, & Schweinberger, 2012); in other words, people seems to have superior facial perception ability when the age of the presented face is congruent with their own age. This phenomenon has been referred to as 'own age bias. A recent meta-analysis of face perception studies has revealed that all age groups exhibited superior face perception ability for same-age compared with other-age age faces (Rhodes & Anastasi, 2012). Thus, the own age bias appears to be a robust effect that influences the accuracy of face perception.

The first aim of experiment two is to investigate to what extent these results hold when controlling for perceptual biases that may aid younger adults over older adults. Prior work examining low intensity emotion perception in older adult has tended to use young adult faces as target stimuli, in this regard one could argue that declines in performance displayed by older adults in previous research were related to the use of young adult actors in the task, which favours young adult participants. To investigate further if all observed face perceptual deterioration might be due to face stimuli age bias (all face stimuli were young faces), experiment two was carried out to see if the age-related difference still exists when all facial stimuli were changed into older faces.

Extensive evidence ranging from behavioural, brain lesion and brain imaging studies has suggested that domain-specific mechanisms are involved in processing faces (e.g. Bentin et al., 1996; Kanwisher, 2000; Moscovitch et al., 1997), which is dissociable from the processing of non-face objects. However, the view of domain-specificity for faces has been challenged by the expertise view, which proposed that the identification of fine-detailed, subordinate objects shares the same mechanism as face perception. It was found that people with expertise with objects showed large activations in the face fusiform areas during these subordination object perception (Gauthier et al., 1999; Bukach, Gauthier, & Tarr, 2006). Furthermore, it was found that prosopagnosia patients are also impaired in discriminating non-face stimuli at subordinate level (Lhermitte, Chain, & Escouroole, 1972). In Chapter 1, it was shown that older people exhibited lower accuracies than younger adults in both upright- and inverted- facial identity perception, which suggested that normal aging is also associated with declined facial perception abilities. However, not many prior studies have investigated whether the age-related face perception decline is specific or it also extends to object perception. For these reasons, it is important to include control conditions to examine if this is a face-specific perception deficit, or whether this deficit also extends to non-face stimuli, an object perception task will be carried out in experiment two. In addition, inverted face trials were included in the face identity task in the present study, this allowed investigation of the inversion effect for face perception (Yin, 1969). Moreover, face inversion is linked with reduced performance compared to upright facial perception, which is often thought to relate to configural processing being disrupted by facial inversion (Farah et al., 1995; Leder & Carbon, 2006). By including inverted faces enables me to check whether differences in performance on the identity-processing task were specific to perceptual processes associated with upright versus inverted face processing.

In view of the above, the present study sought to assess social perception of subtle changes in facial emotion and facial identity shown by older adult actors using same experimental paradigm and levels of difficultly. Additionally, in order to ensure that any differences in performance were specific to social perception I sought to examine the extent to which age related differences in the perception of subtle visual cues extended to the perception of non-social stimuli (object perception). This approach permits the ability to draw inference about how aging is related to differences in social perception when task demands remain similar. If emotion perception is affected by normal aging, but facial identity and object perception remains intact, this would point to the possibility that age-related decline in social perception is emotion-specific; whereas if normal aging also affects facial identity perception, it may suggest that there is a general face processing decline. Finally, if aging affects all tasks (identity, emotion and object) it suggests a domain-general (i.e. non-social specific) decline may account for changes in subtle emotion perception associated with typical aging.

To achieve these aims I developed a series of novel tests that built upon a well utilised paradigm for studying fine-grained visual discrimination of facial identity and facial emotion in younger adult participants - the Cambridge Face Perception Test (CFPT). The CFPT was originally developed to study subtle differences in the perception of facial identity perception (hereafter referred to as CFPT-Identity) under conditions in which working memory demands are minimal (Duchaine, Germine, & Nakayama, 2007a; Duchaine, Yovel, & Nakayama, 2007b), and has since been adapted to examine subtle differences in the perception of happiness (CFPT-Happy), anger (CFPT-Anger), and facial traits (e.g. trustworthiness) (Janik, Rezlescu, & Banissy, 2015; Rezlescu, Susilo, Barton, & Duchaine, 2014). During CFPT-Identity participants are presented with a target face and six faces morphed between the target and one of six distractor faces in varying proportions so that they vary systematically in their similarity to the target face. The participants task is to sort the six morphed faces from most to least like the target face. During CFPT-Happy, participants are presented with six faces that show morphs between the expression of ‘happiness’ and a ‘neutral’ expression in varying proportions; the participants task is to sort the faces from most to least happy (in CFPT-Happy). Each of these tasks has been used successfully to assess fine-grained social perception abilities in younger adult participants (e.g. Janik et al., 2015; Romanska, Rezlescu, Susilo, Duchaine, & Banissy, 2015), and to distinguish between groups (e.g. social perception in prosopagnosia – Duchaine et al., 2007a; Duchaine et al., 2007b; Rezlescu et al., 2014; Shah, Guale, Sowden, Bird, & Cook, 2015). Due to task parameters and accuracy being similar across the CFPT tasks, and given that working memory demands are minimal, the CFPT format offers an ideal means to study fine-grained social perception changes in aging. To date, however, current CFPT tasks only use young adult target faces as stimuli. Given that this may bias performance in favour of younger adult participants (e.g. due to the other age-effect) I sought to develop modified versions of the CFPT-Identity and CFPT-Happy using older adult faces as stimuli. In addition, to date the CFPT measures only assess the perception of faces, but to highlight specificity of any differences to face perception a comparison task assessing object perception is required. To date there exists no object-based CFPT measure, to address this gap I developed a novel version of the CFPT assessing perception of cars (CFPT-Car).

3.1.1 Summary of Experiment 2

To summarise, there is a good degree of evidence suggestive of age-related declines in social perception of faces, but several methodological issues limit the conclusions that can be drawn regarding the nature and factors contributing to these declines (e.g. own-age bias; use of high intensity emotions; lack of systematic comparison across stimuli type [e.g. identity versus emotion] using the same task parameters). This study sought to address this by developing novel measures that assess fine-grained changes in social and non-social perception when task demands and difficultly remain similar. In addition, I sought to ensure that any differences between young and old adult participants were a consequence of own-age biases favouring young adult performance, by using older adult stimuli as target faces. This permitted the ability to contrast social perception abilities for a range of social facial cues (emotion, identity) and non-social perceptual abilities (car perception) in the same participants using similar task parameters, and to assess the relationship between age-related performance differences across each type perceptual cue.

3.2 Methods

Participants

Twenty-six younger adults (seven male and nineteen female; age range 18 – 36 years, mean age = 24 years, SD = 6 years) and twenty-seven older adults (twenty female and seven male; age range 60 – 77 years, mean age = 69 years, SD = 6 years) took part. All participants were native-English Caucasians, with no known history of neurological problems, dyslexia or other language-related problems, and with normal or corrected-to-normal vision. Younger participants were recruited through the university's undergraduate participant pool, and older participants were recruited from the Goldsmiths Psychology Department participant pool.

Level of education, premorbid intelligence (NART), and handedness were recorded at the beginning of experiments; the two groups did not significantly differ in these factors (details given in the Results section). The Mini-Mental State Examination (MMSE) was also used as a screening evaluation to test older participants for possible dementia (Folstein, Folstein, & McHugh, 1975). The MMSE is a commonly used measure to screen for cognitive status. A cut-off limit of < 24 was used, which has a good sensitivity for dementia in the older population (Chayer, 2002). No participants were excluded from the study on the basis of this criterion. All participants gave informed consent prior to beginning the experiment and were fully informed about the experimental procedure. The local ethics committee approved the study.

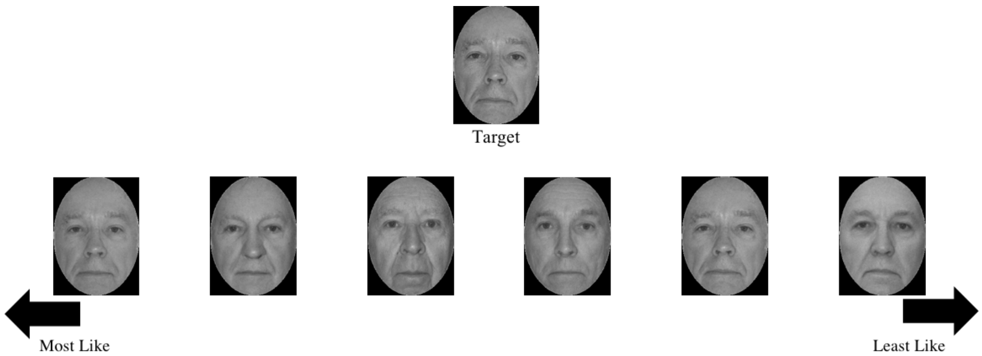
Materials and procedure

Three main tasks were carried out: *CFPT-Identity Older Adult*, *CFPT-Happy Older Adult*, *CFPT-Car*. All tasks were developed specifically for this study using the same task parameters as used previously for younger adult versions of the CFPT (e.g. CFPT-Identity – Duchaine et al., 2007a, Duchaine et al., 2007b; CFPT Happy – Janik et al., 2015). The orders of the three tasks were counterbalanced across participants. Details of each task are provided below.

CFPT-Identity Older Adult

This task followed the same procedure as the standard CFPT-Identity (previously called CFPT, see Duchaine et al, 2007a; Duchaine et al, 2007b), but here I used older adult faces rather than younger adult faces. During the task, participants were displayed a target face and six faces (from a frontal view) morphed between the target and distractor in varying proportions (88%, 76%, 64%, 52%, 40%, 28%). In each trial, participants were asked to sort the six faces by similarity to the target face with a one-minute time limit. If participants completed the trial before the time limit expired they were able to click an option on screen to begin the next trial. The task involved eight upright and eight inverted trials that alternated in a fixed pseudo-random order. This allowed investigation of the inversion effect for face perception (Yin, 1969).

Stimuli were created using the software FantaMorph. All facial stimuli used were from Park Aging Mind laboratory face database (http://agingmind.cns.uiuc.edu/facedb/), which contain standardised pictures of male and female from different ages. In order to match the older facial stimuli to the young facial stimuli used in the original CFPT-Identity (Duchaine et al., 2007a, 2007b), external facial features were removed from images and coloured images were transformed in to grey scale images (Figure 1a). Performance was measured using percentage of correct responses. Chance performance is 36%.



a.

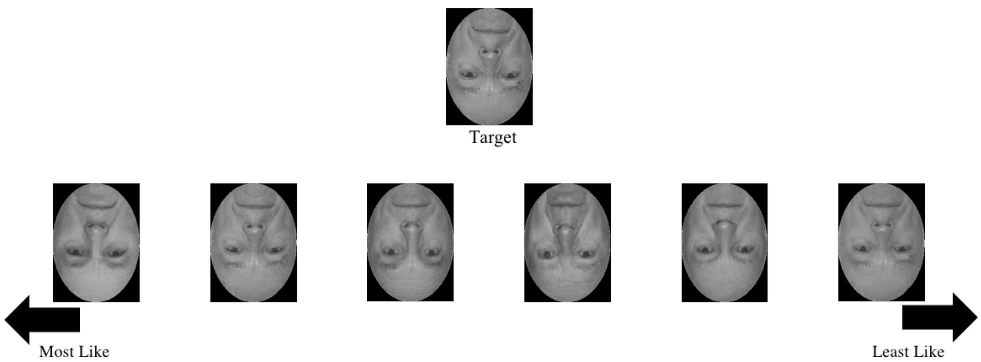
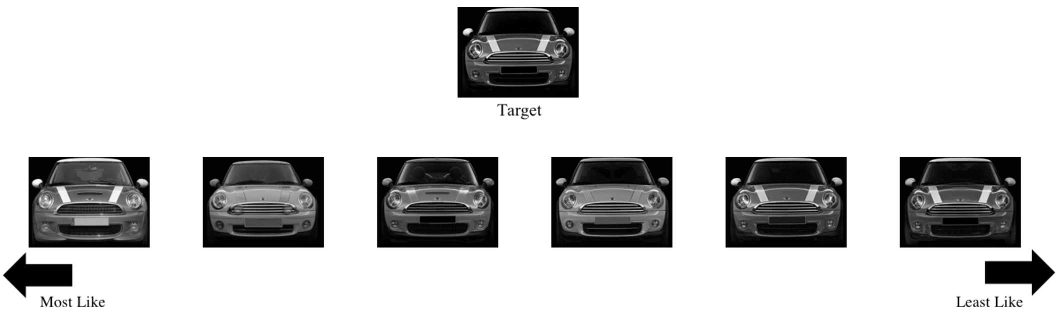


Figure 3.1. (a) Example trials of *CFPT-Identity Older Adult* task. In *CFPT-Identity Older Adult* trials, participants were displayed a target face and six faces (from a frontal view) morphed between the target and distractor in varying proportions (88%, 76%, 64%, 52%, 40%, 28%). Participants' task is to sort the six faces according to the degree of similarity to the target. Half of the trials contain upright faces (upper graph) and half inverted faces (lower graph).

CFPT-Cars

To test object perception I also developed another new version of the CFPT involving using car stimuli as oppose to faces. This test adapted the same experimental paradigm of the original CFPT-Identity (Duchaine et al., 2007a and 2007b) and the CFPT-Identity Older Adult Task described above. That is to say that during the task, participants were shown a target car and six cars (from a frontal view) morphed between the target and one of six distractor cars in varying proportions (88%, 76%, 64%, 52%, 40%, and 28% of the target car; Figure 1b). In each trial, participants were asked to sort the six cars by similarity to the target face with a one-minute time limit, and as per all tasks participants could click on an option to begin the next trial if they completed the trial before this time. As with the CFPT- Identity Older Adult task, the stimuli were created using the software FantaMorph; all car stimuli used were from laboratory stimuli database. The task involved eight upright and eight inverted trials that alternated in a fixed pseudo-random order. Performance was measured using percentage of correct responses. Chance performance is 36%.



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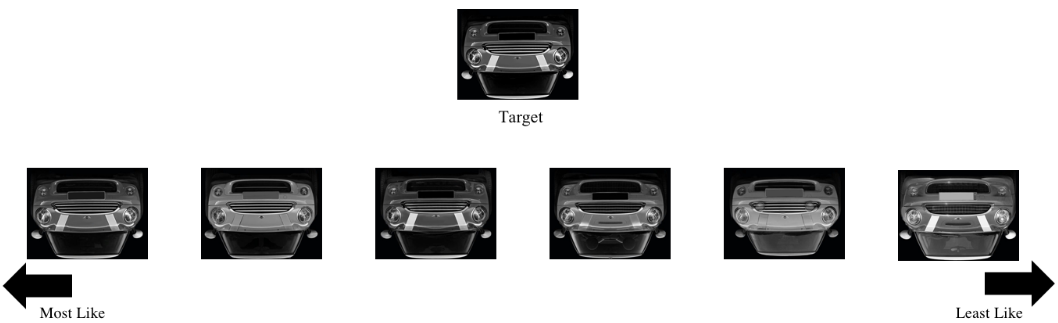


Figure 3.1. (b) Example trials of *CFPT-Car* task. In *CFPT-Car* trials, participants were displayed a target car and six cars (from a frontal view) morphed between the target and distractor in varying proportions (88%, 76%, 64%, 52%, 40%, 28%). Participants' task is to sort the six cars according to the degree of similarity to the target. Half of the trials contain upright cars (upper graph) and half inverted cars (lower graph).

CFPT-Happy Older Adult

This task followed the same procedure as the standard CFPT-Happy (Janik et al., 2015), but here I used older adult faces rather than younger adult faces. During the task, participants were presented six faces (from a frontal view) morphed between the expression of 'happiness' and a 'neutral' expression in varying proportions (25%, 20%, 15%, 10%, 5%, and 0% happiness). These proportions were used based on piloting to establish the most optimal parameters for sensitive task difficult (e.g. to avoid ceiling effects) and to permit comparability to the original young adult CFPT-Happy (note that the percentage morphs are slightly higher than the original young adult CFPT-Happy, but performance accuracy is comparable). Participants were required to sort the faces according to how happy they appeared from the face that looks least happy to the face that looks most happy (note all images appeared in the same fixed random order as per young adult CFPT-Happy at the start of each trial). The time limit for each trial was 60 seconds, and as per all tasks participants could click on an option to begin the next trial if they completed the trial before this time. As with the CFPT-Identity Older Adult task, the stimuli were created using the software FantaMorph; all facial stimuli used were from Park Aging Mind laboratory face database (http://agingmind.cns.uiuc.edu/facedb/); and external facial features were removed from images and coloured images were transformed in to grey scale images (Figure 1c). Performance was measured using percentage of correct responses. Chance performance is 36%.

c.

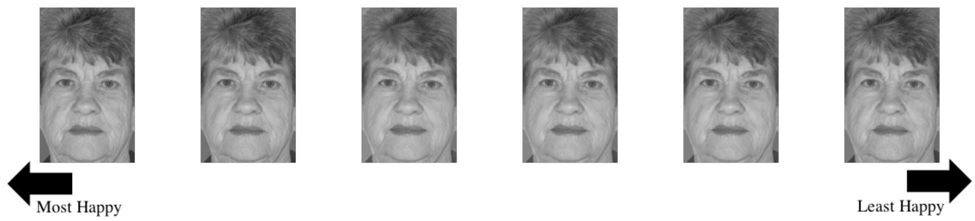


Figure 3.1. (c) Example trials of *CFPT-Happy Older Adult* task. In the *CFPT-Happy Older Adult trials,* participants were presented six faces (from a frontal view) morphed between the expression of 'happiness' and a 'neutral' expression in varying proportions (25%, 20%, 15%, 10%, 5%, 0%). Participants were required to sort the faces according to how happy they appeared from the face that looks least happy to the face that looks most happy.

3.3 Results

Prior to analysis, three younger adult participants were withdrawn from analysis due to them being identified as outliers in at least one task. More specifically, each participant that was withdrawn performed three standard deviations away from the group mean on either one or more task, and was verified as an outlier using Grubb's Test.

Demographic differences

Following outlier removal, the mean age of young group was 25 years (SD = 6 years) and the mean age of old group was 69 years (SD = 6 years). The years of education (young group: mean = 15 years, SD = 3 years; old group: mean = 16 years, SD = 3 years) and NART scores of the two age groups were compared and they were not significantly different (young group: mean = 118.71, SD = 6.92; old group: mean = 120.67, SD = 7.79). The younger group comprised of 16 females and 7 males, with 2 left handed participants. The older group comprised of 20 females and 7 males, with one left handed participant.

Social perception performance differences

Perceptual performance of the two groups were analysed using a 2 (group) × 5 (task type) mixed-ANOVA with the between-participants factor of group (young and old) and within-participants factor of trial type (happiness, upright identity, inverted identity, upright car and inverted car). Mauchly's test indicated that the assumption of sphericity had been violated so the Greenhouse-Geisser correction was employed. The results revealed a significant effect of task type [$F\ (3.048,\ 146.311) = 32.84,\ p < .001,\ \eta^2 = .406$]. Bonferroni corrected post-hoc comparisons revealed that this was because overall participants performed better on the happiness perception relative to inverted face perception and car perception (for both Upright and Inverted conditions), and because overall participants were more accurate on Upright Facial Identity trials relative to inverted face perception and car perception (for both Upright and Inverted conditions). There was also a significant main effect of group [$F\ (1,\ 48) = 20.54,\ p < .001,\ \eta^2 = .300$], which was due to older adult participants performing worse overall compared to young adult participants.

Importantly, the ANOVA also revealed a significant interaction between group and task type [$F\ (3.048,\ 146.311) = 11.103,\ p < .001,\ \eta^2 = .188$]. In view of this, pairwise comparisons with Bonferroni correction were performed between the older and young group on the five face perception tasks. This revealed a significant difference found in happiness perception [$p = .001,\ d = 1.031$] (figure 3.2a), upright facial identity perception, [$p < .001,\ d = 1.437$] (figure 3.2b) and inverted face perception [$p < .001,\ d = 1.316$] (Figure 3.2c). Accuracy performance of upright and inverted car perception did not differ significantly between the two age groups (Figure 3.2d and 3.2e). Therefore, older participants showed reduced performance relative to young old adults in their ability to make fine-grained perceptual judgments of faces (emotion and identity), but not objects.

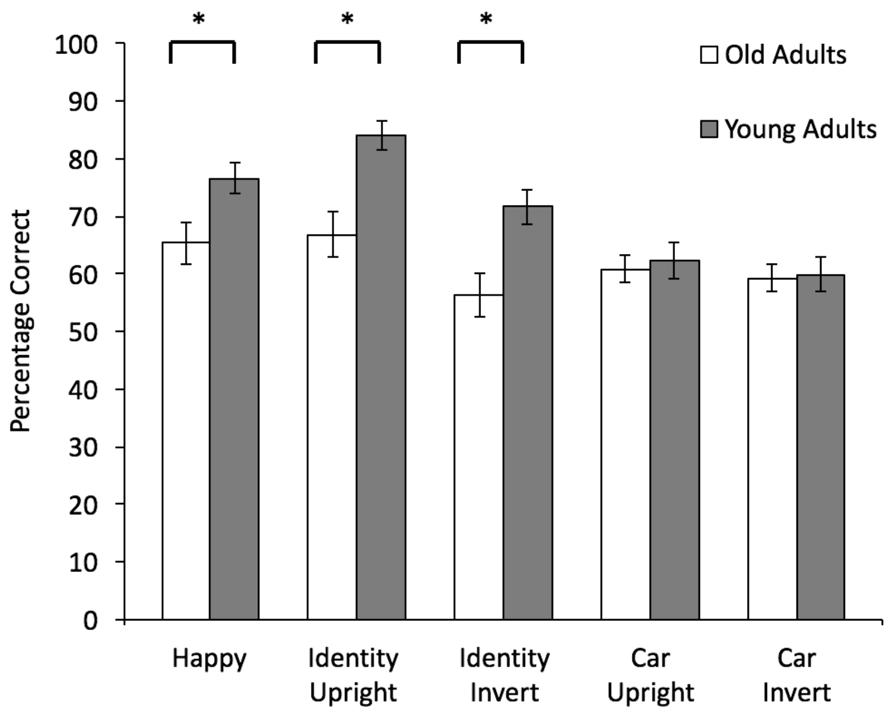


Figure 3.2. Mean perceptual accuracies (± one S.E.) of two age groups on (a) *Happy,* (b) *Identity-Upright,* (c) *Identity-Invert,* (d) *Car-Upright and* (e) *Car-Invert*. Results revealed a significant difference in happiness perception [$p = 0.001$, $d = 1.031$], upright facial identity perception [$p < 0.001$, $d = 1.437$] and inverted face perception [$p < 0.001$, $d = 1.316$] (Figure 3.2 a-c). Accuracy performance of upright and inverted car perception did not differ significantly between the two age groups (Figure 3.2 d, 3.2 e).

Given the moderate differences in gender between the groups I also ran the above analyses when controlling for gender; a similar pattern of data was found, indicating that the differences described above were not due to any gender differences between older and younger participants.

The trajectory of age-related changes differences in social perception

I also examined the trajectory of age-related changes in social perception in experiment 2. Firstly, the correlation between age and performance accuracy on each perceptual task revealed significant negative correlations between age and performance on the CFPT-Identity

Older Adult (both Upright [*R = -.585, p = <.001*, and Inverted Trials [*R = -.528, p = <.001*] and the CFPT-Happy Older Adult [*R = -.488, p = <.001*], but no significant relationship between CFPT-Car performance and age was observed (Upright trials [*R = -.149, p = .302*]; Inverted Trials R = *-.025, p = .865*]). Whilst negatively correlated overall, plotting the data for the relationship between performances on each perceptual task and age revealed evidence towards an inverted parabola for CFPT-Happy Older Adult performance. With this in mind, I next fitted the data to a quadratic function and examined this using polynominal regression. This revealed a significant quadratic relationship between age and performance on the CFPT-Happy Older Adult task [*β = -3.05, t = 2.99; F (2, 47) = 13.22, p <.001*], with performance increasing in younger participants from 18 to 36 years but declining in older participants from 60 years and over (Figure 3.3a). In this regard, while aging does affect the perception of subtle facial cues related to happiness perception, it appears that performance continues to improve during young adulthood (potentially peaking in middle adulthood) before a decline during later life. In contrast, for identity perception, age was a significant predictor of CFPT-Identity (Older) Upright trial performance [*β = -.585, t = 5.00; F (1, 48) = 13.22, p <.001*] and Inverted trial performance [*β = -.528, t = 4.31; F (1, 48) = 18.59, p <.001*] in a linear fashion (Figures 3.3b and 3.3c). This suggests that, contrary to facial emotion, the ability to perceive subtle cues to facial identity steadily declines with from young to older adulthood.

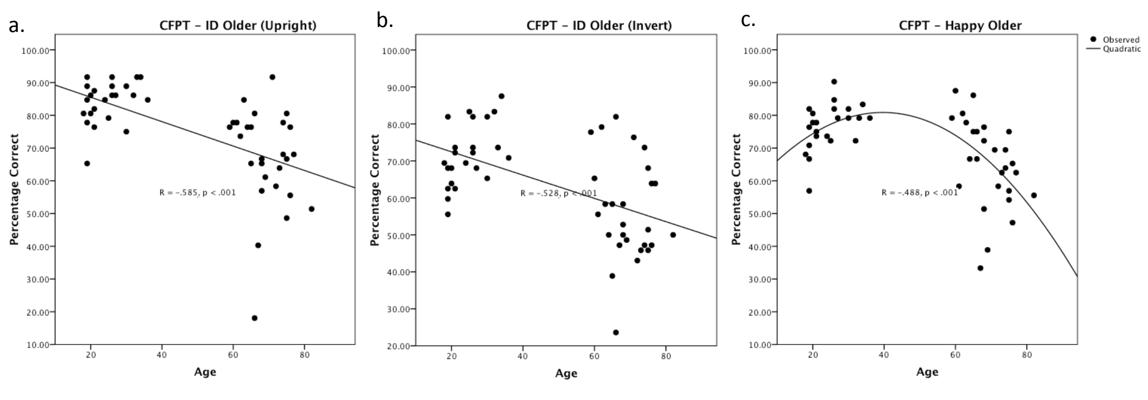


Figure 3.3. The trajectory of age-related changes on perception of (a) *facial happiness*, (b) *upright-* and (c) *inverted- facial identity*. Results revealed a significant quadratic relationship

between age and performance on the *CFPT-Happy Older Adult* task ($p < .001$), with performance increasing in younger adult participants from 18 to 36 years but declining in older participants from 60 years and over (figure 3.3 a). In contrast, for identity perception, age was a significant predictor of *CFPT-Identity (Older) Upright* trial performance ($p < .001$) and *Inverted* trial performance ($p < .001$) in a linear fashion (figure 3.3 b and 3.3 c).

3.4 Discussion

This study sought to investigate the relationship between normal aging and the perception of subtle changes in facial emotional and facial identity in older adult faces. I found that aging is related to linear declines in the ability to make fine-grained visual discriminations regarding the perception of facial identity (for both upright and inverted faces). In contrast for the perception of subtle changes in facial emotion, I found evidence suggestive of an inverted parabola, whereby the perception of happiness from subtle facial cues improved during young adulthood (up to 40 years in the present study), but declined in old adulthood (from 60 years and up in the present study). Importantly, no differences were observed between young and old adults for the perception of subtle changes in non-face stimuli, indicating that age-related differences in the perception of facial emotional and facial identity in older adult faces are specific to social perception and do not reflect domain-general changes in fine-grained visual discrimination with age.

Perception of facial happiness (older faces)

The general pattern of change in facial emotion and identity perception associated with aging that I observe is consistent with prior work that has typically tested these abilities in isolation. That being said, there are a number of studies that have suggested that the perception of happiness remains stable during aging (Moreno et al., 1993; Calder et al., 2003; Orgeta and Philips, 2007); our findings conflict with this conclusion. The reasons for the difference between our findings related to declined happiness perception in older adults and prior work may be due to the use of more subtle low intensity emotion stimuli used in the current study. Moreover, a number of prior studies have tended to use more prototypical exemplars of happiness that use high intensity emotion. While helpful to study emotion perception, arguably high intensity emotions are less commonly encountered in daily life interactions (i.e. we tend to encounter more subtle facial expression that have lower intensities on a daily basis) and often have led to ceiling effects in past research, thus potentially may masking a perceptual deficit (e.g. Moreno et al., 1993; Orgeta & Phillips, 2007; McDowell et al., 1994; Brosgole & Weisman, 1995; Isaacowitz et al., 2007). By testing the perception of low-to-medium intensity expressions of happiness I was able to a) test happiness perception in conditions that were not at ceiling and b) examine older adult's perceptual abilities to determine subtle emotional expressions that may be important in everyday life (Hess, Blairy, & Kleck, 1997). In addition by ensuring similar task demands for our identity, happiness, and non-face perceptual tasks I was able to ensure that differences in the pattern of relationship between aging and performance is not due to not specific task demands (e.g. working memory).

The trajectory of age-related changes

That facial happiness and facial identity perception follow different development trajectories is interesting, and suggests that while both processes are linked with declines in older adulthood the trajectory and mechanisms by which this occurs may to some extent be independent. This is consistent with models of face processing that suggest some degree of independence in the mechanisms involved (e.g. Bruce & Young, 1986; Haxby, Hoffman, & Gobbini., 2000; Calder & Young, 2005). I note, however, that a general caveat of our study is that I lack data from participants in the middle adulthood range (from 40 years to 60 years), thus while our data are indicative that subtle facial happiness perception peaks in middle adulthood before declining in older adulthood, further work is required to test this explicit prediction. In addition it will be important to examine the extent to which age-related differences in facial emotion perception that I observe here for happiness perception hold for other emotion types. What is clear, however, is that there is a steady increase in the ability to perceive subtle expressions of happiness in young adults (from 18 to 36 years in the current study), followed by a decline in older adults (from 60 years upwards in the current study). In contrast, the perception of facial identity shows evidence of more linear declines in both young and old adult participants.

Perception of non-facial objects

The finding that older adults do not differ from younger adults in their perception of objects is also consistent with previous findings reporting that aging is associated with declined face perception, while object perception remains intact (Boutet and Faubert, 2006) or is less affected by aging (Meinhardt-Injac, Persike & Meinhardt, 2014). By assessing the perception of subtle changes in object stimuli under similar conditions to facial identity and facial emotion I am able to ensure that the age-related differences are not due to differing task demands that might influence performance (e.g. working memory). Our object control stimuli, namely cars, were carefully chosen since this class of stimuli includes configural relations between individual features (as with faces). The main difference between faces and cars are the individual features and fine spatial relationships between these features. Different spatial frequencies encode different aspects of faces and objects, and visual cues used for face and object discrimination might be associated with distinct spatial frequencies (Morrison and Schyns, 2001). Gaspar et al. (2008) measured face identification thresholds for upright and inverted faces embedded in different types of noise and concluded that people use information conveyed by similar narrow bands of spatial frequencies to identify upright and inverted faces. Older people's relatively intact performance on object perception, but significantly declined face perception for upright and inverted facial stimuli might be due to their deficits in handling fine internal features that involve perception of fine spatial frequencies (e.g. Meinhardt-Injac, Persike & Meinhardt, 2014). This will be an interesting avenue to explore with future work.

Age-related face perception decline and own-age bias

A further important addition of our study is the development and inclusion of comparable tests for facial identity and facial emotion perception that involve the use of older adult stimuli. Moreover, a common caveat of past work on aging and social perception is the use of young adult faces as task stimuli, which may weight performance in favour of young adult participants due to own-age biases (e.g. own-age effect whereby we are better at perceiving faces of a similar age to ourselves, Anastasi & Rhodes, 2005; Wright & Stroud, 2002). In developing new versions of the CFPT specifically involving older face stimuli and non-face stimuli I hope that my study provides the research community with novel tasks that will be useful for future work. For example, by overcoming the potential for own-age biases the tasks may be helpful for other researchers examining social perception in aging, and in atypical groups where age appropriate task stimuli may be useful (e.g. in prosopagnosia research where the original CFPT-Identity involving young adult stimuli is commonly used as part of diagnostic batteries). Further, by using these tasks, it was found that declined face perception of subtle facial emotion and facial identity in older adults is evident for older face stimuli, implying that declines in social perception associated with aging are not fully accounted for due to an own-age bias. One might suggest that the steady increase in facial happiness perception in young adults could to some extent be to do with own-age bias because as the gap between the younger adult participant's age and the target face decreases (i.e. as they get older) the participant's performance increases. However, if this was the case then one would expect a similar pattern of performance in the facial identity perception (where linear declines with age were found) and it would seem unlikely that we find a decline in facial emotion perception in the older adult group for whom target faces were more optimally matched in terms of the age of participant (i.e. the participant and target face were of a similar age group). It is also important to put our findings in the context of prior work that has sought to examine facial identity processing differences associated with aging. For instance, Bowles et al. (2009) found younger and middle-aged adults did not differ in perceiving different facial identities with minor changes whereas older adults (50+ years) showed significantly poorer performance than the younger group in the CFPT (young faces). The face identity results of present study are line in with this previous finding, which suggest that older people's deficits in discriminating facial identity is not dependent on the age of faces.

3.5 Summary

In summary, here I assessed how aging is associated with changes in the perception of subtle cues related to facial identity of older adults and facial emotion (happiness) displayed by older adults. I also examined how aging is linked to object identity (cars) perception. I found that both facial identity and facial emotion are associated with declines in older adulthood, indicative of declines in the ability to process social facial cues in aging. Interestingly, the trajectory of the age-related differences in the perception of facial identity of older adults and facial emotion of older adults differed; with emotion perception being associated with increases in perceptual abilities in young adulthood followed by declines in older adulthood, while identity perception was linked to linear declines in perception across the lifespan.

CHAPTER 4: METHODOLOGICAL INTRODUCTION TO TRANSCRANIAL CURRENT STIMULATION

This chapter will give an overview of the methodological principles of transcranial current stimulation (tCS) with a particular emphasis on transcranial random noise (tRNS) as this is the method used in my brain stimulation study. In this chapter, neurophysiological mechanisms underlying each transcranial current stimulation (tCS) method will be introduced and the effectiveness of each stimulation on improving perceptual and cognitive functions in healthy populations will be discussed with examples of related studies. In addition, factors that can influence efficiency of stimulation and ethical considerations will be demonstrated. Chapter 5 of this thesis will present the brain stimulation study where high-frequency tRNS was employed to demonstrate whether the cortical excitability of inferior frontal gyrus can be enhanced in older people and the cortical overactivation within this particular region can lead to improved ability in recognising facial emotional expressions.

4.1 Background

Traditional neuroimaging tools, such as electroencephalogram (EEG) and functional magnetic resonance imaging (fMRI), have contributed in exploring human neural mechanisms during cognitive tasks. Although these methods provide excellent spatial (i.e. fMRI) and temporal (i.e. EEG) resolutions, one important limitation within them is that they can only reveal correlations between neural regions and cognitive behavioural performance but cannot account for causality (Lavidor, 2016). As they are either based on measuring indirect activation (positron emission tomography, PET; functional magnetic resonance imaging, fMRI); or recording electrical activity (event-related potential, ERP;

electroencephalogram, EEG; and magnetoencephalography, MEG) during cognitive tasks. An alternative way to study perceptual and cognitive neural mechanisms is to use transcranial magnetic stimulation (TMS), first used in the mid-80s and attracted lots of interest in the field (Stewart, Battelli, Walsh & Cowey, 1999). Over the last decade there is a fast growth in the use of transcranial current stimulation (tCS) for both cognitive neuroscience research and clinical applications (Ruffini, Wendling & Merlet, 2012) (see figure 4.1). Using tCS, brain functions can be modified by generating electric fields (can modulate neural activity) through the delivery of weak electrical currents transcranially over the scalp. The idea behind tCS is that the stimulation (anodal or cathodal mode) of a specific brain region can cause enhancement or inhibition of certain cognitive or perceptual performance, and thus establish a causal link between the stimulated brain regions and the cognitive function (Lavidor, 2016). There are different versions of tCS, including transcranial alternating current (tACS), transcranial direct current (tDCS), transcranial random noise current stimulation (tRNS). This chapter will give an overview of different tCS methods with an emphasis on tRNS.

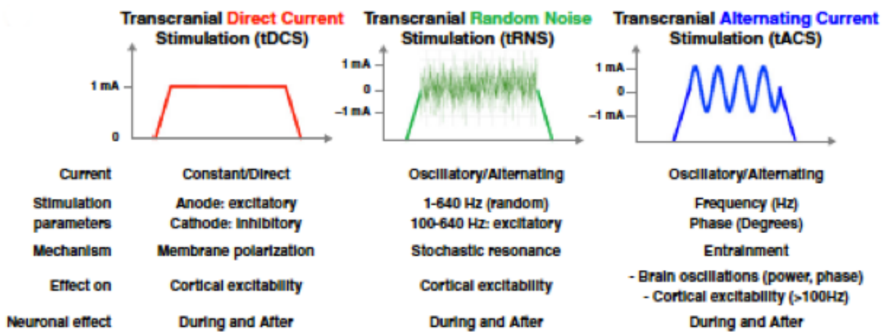


Figure 4.1. Basic characteristics of transcranial direct current (tDCS), transcranial random noise current stimulation (tRNS), and transcranial alternating current (tACS).

4.2 Transcranial direct current stimulation (tDCS)

To date, the most studied tCS is tDCS, which is able to induce long-lasting changes in cortical excitability in a reversible, relatively selective and non-invasive manner (Ambrus, Paulus and Antal, 2010). In tDCS, an "active" or stimulating electrode is placed over the target region to be affected where the weak current (typically 1–2 mA) is consistently delivered, at the same time, a "reference" electrode is placed over a brain region where the effect of the current is minimal. The mechanism underlying tDCS is to manipulate brain excitability via resting membrane polarisation: cathodal stimulation causes hyperpolarisation hence decreased cortical excitability, whereas anodal stimulation depolarises the resting membrane potential and leads to improved cortical excitability (Paulus, 2011; Lavidor, 2016). At the cellular and molecular level, the tDCS after effect reflects the mechanism of synaptic plasticity such as long-term potentiation and long-term depression (Fritsch et al., 2010), and it was found anodal tDCS causes locally reduced inhibitory GABA neurotranmitters while cathodal stimulation causes reduced excitatory glutamatergic neurotransmitters (Stagg et al., 2009). The consequence of this is that the stimulated brain region becomes more responsive to the signals that it normally processes, thus if the brain area is involved in a particular task then performance on that task can be improved. This tDCS induced cortical excitability enhancements or reductions emerge during stimulation and can last after stimulation (Nitsche et al., 2003). Repetitive sessions of tDCS within specific time windows (within 24 hours at least) have shown long-lasting effects (Cohen Kadosh, Soskic, Iuculano, Kanai, & Walsh, 2010; Vestito, Rosellini, Mantero, & Bandini, 2014; Monte-Silva, Kuo, & Hessenthaler et al., 2013).

Studies have claimed that tDCS induces persisting activity changes in the human motor cortex (Nitsche and Paulus, 2000), memory (Javadi and Cheng, 2012; Javadi and Walsh, 2012), and attention (Moos, Vossel, & Weidner et al., 2011). The induced stimulation after-effects depend on "polarity, duration and intensity of the stimulation" (Paulus, 2011). For example, polarity determines the direction of the field relative to the stimulated neurons

(Ruffini, Wendling & Merlet, 2013), in general terms, anodal stimulation (current is injected into the brain) increases cortical excitability (Nitsche and Paulus, 2000; Boggio et al., 2009) whereas cathodal stimulation (current is collected from the brain) decreases it (Nitsche and Paulus, 2000; Berryhill, Wencil, Coslett, & Olson, 2010). However, cathodal tDCS effects on cognition have been questioned (Jacobson, Koslowsky, & Lavidor, 2012) as it showed a null effect (Fregni et al., 2005) or even enhancement (i.e. Weiss & Lavidor, 2012). The 'anodal-excitation and cathodal-inhibition effects (AeCi)' might not be consistent for different brain regions. Jacobson, Koslowsky & Lavidor (2012) investigated the effect sizes of 'anodal-excitation and cathodal-inhibition effects (AeCi)' in both motor and cognitive functions in a meta-analysis study. The AeCi effect was found to occur quite consistently in motor investigations and less commonly in cognitive studies. Specifically, anode electrode applied over a non-motor area normally cause an excitation effect, whereas the cathode electrode rarely causes an inhibition. In addition, Batsikadze, Moliadze and Paulus (2013) suggested an increase of cathodal tDCS intensity might not enhance the inhabitation effect, but might cause a shift of the stimulation direction. In the study, application of 2 mA cathodal tDCS for 20 min resulted in cortical excitability enhancement instead of inhibition.

4.3 Transcranial altering current stimulation (tACS)

tACS is a non-invasive brain stimulation and it has been less intensively studied than tDCS (Hamid, Gall, & Speck, 2015). It can be achieved via the same device as tDCS, but uses different current wave forms and modulate cortical activity in a frequency dependent manner (Antal and Paulus, 2013). During tACS, a specific frequency is applied at a target brain region, and the targeted neurons mirror or synchronise frequencies induced from the cortex by the stimulation, thereby interacting with specific functions of the stimulated region (Lavidor, 2016). It also helps to explore the functional roles of neural oscillations across different cognitive tasks by stimulating the brain with specific frequencies during cognitive tasks. Previous studies suggested the causality of phase-coupling of distant cortical areas for cognitive performance in healthy humans, as it was found that tACS induced neural oscillation synchronization significantly enhanced cognitive performances (Polanía, Nitsche and Korma et al., 2012; Helfrich, Schneider, and Rach et al., 2014). In contrast, tACS induced neural oscillation desynchronization deteriorates performance (Polania, Nitsche and Korma et al., 2012).

Although this technique is still largely unexplored and the underlying stimulation neurophysiology mechanism is not fully understood (Lavidor, M., 2016), some preliminary studies have shown that tACS has observable effects on modulating cortex excitability. For example, Kanai et al. (2010) applied tACS to the visual cortex at different frequencies which varied from 5–40 Hz, and they found that tACS at 20 Hz increased the excitability of the visual cortex during the stimulation, whereas other frequencies did not affect it. Several studies have also shown that tACS can be used to modulate cognitive or perceptual abilities, such as fluid intelligence (Santarnecchi et al., 2013), visual memory (Polanía, Nitsche, & Korman et al., 2012), decision making (Sela, Kilim, and Lavidor; 2012), working memory (Jaušovec and Jaušovec, 2014) and facial expression perception (Janik, Rezlescu, and Banissy, 2015). For instance, in Janik et al.'s (2015) study, it was found that modulating occipital gamma with 40 Hz tACS enhances facial anger perception but not other face identity tasks. This finding implicates an important role of occipital gamma oscillations in facial emotion perception.

4.4 Transcranial random noise stimulation (tRNS)

Another form alternating current stimulation is tRNS (transcranial Random Noise Stimulation). This approach has been recently begun to be used to study cognitive and perceptual function. It is therefore a relatively novel type of tCS in the context of studies of human cognition. During tRNS a random electrical oscillation spectrum is passed between the two electrodes (Ruffini, Wendling & Merlet, 2012). Unlike transcranial direct current stimulation (tDCS) that consisted of an active stimulation electrode and a reference electrode, tRNS stimulation is absent of directionality and both electrodes are considered to have excitatory stimulation effect (Pirulli, Fertonani, & Miniussi, 2016). That is to say that increased cortical excitability can be found under both stimulating electrodes.

4.4.1 Mechanisms of tRNS

During tRNS, a random electrical oscillation spectrum is delivered by a battery-driven electrical stimulator (DC-Stimulator-Plus, neuroConn) through a pair of conductive rubber electrodes which are covered in saline-soaked sponges or conductive gels. In the random "noise" stimulation mode, random level of current was generated for every sample (sampling rate 1280 samples/s), the random numbers are normally distributed and the probability density function follows a bell-shaped curve; in the frequency spectrum all coefficients have a similar size ("white noise") (Chaieb, Paulus and Antal, 2011). The frequency spectrum was separated into a low (0.1–100 Hz)- and high (101– 640 Hz)-frequency spectrum (Terney, 2008). The main effect of tRNS is an increase in cortical excitability under both electrodes placed on the scalp (Terney et al. 2008; Chaieb et al., 2011), although recently it was found that lower intensities at around 0.4 mA tRNS lead to inhibitory aftereffects (Moliadze et al., 2012). tRNS has been proven to have successfully modulated the motor cortex (Terney et al., 2008; Moliadze et al., 2010, 2012; Chaieb et al., 2011), arithmetic learning (Snowball et al., 2013), perception of numerosity (Cappelletti et al., 2013), and facial identity perception (Romanska, Duchaine, & Banissy et al., 2015).

Previous studies suggested that the tRNS induced cortical excitability was due to strengthening of synapses and inducing long-term potentiation (LTP), which is similar to the effect of anodal tDCS (Rioult-Pedotti et al., 2000; Antal, Chaieb, & Moliadze, 2010; Terney et al., 2008). However, the underlying neurophysiology mechanism between tDCS and tRNS are different; tDCS modifies the resting membrane potential directly thus changing the firing rate of individual neurons, whereas the tRNS does not possess a direct current component (Terney et al., 2008). The physiological mechanism underlying tRNS is not fully confirmed, there are several explanations. One explanation is "stochastic resonance" (Wiesenfeld & Moss, 1995), which claimed that the fine-tuned noise from tRNS can sensitize targeted neurons and lower their threshold to detect signals, in other words, the random-noise enhances weak neuronal signal detection in the sensory system (Lavidor, 2016; Terney, 2008; Moss et al., 2004). Another possibility is tRNS might work like tACS, it can possibly interact with ongoing neural oscillations in the brain and thus result in increased cortical excitability (Terney et al., 2008). At the neurophysiological level, during tRNS, repeated activations of sodium channels by higher frequencies (100 – 640 Hz) can lead to neuron membrane depolarization, as observed in both animal and physiological studies (Schoen and Fromherz, 2008; Chaieb, Antal, & Paulus, 2014).

4.4.2 Frequency range of stimulation

Frequency range (Hz) and intensity (amplitude) are the major factors determining intervention outcome (Paulus, Antal, & Nitsche, 2012). High-frequency (100- 640 HZ) was most commonly used in tRNS studies and it showed similar excitatory effect as anodal tDCS. For example, Terney et al. (2008) used 10min tRNS with the frequency between 0.1 and 640 Hz and showed that tRNS was also able to increase the excitability of the motor cortex with the similar effect as tDCS, higher frequencies (100 – 640 Hz) appeared to be responsible for generating this effect, which might be attributed to the repeated opening of Na+ channels. Furthermore, Fertonani, Pirulli, & Miniussi (2011) compared the effect of different types of tCS [high-frequency tRNS (100 – 640 Hz), low-frequency tRNS (0.1–100 Hz), anodal-tDCS, cathodal- tDCS, and sham stimulation] on perceptual learning and the results showed that high-frequency tRNS had a significantly superior simulating effect compared to others tCS, which was possibly due to the stimulating mechanism of tRNS to “prevent homeostasis of the system and potentiate task-related neural activity”. In addition, Romanska, Duchaine, & Banissy (2015) showed that single-session high-frequency tRNS targeted at the lateral occipitotemporal cortex significantly improved facial identity perception. This evidence suggests that high-frequency tRNS is an effective brain stimulating method, which has similar or even better after-effect results as tDCS. There are inconsistent findings (Saiote, Paulus, Antal et al., 2013; Mulquiney et al., 2011), for instance, Mulquiney et al. (2011) found high-frequency tRNS cannot enhance working memory in the way tDCS does after comparing the effect of tDCS and high-frequncy tRNS on working memory following stimulation over the DLPFC.

4.4.3 Spatial resolution

Quite a few studies have shown that tRNS can selectively stimulate a specific neural region and enhance its cortical excitability. For instance, Terney (2008) showed that tRNS can selectively modulate the excitability of the motor cortex. Specifically, it was found that delivering 10 minutes high-frequency (101-640 Hz) tRNS to primary motor cortex induced increased excitability by 20-50% (lasts for up to 90 minutes), as revealed by measuring motor-evoked potentials (MEPs) using single-pulse transcranial magnetic stimulation (TMS). Using the same method, Chaieb, Antal and Paulus (2014) also found that application of transcranial random noise stimulation (tRNS) between 0.1 and 640 Hz over the primary motor cortex (M1) for 10 minutes induces a persistent excitability increase lasting for at least 60 minutes.

Earlier studies have suggested that the spatial resolution or the focality of tDCS can be improved by reducing stimulation electrode size, but keeping current density constant (Nitsche et al., 2007). However, this approach has not been tested in tRNS and related demonstration is required. In addition, some tDCS studies have found that the stimulation effect might not be restricted to the targeted neural region, but rather spread into neural tissue between electrodes (Opitz, Paulus, & Will, 2015). No tRNS studies thus far have demonstrated this issue, and not many tCS studies have investigated this in depth. In future studies, combining tRNS and with neuroimaging methods and connectivity analysis can help to reveal a more comprehensive picture of the stimulation effect on neural cortex and neural network.

4.4.4 Temporal resolution

Understanding of the time course of both online (during stimulation) and offline (after stimulation) tRNS effect is important, as it can help to identify how it interacts with the underlying neural system, and be useful for developing interventions to help people with impaired or declined cognitive abilities. Most studies that have explored the temporal resolution of tRNS are related to the motor cortex, which might be due to the accessibility of measuring motor cortical excitability. For example, In Terney et al.'s (2008) study using motor-evoked potential (MEP) recordings and psychophysical measurements, it was shown that a 10-minute application of transcranial random noise stimulation (tRNS) can enhance cortical excitability for up to 90 minutes (Terney et al. 2008). Chaieb, Antal and Paulus (2015) applied transcranial random noise stimulation (tRNS) between 0.1 and 640 Hz over the primary motor cortex (M1) for 10 minutes and it induced a cortical excitability which lasted for at least 60 minutes.

Some prior studies have found that online- and offline- stimulation can produce different stimulation aftereffect (Barbieri, Negrini, Nitsche, & Rivolta, 2016). For example, Barbieri and colleagues (2016) delivered online (a-tDCS during task execution) and offline (a-tDCS before task execution) targeted at the right lateral occipital cortex. The results showed that only offline a-tDCS improved the perceptual and memory performance of both faces and objects. However, online a-tDCS did not help to improve either perceptual or memory performance. In another study, Prichard and his colleagues (2014) have directly compared the time course of the effect of tDCS and tRNS in modulating cognitive or perceptual abilities (Prichard, Weiller, Fritsch & Reis, 2014). They (2014) investigated whether tRNS and tDCS have different online (within session) and offline (between session) effects in modulating motor skill learning over three consecutive days. It was found that both tRNS and tDCS have online effect and short offline effect in enhancing motor skill learning, but the offline effect cannot persist overnight. The main differences between tDCS and tRNS on temporal aspect was tDCS enhanced perceptual learning immediately following the onset of stimulation, whereas tRNS exerted more gradual effects. In another study, Pirulli, Fertonani, & Miniussi (2013) applied high-frequency tRNS, anodal tDCS and sham tDCS on V1 before or during the execution of an orientation discrimination task. They found that tRNS enhanced task performance only when it was applied during task execution, whereas anodal tDCS can improve the performance if it was applied before task execution. These findings suggested that timing of identical tES protocols can yield different effects on performance and each tCS have temporally distinct interactions with the neurological process of motor skill learning.

4.4.5 Intensity of stimulation

Most tRNS studies only use one intensity parameter, therefore this aspect of tRNS is not well addressed in the current field of research. Previous studies have shown that application of 1mA high-frequency tRNS is sufficient to modulate motor cortical excitability (Terney et al., 2008; Chaieb, Antal and Paulus, 2015), or improving cognitive (Snowball et al., 2013) or perceptual (Romanska, Duchaine, & Banissy, 2015) abilities. Moliadze, Atalay, and Antal et al. (2012) applied different stimulation intensities (0.2, 0.4, 0.6, 0.8 and 1mA, respectively) tRNS in order to determine what is the lowest intensity capable of inducing observable cortical excitability for tRNS. In the study, 14 participants received sham stimulation and tRNS using different intensities and 11 participants received sham stimulation and tACS using different intensities in a randomized order. Stimulation sessions were delivered on separate days with at least 3 days apart to avoid a "carry-over effect". Cortical excitability was measured immediately after each simulation using single test-pulse MEPs at 0-minute, 5-minute and 10-minute post stimulation, and then every 10 minutes up to 60 minutes and then again at 90 minutes. The results showed that 1 mA tRNS significantly increased MEPs at the immediately after the stimulation and the aftereffect persisted for 90 minutes compared to the sham stimulation. Surprisingly, it was found that 0.4 mA stimulation significantly decreased MEPs between 20-minute and 90-minute post stimulation compared to sham stimulation. tRNS with 0.2, 0.6 and 0.8 mA did not exhibit any aftereffect. This finding suggests that aftereffect of tRNS is intensity dependent, and the threshold for producing cortical excitability is 1mA, at least for motor cortex modulation. Further studies are needed to test if the threshold also applies to other parts of cortex that are responsible for other cognitive domains.

4.4.6 Duration of stimulation

The effect of tRNS duration on modulating cortical excitability has not been extensively studied. Studies involving modulating motor cortex have established that a 10-minute application of transcranial random noise stimulation (tRNS) over the primary motor cortex (M1) increases the cortical excitability, which lasts around 60-90 minutes (Terney et al., 2008;

Chaieb, Antal and Paulus, 2015). Chaieb and her colleagues (2009) firstly demonstrated the aftereffect of a shorter duration of tRNS. In the study, they found that a 4-minute application of 1mA tRNS over the sensorimotor cortex induces a transient reduction in BOLD response during the performance of a simple finger-tapping task. However, this study only tested nine participants therefore the power of the study is questioned. Later, Chaieb, Paulus and Antal (2011) further investigated whether there is a "threshold stimulation duration" that is necessary to modulate cortex excitability and generate noticeable and lasting aftereffect. In the study, they demonstrated the applications of 4-, 5-, 6- minute tRNS using single-pulse monophasic transcranial magnetic stimulation (TMS) to measure cortical excitability before and after tRNS. It was found that 5- and 6-minute tRNS induced significant enhanced cortical excitability, whereas 4-minute tRNS produced no significant aftereffect on cortical excitability. These studies suggest that tRNS induced cortical excitability require a minimal stimulation duration of 5 minutes. This finding is awaiting confirmation from more studies, and the underlying mechanism for this phenomenon is not well understood, future studies should try to clarify the question.

4.4.7 Ethical considerations

Generally speaking, tCS including tRNS are safe brain stimulation techniques, and the induced effect is reversible, relatively selective and non-invasive if stimulation parameters are controlled by related safety guidelines (Ambrus, Paulus and Antal, 2010; Davis, 2015). There are some safety protocol guidelines for tDCS (i.e. Bikson, Datta and Elwassif, 2009), however, specific safety guidelines and related ethical considerations for tRNS are currently lacking. Safety stimulation parameters and stimulation time which were defined in papers mentioned above were strictly followed in my stimulation study.

Poreisz et al. (2007) investigated potential risks associated with tDCS by summarising the partially adverse effects of 567 tDCS sessions over motor and non-motor cortical areas. They concluded the most reported adverse effect associated with tDCS is a mild tingling skin sensation during the stimulation. It should be noted that the reported minor adverse effects of tDCS on skin are not necessarily linked with brain tissues and should be considered independently (Bikson et al., 2009). tRNS possesses advantages over tDCS regarding skin sensation. Specifically, tRNS delivers oscillatory current and thus does not have the polarity constraints as tDCS which might cause perceptible skin sensations when applied (Chaieb et al., 2009). Therefor tRNS is a possible alternative to tDCS with a better blinding control as it has similar excitability effect as anodal tDCS but it is not as noticeable as tDCS regarding skin perception (Ambrus, Paulus and Antal, 2010).

The occurrence of seizures has not reported in tCS studies, but rare cases were reported in rTMS studies with epileptic patients under treatment with drugs which potentially lower the seizure threshold (Rossi, Hallett and Rossini et al., 2009). Therefore, it is very important to screen participants for any contradictions to tRNS in order to eliminate any potential hazards of stimulations. In tCS brain stimulation study, participants are not permitted to receive stimulation if they have a heart pacemaker, cochlear implant, aneurysm clip or any other metallic object or electronic device within their bodies; if they have a personal or family history of epilepsy or any other medical, psychiatric or neurological disorders; female participants who are pregnant or anyone who has taken part in a brain stimulation study within 24 hours prior to the experiment which uses tCS. The study reported in Chapter 6 of this thesis only used healthy younger and older participants and the screening process mentioned above was followed. The stimulation parameters were carefully controlled according to the safety guidelines and the brain stimulation study was approved by the local ethics committee at Goldsmiths college.

TCS studies have been suggested as a promising tool for enhancing various cognitive and perceptual abilities, such as mathematical skills (Snowball et al., 2013), facial perception (Romanska et al., 2015), and depression (Nitsche et al., 2009). However, there is a potential risk with DIY users who wish to explore the use of brain stimulation, as they might be lacked of proper safety training and sufficient neuroscience knowledge (Danis et al., 2013). In addition, it should be cautious to apply tCS to children whose brain are still developing and they might have different safety stimulation thresholds, there is still a large amount to be done in establishing safety protocols for children (Davis, 2014). Furthermore, tCS induced stimulation has shown spreading from targeted neural regions to surrounding tissues and might cause unplanned effects (Miranda et al., 2006). It is important to leave at least 24 hours between stimulations to reduce build-up effect on untargeted neural regions (Danis et al., 2013).

CHAPTER 5: ENHANCING EMOTION PERCEPTION USING NON-INVASIVE BRAIN STIMULATION

Extensive behavioural evidence has shown that older people have declined ability in facial emotion perception. Recent work has begun to examine the neural mechanism that contribute to this, and potential tools to support emotion perception during aging. The aim of this study was to investigate whether high frequency tRNS applied to the inferior frontal cortex would enhance facial expression perception in older adults. Healthy aged adults (60+ years) were randomly assigned to receive active high-frequency or sham tRNS targeted at bilateral inferior frontal cortices. Each group completed tests of facial identity perception, facial happiness perception and facial anger perception. These tasks were completed before and after stimulation. The results showed that, compared to the sham group, the active tRNS group showed greater gains in performance after stimulation in anger perception (relative to performance before stimulation). The same tRNS stimulation did not significantly change performance on the two other face perception tasks assessing facial identity and facial happiness perception. Examination of how inter-individual variability related to changes in anger perception following tRNS indicated that the degree of performance change in anger perception following active tRNS to inferior frontal cortex was predicted by baseline ability and gender of older adult participants. The findings suggest that high frequency tRNS may be a potential tool to aid anger perception in typical aging, but flag that performance variability and gender may interact with stimulation leading to different outcomes.

5.1 Introduction

Emotional facial expression perception plays an important role in interpersonal communication. Difficulties with emotion perception are associated with specific types of social impairment, including poor interpersonal interaction, reduced social competence, loneliness, and inappropriate social behaviours (e.g., Spell & Frank, 2000; Kanai et al. 2012). Numerous studies have focused on establishing how emotion perception is affected as a function of normal adult aging, as well as the extent and implications of any observed difficulties (e.g. Sullivan and Ruffman, 2004; Isaacowitz et al., 2007; Ebner et al., 2013; Ebner & Fischer, 2014). The overall pattern of results regarding age group differences in facial expression perception is quite consistent: a recent meta-analysis reviewed papers examining age differences in emotion perception and concluded that older adults (60+) have increased difficulty in perceiving at least some basic emotions (particularly anger, sadness, and fear) from faces, but that others remain spared (e.g. disgust perception; Ruffman et al. 2008).

Although many studies have investigated the cognitive and neural basis of decline in emotion perception during typical aging, little attention has been directed towards improving face emotion processing in these individuals. In other areas of research one tool that has proved to be useful in aiding social perception is transcranial current stimulation (tCS). TCS is a safe and noninvasive technique for brain stimulation that can be used to increase or decrease brain activity under a targeted brain region. It refers to a range of techniques, including transcranial direct current stimulation (tDCS), transcranial random noise stimulation (tRNS), and transcranial alternating current stimulation (tACS), which involve passing a weak current between electrodes placed on the scalp (Miniussi, Harris, & Ruzzoli, 2013). For instance, in high-frequency tRNS, an alternating current ranging randomly between 100-640Hz is passed between electrodes leading to bilateral increases in cortical excitability under two stimulating electrodes (Terney et al., 2008).

Prior work has shown that tCS can be effective in improving performance on several tasks in young adults, including memory, perception, social cognition, social perception, learning and motor abilities (e.g. Cohen Kadosh et al., 2010; Snowball et al., 2013; Fertonani et al., 2011; Sellaro et al., 2016; Romanska et al., 2015). While tCS has been employed to study young adults, it has been used less frequently to study older adult participants (see Tatti et al., 2016 for review). This is surprising given a) the psychosocial consequences of reduced emotion perception ability (Spell & Frank, 2000), b) the consistent pattern of age-related decline in emotion perception ability (e.g. Ruffman et al., 2008), and c) prior work showing that social processing (including emotion perception) can be improved following tCS in young adult participants (e.g. Santiesteban et al., 2012, 2015; Hogeveen et al., 2014, 2016; Janik et al., 2015; Romanska et al., 2015; Barbieri et al., 2016; Liepelt et al., 2016; Sellaro et al., 2016), implying that tCS may have potential efficacy as a tool to enhance facial processing skills in older adults. Indeed, in other domains (e.g. memory, motor performance) non-invasive brain stimulation techniques have been shown to offer promise in enhancing performance of healthy older adults. For instance, Hsu et al. (2015) investigated the effect of non-invasive brain stimulation on healthy older adults by conducting a meta-analysis of fourteen studies with a total of 331 healthy older adults. The meta-analysis revealed that applying a single session of non-invasive brain stimulation typically positively influenced older adults' performance. With this in mind, assessing the effect of using non-invasive brain stimulation as a tool to improve older adults emotion perception seems an important avenue of investigation.

One form of tCS that might be particularly useful in the context of aging is the use of high-frequency tRNS, which can induce bilateral changes in cortical excitability. This is important because age-related neural functions are often associated with shifts from unilateral functional brain activation to bilateral activation. For instance, the compensation-related utilisation of neural circuits hypothesis (CRUNCH) suggests that older people shift from unilateral functional brain activation to bilateral activation to achieve similar performance output as younger people who might only use unilateral neural activation (Reuter-Lorenz & Cappell, 2008). Similarly, aging has been linked with hemispheric asymmetry reductions and the recruitment of compensatory mechanisms (e.g. the hemispheric asymmetry reduction in older adults model [HAROLD], Cabeza, 2002). In this context high frequency tRNS may be useful to increase compensatory potential by inducing greater bilateral functional brain activation.

Prior work also suggests that age-related declines in emotion perception are related to changes in perceptual strategies employed by old relative to young adults; for example, older adults tend to use perceptual information from upper parts of the face (e.g. eye region) less often and less efficiently (i.e. they are worse at detecting changes in this region) than young adult participants (Circelli et al., 2013; Murphy & Isaacowitz, 2010; Sullivan et al., 2007; Slessor et al., 2012; Chaby et al., 2011; Wong et al., 2005). This perceptual strategy of privileging information from lower parts of the face appears to predict patterns of change in older adult emotion perception (Wong et al., 2005; Mather, 2016). In this regard, it has been argued that older adults have weaker perceptual representations of emotions that typically rely more heavily on information from the top half of the face (e.g. fear, sadness, and anger; Mather, 2016). One way in which high frequency tRNS is thought to aid performance is via mechanisms of stochastic resonance, with random noise amplifying weak neural signals (e.g. Moss et al., 2004). With this in mind, tRNS may offer a useful intervention to amplify weak signals in brain regions associated with emotion processing in older adults.

One brain region commonly linked with emotion perception is the inferior frontal cortex. For instance, a number of meta-analyses point to the involvement of inferior frontal cortex during expressive face perception (e.g. Sabatinelli et al., 2011; Fusar-Poli et al., 2009). Of particular interest in the context of aging is that activation within inferior frontal cortex has commonly been linked with the perception of facial emotions that older adults show impairments in perceiving (e.g. fear, sadness, and anger; Fusar-Poli et al., 2009; Fischer et al., 2010). Indeed in the meta-analysis by Fusar-Poli and colleagues (2009) it was found that bilateral inferior frontal cortex activity was most prominently associated with processing anger perception (typically impaired in aging). With this in mind, the inferior frontal cortex is a particularly interesting target region to assess whether high frequency tRNS could improve the emotion perception.

When investigating the utility of non-invasive brain stimulation for improvement, it is also important to consider individual variation within the target cohort and how this might interact with stimulation effects. One key feature that can interact with the effects of brain stimulation is baseline performance (e.g. Feurra et al., 2013; Hsu et al., 2015; Tseng et al., 2012). This is particularly important in aging research, since a number of studies point to differences in the functional brain networks recruited between high and low performing older adults (Cabeza et al., 2002, Reuter-Lorenz & Cappell, 2008). For example, in the context of face processing it has been shown that high performing older adults show activation in compensatory brain networks (i.e. different brain networks) when compared to young adults and when compared to low-performing older adults (Lee et al., 2011). These findings are often interpreted with the suggestion that low-performing older adults recruit similar brain networks as young adults but in an inefficient manner, whereas high-performing older adults show greater plastic reorganization of neurocognitive networks (and therefore compensate for deficiencies associated with typical aging; Cabeza et al., 2002, Reuter-Lorenz & Cappell, 2008). This highlights an important consideration for non-invasive brain stimulation studies since identifying a target brain region based on young adult or low-performing older adult brain networks may lead to differential patterns of behavioural change in low-performing versus high-performing older adults (i.e. low performing older adults may benefit from stimulating brain regions that younger adults use, but high performing older adults may benefit from stimulating a compensatory brain network).

5.1.1 Summary of Experiment 3

To my knowledge no studies to date have examined a) if high-frequency tRNS can modulate emotion perception or b) if any effect can differ across older adults depending on baseline performance (i.e. high versus low performing older adults). With this in mind, this study sought to examine whether high-frequency tRNS targeted at the inferior frontal cortex could modluate older adults' abilities to perceive facial emotion (anger and happiness perception) and facial identity. I also assessed the extent to which any changes in performance following stimulation would be influenced by pre-stimulation (i.e. baseline) perceptual abilities. Based on prior work highlighting the involvement of bilateral inferior frontal cortex activity in anger perception (Fusar-Poli et al., 2009) and work suggesting that low-performing older adults tend to recruit similar brain networks as young adult participants (but high performing older adults tend to recruit compensatory brain networks) I predicted a specific improvement in low-performing older adults in anger perception.

5.2 Methods

Participants

Thirty-two healthy older adult volunteers (mean age = 70 years, SE = 3 years; fourteen males) participated in this study. Participants were randomly assigned to the active high frequency tRNS (n = 16, mean age = 69 years, SE = 2 years; eight males) or sham stimulation (n = 16, mean age = 71 years, SE = 2 years; six males) groups.

Participants were recruited from the community using fliers in, for example, retirement communities or senior citizen centers. All participants were native-English Caucasians, with normal or corrected-to-normal vision, with no known history of neurological problems, dyslexia or other language-related problems. Information on handedness, education level, and National Adult Reading Test (NART) score (Nelson and Willison, 1991) were obtained and recorded from each subject. All participants were asked to complete mini-mental state examination (MMSE) (Folstein et al., 1975) to evaluate mental states, and none of them scored lower than 24. Informed consent from all participants were obtained prior to beginning the experiment who were fully informed about the experimental procedure. The experimental protocol was approved by the Ethics Committee of Goldsmiths (University of London).

Equipment and procedure

Participants completed three tests before and after tRNS. The tests were the Cambridge Face Perception Angry (CFPT-Angry; Janik et al., 2015), Cambridge Face Perception Happy (CFPT-Happy) and the Cambridge Face Perception Identity (CFPT-Identity; Duchaine et al., 2007a, 2007b) tests (Figure 1). All participants completed the tasks before stimulation to measure their baseline performance and after stimulation to measure post-stimulation performance change. The order of the tasks (both pre- and post- stimulation) was randomised and counterbalanced for each subject. The approximate completion time for all tests was 30 minutes, after which they received 20 minutes of brain stimulation (see details below), followed by the post-stimulation tests. Details of each test and the brain stimulation parameters can be found below.

CFPT-Angry

In the CFPT-Angry participants were presented six faces (from a frontal view) morphed between the expression of 'anger' and a 'neutral' expression in varying proportions (40%, 32%, 24%, 16%, 8%, 0%). All faces were of young adult participants and were adapted from the Radbound Facial Database (Langer et al., 2010). These six faces were presented simultaneously on the screen in fixed pseudo-random order. Memory demands are minimal in this task because faces are presented simultaneously; it is therefore an ideal measure to assess facial identity perceptual abilities. Participants were required to sort the faces according to how angry they appeared, from the face that looks least angry on the left to the face that looks most angry on the right. The time limit for each trial was 60 seconds, but participants could move on to the next trial earlier if they completed the trial before the time limit expired. Participants completed ten trials in total. Performance was measured using percentage of correct responses. Chance performance is 36%.

CFPT-Happy

In the CFPT-Happy task participants were presented six faces (from a frontal view) morphed between the expression of 'happiness' and a 'neutral' expression in varying proportions (15%, 12%, 9%, 6%, 3%, 0%; lower morphs were used than CFPT-Angry in order to avoid ceiling effects that commonly occur with happiness perception tasks). All faces were of young adult participants and were adapted from the Radbound Facial Database (Langer et al., 2010). The six faces were presented simultaneously on the screen in a fixed pseudo-random order. Memory demands are minimal in this task because faces are presented simultaneously; it is therefore an ideal measure to assess facial identity perceptual abilities. Participants were required to sort the faces according to how happy they appeared, from the face that looks least happy on the left to the face that looks most happy on the right. The time limit for each trial was 60 seconds, but participants could move on to the next trial earlier if they completed the trial before the time limit expired. Participants completed ten trials in total. Performance was measured using percentage of correct responses. Chance performance is 36%.

CFPT-Identity

To investigate facial identity perception the CFPT-Identity was used in the experiment (previously called CFPT; Duchaine et al., 2007a, 2007b). This test assessed participants' ability to perceive differences between facial identities. During the task, participants were shown a target face (from a 3⁄4 viewpoint) and six faces (from a frontal view) morphed between the target and a distractor face (six unique distractors per target) in varying proportions (88%, 76%, 64%, 52%, 40%, 28%) so that they vary systematically in their similarity to the target face. All faces stimuli used were young adults. In each trial, participants were asked to sort the six faces by similarity to the target face within 60 seconds. If the participant completed the trial before the end of the one-minute time window they had the option to click on a button to begin the next trial (i.e. the task was self-paced). Memory demands are minimal in this task because faces are presented simultaneously; it is therefore an ideal measure to assess facial identity perceptual abilities. Normally, the CFPT contains, eight upright and eight inverted trials that alternated in a fixed pseudo-random order (Duchaine at al., 2007a, 2007b), but for the purpose the present study eight upright trials were completed (i.e. there were no inverted trials). Performance was measured using percentage of correct responses. Chance performance is 36%.

a.

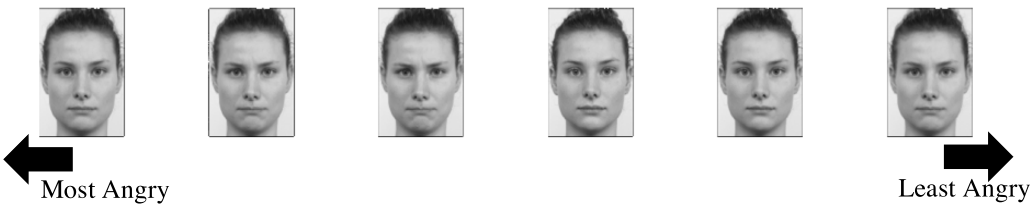


Figure 5.1. (a) Example trial of the CFPT-Angry. Participants were displayed six faces containing varying levels of anger ranging from 0 to 40% on the screen in a random order. Participants were required to sort them from most angry to least angry.

b.

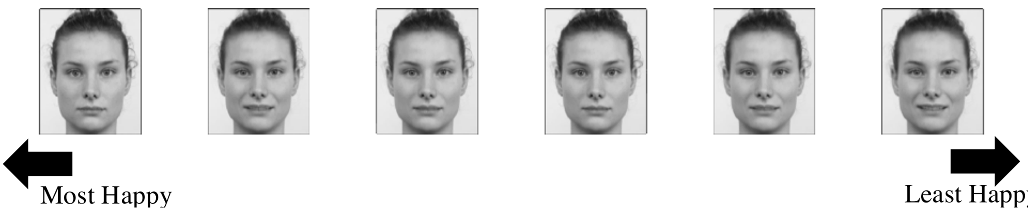


Figure 5.1. (b) Example trial of the CFPT-Happy. Participants were displayed six faces containing varying levels of happiness ranging from 0 to 15% on the screen in a random order. Participants were required to sort them from most happy to least happy.

c.

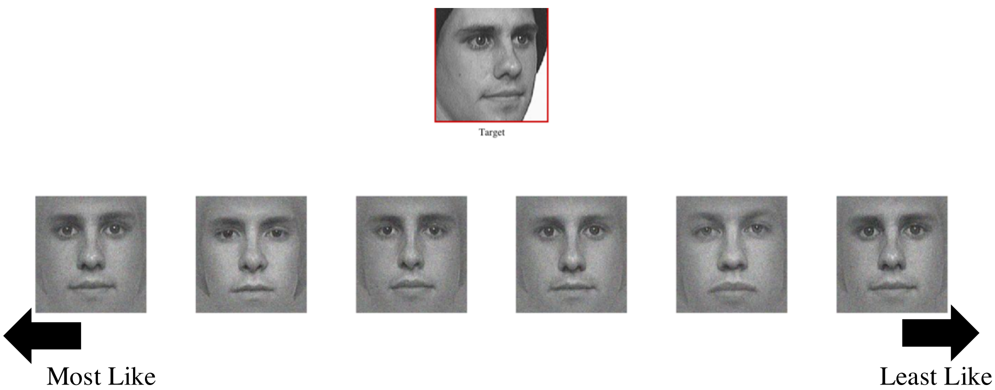


Figure 5.1. (c) Example trial of the CFPT-Identity. Participants were displayed a target face and six faces (from a frontal view) morphed between the target and distractor in varying proportions (88%, 76%, 64%, 52%, 40%, 28%). Participants were required to sort the six faces according to the degree of similarity to the target.

Brain stimulation parameters

Participants were randomly assigned to two groups for different stimulation conditions: active high frequency tRNS or sham stimulation. For each group, participants were seated in a comfortable chair, in front of a computer screen and a keyboard. In the active high frequency tRNS group 20-minute of brain stimulation was administered using a pair of saline-soaked surface sponge electrodes and a battery- driven, programmable, constant current DC-Stimulator (neuroConn). The stimulation electrodes were placed over both sides of the inferior frontal cortex, which has been previously identified as F7 and F8 (international 10–20 system for electrode placement sites; Towle et al., 1993). The size of both stimulation electrodes were 5 × 5 cm and they were fixed by rubber straps. High frequency tRNS (100-640 Hz) was applied for 20-minutes with a current strength of 1000 μA, 15s fade in/out. For sham stimulation the current was applied for 5s with a 15s fade in/out. This length of stimulation does not lead to changes in cortical excitability beyond the period of stimulation. It has been shown that participants cannot distinguish between active and sham stimulation (Ambrus et al., 2011). During the 20-minute brain stimulation, all participants were shown a neutral video to ensure consistency of personal activity during stimulation and to reduce boredom before continuing to the next stage of the experiment. Participants were blind to the stimulation group that they were assigned to.

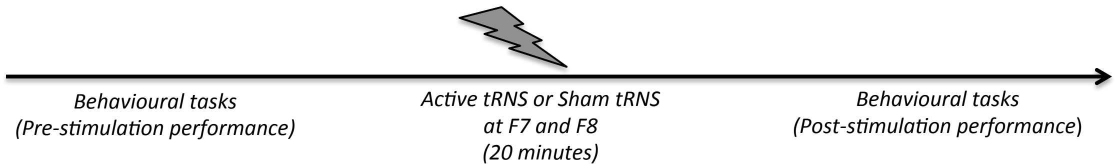


Figure 5.2. Experimental procedures. All participants were required to complete all three behavioural tasks (CFPT-Anger, CFPT-Happiness, and CFPT-Identity) in a randomised and counterbalanced order, then participants received 20 min of active or sham high-frequency tRNS targeted at F7 and F8 prior to completing the same tasks (CFPT-Anger, CFPT-Happiness, and CFPT-Identity) in a randomised and counterbalanced order.

5.3 Analysis and Results

Preliminary analyses and baseline characteristics

Prior to the statistical analysis, two participants (one from the Sham Group and one from the Active tRNS Group) were identified as outliers (using a criteria of > 3 standard deviations from the mean on any individual variable of interest; and significance using Grubb's Test). Following removal of these outliers the mean age of Sham and Active tRNS Groups still did not significantly differ from each other (Active-tRNS: mean = 68 years, SE = 2 years; Sham: mean = 71 years, SE = 2 years). Handedness, level of education (Active-tRNS: mean = 14 years, SE = 1 year; Sham: mean = 15 years, SE = 1 year), and NART scores (Active-tRNS: mean = 118, SE = 3.80; Sham: mean =121, SE =1.56) of two groups were matched between two groups. Baseline performance on the three face perception tasks (happiness, anger and facial identity perception) also did not significantly differ between two groups [happiness baseline t = .465 p = .645; anger baseline t = .013, p = .990; identity baseline t = 1.18 p = .250].

Performance differences following tRNS

To examine the extent to which performance on each task was modulated by active or sham tRNS a performance change score was calculated by subtracting performance following tRNS (active or sham) from baseline performance (i.e. performance before stimulation). This provides a measure of the degree of change in performance following stimulation with positive values indicating an improvement in performance and negative values indicating a reduction in performance. To compare whether the degree of change following stimulation differed between Active and Sham tRNS groups across each task (happy, anger, identity) a series of planned Bonferroni corrected paired comparisons were conducted. This revealed that for anger perception participants in the Active tRNS group showed larger gains in performance than participants in the Sham tRNS group [$t(28) = 3.18$, $p = .012$ (Bonferroni corrected)]. This pattern of results was not found for happiness perception [$t(28) = .181$, $p = .858$] or identity perception [$t(28) = 1.95$, $p = .183$ (Bonferroni corrected)] where no significant differences were observed (Figure 5.3).

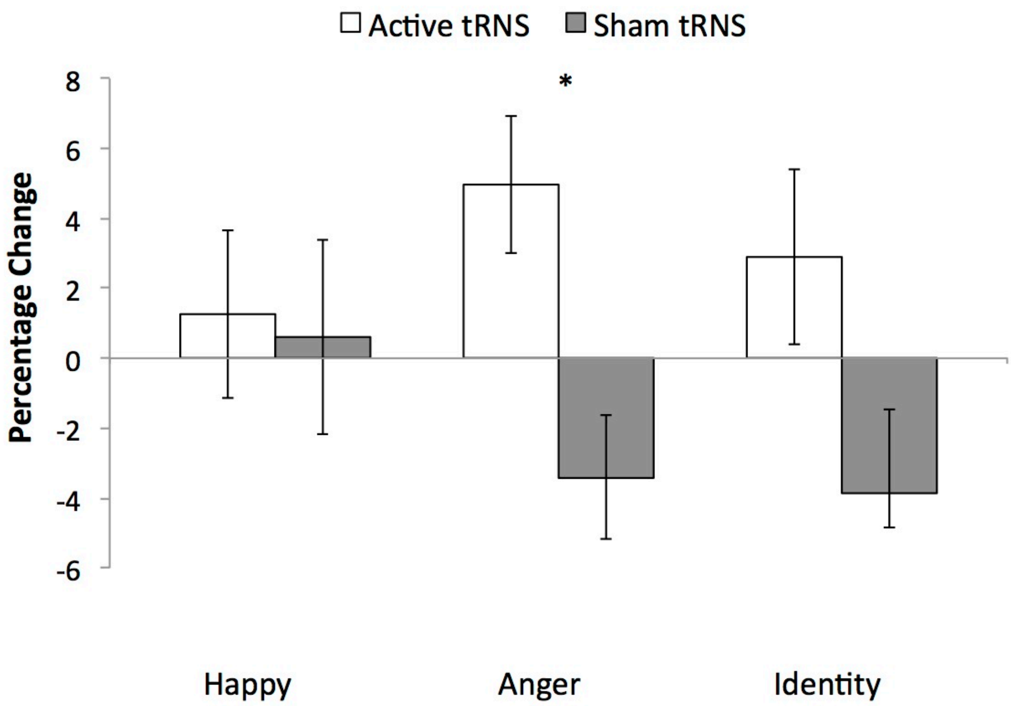


Figure 5.3. Comparison of degree of change following Active (bars in white) and Sham (bars in grey) tRNS across each task (happy, anger, identity).

Given that prior work has linked the efficacy of brain stimulation effects to baseline performance I next sought to examine the extent to which performance in the pre stimulation test was related to performance change following stimulation on the anger perception task. To do so I correlated pre-tests scores with performance change for the Active tRNS and Sham tRNS groups separately. This revealed that for the Active tRNS Group there was a significant negative relationship between pre-test performance and performance change following stimulation [$r = -.572, p = .026$], indicative of lower performance in the pre-test being associated with larger performance gains following active tRNS (Figure 5.4a). This pattern was not observed for the Sham tRNS group, where no significant relationship was found between pre-test performance and performance change scores [$r = -.052, p = .854$] (Figure 5.4b). Similarly, no significant relationship was observed between pre-test performance and performance change scores for either the active tRNS or sham stimulation group on the CFPT-Happy or CFPT-Identity (i.e. happiness pre-test performance did not significantly relate to performance change in happiness perception [Active tRNS Group – $r = -.085, p = .764$; Sham Group – $r = -.297, p = .282$]; identity pre-test performance did not significantly relate to performance change in identity perception [Active tRNS Group – $r = -.282, p = .309$; Sham Group – $r = -.034, p = .906$]).

Simple linear regression indicated that pre-test performance was a significant predictor of performance change following stimulation in the Active tRNS Group [$\beta = -.572, t = 2.51; F (1, 14) = 6.31, p =.026;$ *Adjusted R Square* $= .275$]. In addition to baseline performance, prior work has suggested that brain stimulation effects may be influenced by gender (e.g. Chaieb et al., 2008; Lapenta et al., 2012; Russell et al., 2014). Adding gender (male = 0, female = 1) as secondary predictor in a hierarchical regression model alongside pre-test performance significantly improved the model [$F (1, 12) = 9.30, p = .013$; *Adjusted R Square* $= .542$]], with both pre-test performance [$\beta = -.674, t = 3.66, p = .003$] and gender [$\beta = .540, t = 2.93, p = .013$] acting as significant predictors of performance change in anger perception following stimulation in the Active tRNS Group only. Participants' predicted *Improvement in Performance (Anger)* is equal to 23.2% - 35.5% × *[Baseline Performance (Anger)]* + 7.9% × *[Gender of Participants]*, where Gender of Participants is coded or measured as female =1 and male =0.

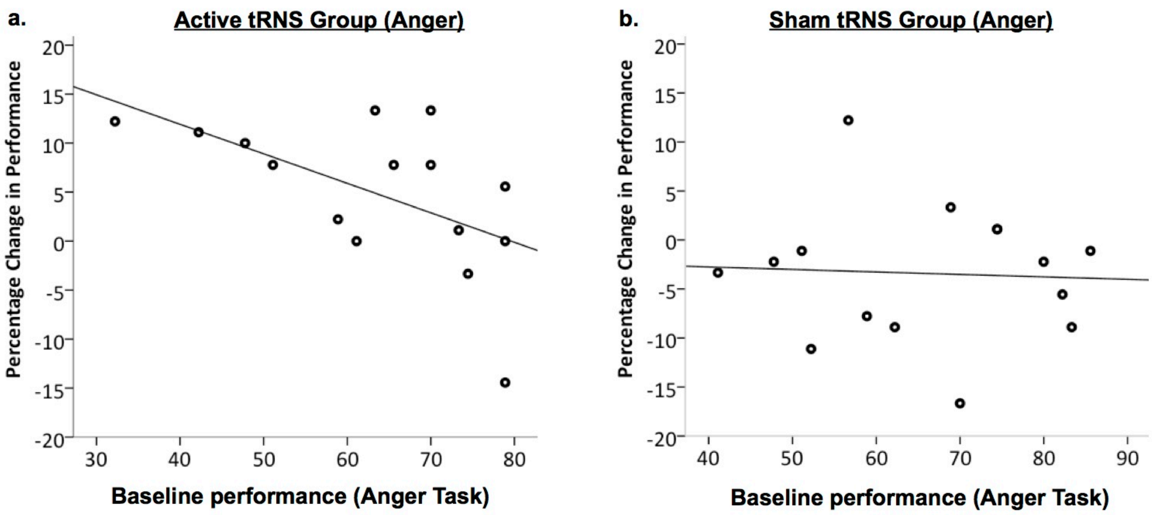


Figure 5.4. Relationship between baseline performance and performance change following stimulation in Anger task. (a) For the Active tRNS Group there was a significant negative relationship between pre-test performance and performance change following stimulation. (b) This pattern was not observed for the Sham tRNS group.

5.4 Discussion

The aim of the present study was to investigate whether high-frequency tRNS targeted at the inferior frontal cortex would enhance older adults' ability to process facial emotion, and in doing so explore the importance of the inferior frontal cortex in older adults' emotion perception. Facial emotion perception (happiness and anger perception) and facial identity perception were assessed before and after active or sham tRNS targeted at the inferior frontal cortex. The results showed that there was a significant improvement for anger perception following high-frequency tRNS relative to sham stimulation. In contrast, the same tRNS paramters did not significantly change the ability to perceive facial identity or happiness. These results indicate that tRNS targeted at inferior frontal cortex enhanced older adults' ability to detect fine grained changes in the expression of anger, and add strength to previous proposals suggesting that the inferior frontal cortex is particularly sensitive to processing anger rather than positive (happiness) emotions (Fusar-Poli et al., 2009).

By providing evidence confirming a link between inferior frontal cortex activity and anger perception in older adult participants, the neuromodulatory approach adopted in the current study could provide avenues for the development of novel approaches to intervention aimed at overcoming age-related declines in anger perception. In this context it important to be aware of factors that might interact with stimulation efficacy. In addition to showing group level differences between active and sham tRNS targeted at inferior frontal cortex on anger perception, the results also showed that the degree of improvement in anger perception displayed by older adults receiving active tRNS to inferior frontal cortex was influenced by both baseline ability (i.e. pretest score) and gender. This pattern was not observed in the sham stimulation group. It was also not found for facial happiness or facial identity perception. Recent findings show that the effects of noninvasive brain stimulation are to some degree dependent on individual differences in susceptibility (e.g. modulation by gender - Chaieb et al., 2008; Lapenta et al., 2012; Russell et al., 2014; modulation by performance variability – Hsu et al., 2015; Krause & Cohen-Kadosh, 2014; Sarkar et al., 2014; Tseng et al., 2012). In line with this, the present pattern of results show that baseline ability was related to degree of change in anger perception following active tRNS; with decreased baseline ability being linked to increased gain following active tRNS. Models of the interaction between aging and performance suggest that low-performing older adults recruit similar brain networks as young adults but in an inefficient manner, whereas high-performing older adults show greater reorganization of neurocognitive networks leading greater compensation (Cabeza et al., 2002; Reuter-Lorenz and Cappell, 2008). In the context of the findings reported here one might speculate that high-performing older adults have successfully applied compensatory strategies and recruited additional neural regions, leading to stimulation being less likely to induce additional benefits. In contrast, low-performing older adults (i.e. those that are inefficient in recruiting additional neural regions) have a greater capacity for stimulation to induce additional benefits.

To our knowledge, no studies have examined the relationship between inter-individual variability in baseline ability and performance change in emotion perception following tRNS in older adult participants. In other domains, there is some evidence for a similar pattern of data to our own. For example, using fMRI in conjunction with transcranial magnetic stimulation (TMS; a different type of non-invasive brain stimulation) to study memory, Solé-Padullés et al. (2006) found that TMS modulates low performing older adults' neural activation patterns (from unilateral to bilateral neural activation), and this change coincides with significant improvements in memory performance. The present finding (and findings of prior work in other domains using other forms of brain stimuation, e.g. TMS; Solé-Padullés et al. 2006; Hsu et al., 2015) suggests that future brain stimulation studies with older adult participants should measure and examine the impact of baseline performance on stimulation efficacy. An additional broader implication of this is that prior studies that found little or small brain stimulation effects in older adults might have been related to the possible recruitment of high performing older adults who have a relatively small capacity for cognitive improvement, which could potentially mask the effect of noninvasive stimulation on lower performing individuals. In future studies there is a need to further clarify the relationship between the effect of brain stimulation and different levels of ability, and the underlying neural compensation mechanisms.

The relationship between gender and change performance in anger perception following active tRNS is consistent with prior work that has shown that gender can influence performance change following tCS (Chaieb et al., 2008; Lapenta et al., 2012; Russell et al., 2014). This has commonly been interpreted in two ways: 1) hormonal differences (Chaieb et al., 2008; Lapenta et al., 2012) or 2) differences in brain structure (cranial bone density differences between males and females; Russell et al., 2014). To date work assessing how gender influences the efficacy of tCS has been focused on young / middle-aged adults[1], therefore future studies will need to assess whether and how gender is likely to act as a moderator of performance change following non-invasive brain stimulation in older adults.

While our findings highlight the importance of stimulation targeted at the inferior frontal cortex in anger perception, it is important to note that it cannot be fully concluded that the improvement on anger perception was only due to the after-effect of stimulating this region, as there is evidence showing that noninvasive transcranial brain stimulation can spread to surrounding neural regions of the targeted stimulation regions (Zheng et al., 2011; Summers et al., 2016). The role of the inferior frontal cortex in processing negative emotions and its inter-connection with other brain regions involved in emotion perception (e.g. amygdala, Nomura et al., 2004; Nakamura et al., 1999; Narumoto et al., 2000) during aging is not clear. To investigate these questions, future studies will need to combine brain stimulation with brain imaging techniques (e.g. EEG, fMRI) to reveal more about network dynamics underlying changes in emotion processing following stimulation of inferior frontal cortex. This will help to discover principles of connectivity between other emotion-related regions and the effect of normal aging on neural connectivity. This would also permit a better

[1] The mean age from Russell et al. (2014) was 53 years for males [range 34-68 years] and 50.5 years [range 21-75 years] for females, however this was tested on 12 males and 12 females thus testing on a larger sample of older adult participants is required.

understanding of the interaction between brain stimulation and neural networks involved in emotion processing (see Luft et al., 2014 for a similar discussion). Further, it will be important for future work to assess the extent to which performance change in emotion perception following stimulation to inferior frontal cortex extends to other emotions that were not tested in the current study (e.g. fear, sadness), and to other emotion processing tasks (e.g. emotion discrimination; tasks involving the older adult rather than younger adult target faces). In addition, one limitation involved in the present study is the lack of control stimulation site. It is not fully confirmed that the aftereffect is purely due to the stimulation targeted on the IFG site, or whether it is a general stimulation effect. Therefore, it would be beneficial to have a follow-up study that includes a control stimulation site (e.g. motor cortex).

As only tested older adult participants were tested in the current investigation it remains important for future work to consider whether the pattern of effects is specific to older adults or evident across different age groups. Prior brain imaging work suggests that the IFC plays a role in younger and older adult emotion perception (Sabatinelli et al., 2011; Fusar-Poli et al., 2009). In this regard, one may expect a similar pattern of results, but whether the effects would be specific to anger versus other emotional cues and perceptual abilities remains unclear. Younger adults tend to outperform older adults in emotion perception, but this can vary according to the emotion type. Anger, sadness, and fear emotions are regularly found to be impaired but that others remain spared (e.g. disgust perception; Ruffman et al. 2008). The reasons for why these emotions are impaired, but the others tend to be spared are unclear. Commonly functions that are spared from decline in aging can be related to activity in different neural correlates to younger adults (Cabeza et al., 2002; Reuter-Lorenz and Cappell, 2008). Given that the responsiveness to brain stimulation can vary according to a number of these effects (e.g. targeted brain region, age, baseline ability) then one may expect some degree of difference in the pattern of results depending on age group. This remains an important question for future investigation.

5.5 Summary

In experiment 3, I assessed the impact of high-frequency tRNS targeted at the inferior frontal cortex on older adults' facial emotion and facial identity perception abilities. I find that high-frequency tRNS targeted at the inferior frontal cortex improved anger perception in older adults, but that the degree of improvement was influenced by baseline ability and gender. In contrast, the same tRNS stimulation did not significantly change the performance on happiness perception or identity perception. The finding highlights high frequency tRNS as a potential tool to aid facial emotion perception in typical aging, but that there are gender and performance specific moderators of this effect that should be considered prior to application.

CHAPTER 6: INVESTIGATION OF EVENT-RELATED POTENTIALS (ERPS) DURING EMOTION PROCESSING

Chapter 2 and chapter 3 have shown that older participants have significantly declined behavioural performance in recognising low intensity happiness (only with older faces) and anger facial emotions. However, the underlying neural correlates of emotion processing in older participants are still unclear from these behavioural investigations. This chapter will record and compare event-related potentials (ERPs) from older and younger participants to investigate age-related neural activation patterns during emotion processing of neutral, anger and happiness facial emotions. In doing so, this chapter will try to provide a novel insights into age-related changes in emotion recognition by using behavioural and EEG measures, and investigating how 'face stimuli age' and different 'emotional intensities' affect both younger and older participants' behavioural performance and neural activations.

6.1 Introduction

Previous functional brain imaging studies have found that older participants exhibit a different neural activation pattern from younger participants during emotion recognition (e.g. Gunning-Dixon, Gur, & Perkins, 2003; Tessitore, Hariri, and Fera et al., 2005). Generally, older people tend to recruit more frontal cortical regions to compensate their lower subcortical neural activations when compared to younger people during emotion processing. For example, Gunning-Dixon, Gur, & Perkins (2003) investigated age-related neural activations in cortical and limbic regions using fMRI by presenting facial displays of a mixture of mostly negative emotions to both young and older participants. In the emotion-discrimination task, younger participants activated the amygdala and surrounding temporo-limbic regions, whereas older participants activated left frontal regions. Tessitore, Hariri, and

Fera et al.'s (2005) compared older and younger subject's neural processing of fearful and threatening stimuli using fMRI and found older participants were associated with increased prefrontal cortical neural responses, including Broca's area and left medial prefrontal cortex; and significantly lower neural responses in the amygdala and posterior fusiform gyri. In addition, my brain stimulation study illustrated in chapter 5 has shown that high-frequency transcranial random noise stimulation (tRNS) targeted at bilateral inferior frontal gyrus significantly enhanced older adults' perception of anger.

These previous studies have uncovered some important points of age-related neural mechanism of emotion processing. However, several limitations apply to these neuroimaging studies. Firstly, most neuroimaging studies only investigated facial displays of negative emotions in their studies (i.e. Tessitore, Hariri, and Fera et al., 2005; Fischer et al., 2010), few studies have compared the young-old neural activations during recognition of neutral and happiness emotions. Therefore, it is not entirely clear whether the age-related compensation pattern reflects older people's general emotion processing, or processing of negative emotions only (Fischer et al., 2005). Secondly, most previous neuroimaging studies have used fMRI to demonstrate the age-related neural activations during emotion perception tasks.

What are ERPs and what do they measure?

Although fMRI has excellent spatial resolution, the temporal resolution is relatively poor. Electroencephalography (EEG) has much better temporal resolution than fMRI and enables inference about the time course of emotional facial expression processing in human brain. ERP is a measurement of the postsynaptic potentials (PSPs) of neurons. PSP occur when "neurotransmitter bind the receptors, changing the flow of ions across the cell membrane" (Luck, 2014). When a PSP occurs within a single neuron, it creates a small electrical dipole.

Measurable ERPs can only be recorded when the dipole from many thousands of similarly oriented neurons sum together (Luck, 2014). Therefore, ERPs provide a direct and high temporal resolution measure of neurotransmission-mediated neural activity. The measurement of event-related brain potentials (ERPs) is most suitable for investigating the time course of the cortical responses during the encoding of affective pictures (Schupp et al., 2003). However, few studies have assessed healthy aged older adult participants' neuronal correlates of emotion processing using EEG (Wieser, 2006). The present study investigates age-related neutral activations during emotion processing by comparing healthy older and younger participants' ERPs.

ERP components involved in facial emotion processing

As discussed in chapter one, younger adults showed three major ERP components: firstly, an enhanced early frontocentral positivity was elicited in response to emotional as opposed to neutral faces within 120ms after stimulus presentation (Eimer and Holmes, 2002; Eimer, Holmes, and McGlone, 2003), followed by a broadly distributed sustained positivity beyond 250ms post-stimulus (Eimer and Holmes, 2002; Eimer, Holmes, and McGlone, 2003), and then followed by an enhanced negativity at lateral posterior sites (EPN) (Eimer, Holmes, and McGlone, 2003; Balconi, Pozzoli, and Possoli, 2003; Kisslerm Herbert, and Winkler et al., 2009). The early frontocentral positivity (within 120ms post-stimulus) and later broadly distributed positivity (beyond 250ms post-stimulus) were found very similar across different types of basic emotional expressions; in other words, these ERP positivities are not modulated by emotion type (Eimer et al., 2003, 2007). In addition, these emotional positivities are modulated by attention, as it was found that these positivities disappeared when attention was directed away from the faces (Eimer et al., 2003). These early and late emotion-related cortical positivities are not modulated by emotion type, and they reflect non-automatic and attentive processing of facial emotions, which is in contrast to the automatic and inattentive subcortical emotion processing (e.g. amygdala) (Eimer et al., 2003, 2007). Prior studies on negativity at lateral posterior sites (EPN) suggested that the amplitudes of the EPN were enhanced by emotional faces, as viewing threatening (Holmes et al., 2003; Schupp, Ohman, et al., 2004) and happy (Schacht & Sommer, 2009) faces elicited an enhanced EPN compared to neutral faces. However, the amplitudes of EPN did not vary between pleasant and unpleasant stimuli (Schupp et al., 2003). In addition, the EPN component was not modulated by different levels of attentional demands, as it was found that the EPN amplitudes remained consistent across a verity of viewing paradigms (e.g. passiving viewing, target detection). EPN only increases when the emotional intensity of facial stimuli increases (Schupp et al., 2003).

Up to now, few studies have investigated the whether the emotion-related ERPs are affected by advancing age. A recent ERP study (Wieser, Mühlberger, Kenntner-Mabiala, & Pauli, 2006) compared older and younger adults' ERPs during displaying facial expressions (neutral, positive and negative) and revealed that early EPN (168–232ms) was reduced in older adults compared to younger adults, but the late EPN (232–296ms) was not affected. However, some questions remain to be answered, such as whether other ERP components are affected by normal aging (e.g. early and late emotion-related positivities); and what are the effects of task difficulty and stimuli age in modulating these emotion-related components.

The effects of 'face stimuli age' and 'task difficulty' in facial emotion perception

In addition, perceptual biases may have influenced previous brain imaging results since most previous neuroimaging studies only used younger faces (Bäckman, 1991; Lamont, Stewart-Williams, & Podd, 2005). This may lead to the other-age effect influencing performance

(Chapter 1; Reuter-Lorenz and Cappell, 2008). Furthermore, another set of issues that have largely been ignored in most previous studies is the variation of emotional intensity, or task difficulty. In most neuroimaging studies, the facial emotion displays only contained high-intensity of emotions that are typically linked with high performance (i.e. ceiling levels of performance) have been used (this can potential mask differences in performance, as discussed and demonstrated in Chapters 2 and 3). This leads to two issues: 1) it is unknown how older people's perception of subtle/low-intensity facial expressions is linked with brain activity and 2) it is unclear how task difficulty interacts with age-related changes in brain function when completing emotion perception tasks.

In other domains, the relationship between task difficulty and age-related neural compensation has been described via the compensation-related utilization of neural circuits hypothesis (CRUNCH) model (Reuter-Lorenz and Cappell, 2008), which attempts to explain younger and older people's behavioural performance and neural activation patterns at low and high task demands and explained the possible underlying mechanisms. This model is based on the assumption that older people's processing inefficiencies cause the aging brain to recruit additional neural resources to achieve the similar output as younger brain. This compensatory strategy is effective at lower level of task demand. However, as task demand increases, when older people's neural resource ceiling is reached, it results in insufficient compensation and age-related behavioural performance decline. This aging compensation model has been supported by studies investigating other cognitive function, such as memory (Daselaar, Fleck, Dobbins, Mad- den, & Cabeza, 2006), language processing (Mattay et al., 2006; Cappell, Gmeindl, & Reuter-Lorenz, 2006; Martin, Joanette, and Monchi, 2015) and executive functioning (Martin, Joanette, and Monchi, 2015). However, to date no one has demonstrated this model in facial emotion perception in aged participants.

The aim of this study was to provide insights into older and young adults' ERPs and behavioral response during perceiving anger and happiness facial emotions with low- and high- emotional intensities. The present study will demonstrate the neural compensation hypothesis by comparing older and young people's neutral activation patterns at neutral (baseline), easy and hard conditions for anger and happiness emotion perception.

6.2 Methods

Participants

Participants consisted of sixteen younger participants (12 female and 4 male; mean age = 24 years, SD = 6 years) and fifteen older participants (12 female and 3 male; mean age = 69 years, SD = 9 years). All participants were native English speakers, with no known history of neurological problems, dyslexia or other language-related problems, and with normal or corrected- to-normal vision. Younger participants were recruited through the university's undergraduate participant pool, and older participants were recruited from local elderly community centres. All participants provided informed consent prior to beginning the experiment and were fully informed about the experimental procedure. The local ethics committee approved the study.

Level of education, premorbid intelligence (NART) (Nelson, 1991), handedness, Screening tests of working memory (digit span) (Turner & Ridsdale, 2004), Toronto Alexithymia Scale (TAS-20) (Bagby, Parker, & Taylor, 1994) were recorded at the beginning of experiments; the two groups did not significantly differ in these factors (details given in the Results section). The Mini-Mental State Examination (MMSE) was used as a screening evaluation to test older participants for possible dementia (Folstein, Folstein, & McHugh, 1975). The

MMSE appears to be the most widely used measure to screen for cognitive status. A cut-off limit of < 24 was used, which has a good sensitivity for dementia in the older population (Chayer, 2002). No participants were excluded from the study on the basis of this criterion. All participants gave informed consent prior to beginning the experiment and were fully informed about the experimental procedure. The local ethics committee approved the study. Demographic characteristics of the two samples can be seen in Table 6.1.

Table 6.1. Basic demographic and descriptive characteristics of the two study groups.

	***Old* (*n = 15*)**	***Young* (*n = 16*)**
Gender (male/female)	*3/12*	*4/12*
Age (years)	*69 (9)*	*24 (6)*
Education (years)	*15 (3)*	*16 (2)*
Handedness (right/left)	*14/1*	*15/1*
Premorbid IQ (NART)	*120.07 (8.430)*	*115.44 (10.295)*
Working memory (digit-span)	*105.27 (16.867)*	*106.63 (12.209)*
TAS-20 score	*43.00 (7.329)*	*44.75 (9.692)*

Experiment task

Participants were seated in a dimly lit, sound-attenuated room. A computer screen was placed at a viewing distance of approximately 50 cm. The task was presented on a PC using the MATLAB (The MathWorks, Inc., Natick, MA)-based toolbox Cogent 2000 (www.vislab.ucl.ac.uk/cogent.php). The faces were approximately 5 × 8 cm when displayed on a 17-in. monitor (screen size, 1,024 × 768 pixels) on a Dell computer.

The facial stimuli used in the experiment were created from FaceGen modeler software (www.facegen.com/products.htm) with no hair or facial hair to avoid gender cues other than facial structure and features. All images were three-dimensional, grey scale, front profile Caucasian faces. Thirty young (18 – 40 years; 15 male and 15 female) and thirty old (15 male and 15 female; 65+ years) faces were used in the task. Each identity displayed anger and happiness in low (30%, 15%), high (60%, 75%), and neutral (0%) intensities (see figure 6.1). Trials with low and high intensities correspond to hard and easy difficulty recognition levels. There were ten stimulus conditions in total, each condition comprised of 60 trials (neutral condition has 30 trials): *old face stimuli-anger-easy, old face stimuli-anger-hard, old face stimuli-happy-easy, old face stimuli-happy-hard, old face stimuli-neutral, young face stimuli-anger-easy, young face stimuli-anger-hard, young face stimuli-happy-easy, young face stimuli-happy-hard, young face stimuli-neutral.*

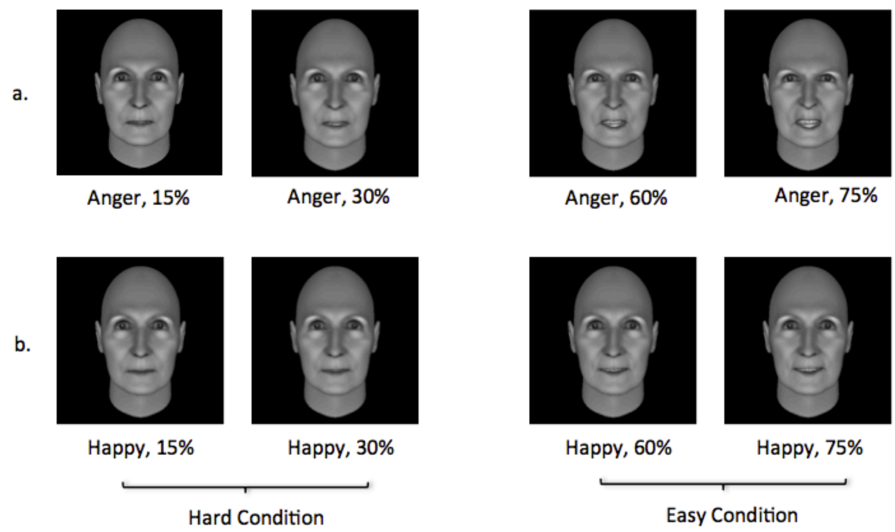


Figure 6.1. Example emotional facial stimuli of anger (a., upper graphs) and happiness (b., lower graphs) used in the experiment. Hard task conditions contain facial stimuli with lower emotional intensities (15% and 30%), and easy task conditions contain facial stimuli with higher emotional intensities (60% and 75%).

In each trial, facial stimuli were presented for 500ms, followed by a blank screen with a fixation cross for 500ms. A screen appeared to ask participants to provide a response, and the screen would not change until the participant's behavioral response. The interval between the response and presentation of subsequent stimulus was 1500ms (see figure 6.2). Participants were shown one facial stimuli at a time, in a randomized order on a black background. Participants were instructed to judge the facial expression they were presented in each trial and to respond as quickly and accurately as possible by pressing one of three buttons (neutral, anger, and happiness) on the response box. They were reminded that some facial expressions were quite subtle. Accuracy and reaction times (RTs) were recorded. Resting state EEG (3 minutes with eyes-open and eyes-closed) was recorded for each participant before the experiment was carried out. The resting state EEG was not analysed.

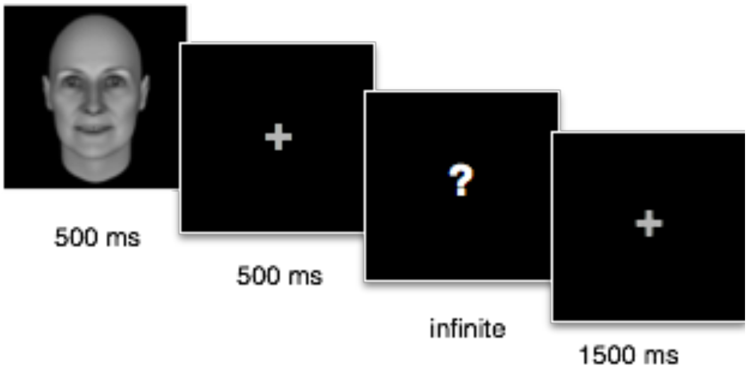


Figure 6.2. An example trial of the emotion perception task. In each trial, a facial stimulus was presented for 500 ms, followed by a blank screen with a fixation cross for 500ms, then followed by a screen that requires participants to provide a response (the screen would not change until the participant's behavioral response). The interval between the response and presentation of subsequent stimulus was 1500ms.

EEG Recording and Analysis

EEG was recorded with a sampling frequency of 512 Hz, band-pass filtered between 0.16 and 100 Hz by 64 active electrodes placed according to the extended 10–20 system of electrode placement and amplified by a BioSemi ActiveTwo amplifier (www.biosemi.com). The vertical and horizontal EOGs were recorded using four additional electrodes to monitor eye blinks and horizontal eye movements, where one pair of electrodes (see figure 6.3, positions

C and D) were used to record horizontal eye movements (HEOG) and a second pair of electrodes (see figure 6.3, positions A and B) were used to record vertical eye movements (VEOG). The EEG data were processed and analyzed using the following MATLAB- based toolboxes: EEGLAB (Delorme & Makeig, 2004) for data preprocessing and FieldTrip (Oostenveld, Fries, Maris, & Schoffelen, 2011) for data analysis and statistical comparisons.

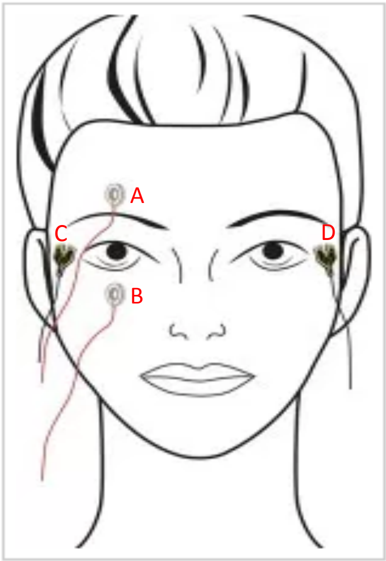


Figure 6.3. Electrode placement for recording horizontal (C and D) and vertical (A and B) EOG, respectively

Preprocessing

The EEG data were re-referenced to a common average reference for ERP analyses. The use of a common average reference has been recommended for ERPs (Picton et al., 2000; Pfurtscheller & Lopes da Silva, 1999) because it is a less biased method for comparing across scalp topographies. The data were high-pass filtered at 0.5 Hz and epoched from −1500ms before and 1500ms after the onset of stimuli. The artifacts were treated in a semi-automated fashion: visual inspection was initially done to remove large muscle artifacts, followed by an independent component analysis for correcting the eye blink-related artifacts. Subsequent to the eye blink correction, epochs containing amplitudes exceeding ±75μV were discarded for future analysis.

After artifact rejection, for the young group an average of 42 trials (SD = 8.04) and 43 trials (SD = 7.93) remained in the easy and hard anger conditions of older face stimuli; 43.19 trials (SD = 8.550) and 42.81 trials (SD = 6.26) remained in the easy and hard happy conditions of older face stimuli. In conditions of using young face as stimuli, the young group remained an average of 43.44 trials (SD = 7.60) and 42.25 trials (SD = 7.91) in the easy and hard anger conditions; 41.69 trials (SD = 9.25) and 41.31 trials (SD = 8.80) remained in the easy and hard happy conditions. For older group the analogous numbers were the following: 41.93 trials (SD = 11.93) and 41.80 trials (SD = 11.18) for easy and hard anger conditions of older face stimuli, respectively; 41.53 trials (SD = 12.40) and 41.53 trials (SD = 12.40) remained in the easy and hard happy conditions of older face stimuli. In conditions of using young face as stimuli, the old group remained an average of 40.47 trials (SD = 11.83) and 40.60 trials (SD = 11.62) in the easy and hard anger conditions; 42.20 trials (SD = 12.36) and 40.80 trials (SD = 12.39) remained in the easy and hard happy conditions.

ERP Analysis

For the ERP analysis, a low-pass filter at 35 Hz was applied, and the filtered epoch of 200ms before the onset of stimuli and 1 sec after the onset of stimuli were averaged over trials to obtain the ERP signals. The ERPs were baseline (–200 to 0 ms) subtracted.

Statistical Analysis

ERP experiments provide extremely rich data sets, to avoid the multiple comparison problems and to be able to effectively control the type I error rate, a non-parametric cluster-based permutation test was used for establishing the significance of the ERPs difference between group comparisons. Non-parametric cluster-based permutation test has been popular in analysing EEG/MEG multidimentional data and it has been successfully applied in EEG studies (Lindsen, Jones, Shimojo, & Bhattacharya, 2010; Sandkuhler & Bhattacharya, 2008; Luft, Takase, & Bhattacharya, 2014). It has the strength of combining "statistical significance with biological/cognitive significance"; the logic is as follows: "for an effect to be both statistically and biologically significant, it needs to be found over a cluster of data points in all analysed dimensions such as time and space (electrodes). An isolated significant difference found at a nonspecific data point would not be considered biologically relevant, therefore would not yield a significant cluster, even if it is highly significant statistically (i.e., $p < .00001$)" (Luft, Takase and Bhattacharya, 2014).

The method consists of finding clusters and then calculating the cluster statistics (Maris & Oostenveld, 2007). First, the multidimensional (time, amplitude and electrode) clusters were detected by grouping neighbouring data points that show a significant effect ($p < 0.05$) of condition in (paired or independent) t-tests, and a cluster-level statistic was calculated by summing the values of t statistics over the cluster (Luft, Takase and Bhattacharya, 2014; Lindsen, Jones, Shimojo & Bhattacharya, 2010). In the present study, electrodes with a distance of less than 5 cm are considered as neighbors, yielding on that significant data points were considered to be part of a cluster if at least four of its neighbours were also found to be significant. Second, Monte Carlo randomisation was used to identity the exact probability that a cluster with the maximum cluster-level statistic was observed under the assumption that the the EEG neural responses for the two compared conditions were not significantly different (Maris & Oostenveld, 2007). A histogram of maximum cluster-level statistics was collected by calculating the cluster-level statistic a great number of times (500 times in the present analysis) on random permutation of the pooled data of the two conditions; this histogram was subsequently used to calculate the p-value for that cluster, and these procedures were then carried out for the lower ranking cluster-level statistics (Lindsen, Jones, Shimojo & Bhattacharya, 2010).

In the present study, the cluster-based permutation to was used to find the main differences between the younger and older groups and to define the ROIs on the multidimensional space (time, electrode), which were subsequently analysed by standard ANOVA as appropriate.

6.3 Results

6.3.1 Behavioral Results

Prior to data analysis, accuracy and RT outliers were withdrawn from further analysis due to them being identified as outliers using Grubb's rule[2]. Participants' anger and happiness perceptual performance (accuracy and RTs) were analysed using 2 (emotion type) × 2 (task difficulty) × 2 (face stimuli age) × 2 (group) mixed ANOVAs with the between-participants factor of group (young and old), within-participants factor of emotion type (anger and happiness), face stimuli age (young and old) and another within-participants factor of task difficulty (easy and hard). Participants' neutral emotion perceptual performance (accuracy and RTs were analysed using 2 (face stimuli age) × 2 (group) mixed ANOVA with the between-participants factor of group (young and old) and within-participants factor of face stimuli age (young and old) was used to analyse the group performance difference on neutral recognition tasks.

Accuracy

[2] (accuracy: two outliers from *older face_neutral* condition, one outlier from *older face_anger_easy* condition, one outlier from *younger face_neutral* condition, one outlier from *younger face_anger_easy* condition, two outliers from *younger face_happy_easy* condition; no RT outliers were found).

Perception of neutral facial expression

For the recognition of neutral emotion tasks, the results revealed a trend for a group difference on the performance accuracy [$F\ (1, 26) = 4.195, p = .051, \eta^2 = .139$], which was due to older participants' higher accuracy on neutral trials compared to younger participants. No other significant main effect or interaction was found.

Perception of anger and happiness facial expressions

A 2 (emotion type) × 2 (task difficulty) × 2 (face stimuli age) × 2 (group) mixed ANOVAs on the accuracy rate of anger and happiness perception tasks revealed a main effect of group [$F\ (1, 26) = 30.357, p < .001, \eta^2 = .539$], which was due to younger adults' overall performance was significantly better than older adults. Main effect of task difficulty was also significant [$F\ (1, 26) = 381.512, p < .001, \eta^2 = .936$], which was due to the overall accuracy for easy tasks were significantly higher than hard tasks. Main effects of emotion type and face stimuli age were not significant.

The interaction of emotion × stimuli age was significant [$F\ (1, 26) = 24.495, p < .001, \eta^2 = .485$], which was due to in anger perceptual tasks, the overall accuracy for older face stimuli was significantly higher than younger face stimuli (anger: $p < .001; d = 1.699$); whereas in happiness perceptual tasks, the overall accuracy for younger face stimuli was significantly higher than older face stimuli (happiness: $p = .008, d = 1.441$, Bonferroni corrected).

The interaction of emotion × stimuli age × task difficulty was significant [$F\ (1, 26) = 15.085, p = .001, \eta^2 = .367$], which was due to in hard level of anger perceptual tasks, the overall accuracy for older face stimuli was significantly higher than younger face stimuli ($p < .001, d$

= *1.744*); whereas in hard level of happiness perceptual tasks, the overall accuracy for younger face stimuli was significantly higher than older face stimuli ($p < .001$, $d = 1.538$).

Interestingly, the interaction of emotion × stimuli age × task difficulty × group was significant [$F (1, 26) = 4.893$, $p = .036$, $\eta^2 = .158$]. Pairwise comparison (with Bonferroni correction) revealed that older group performed significantly poorer than younger group in both easy (old face stimuli condition: $p < .001$, $d = 1.608$; young face stimuli condition: $p < .001$, $d = 1.865$) and hard (old face stimuli condition: $p = .032$, $d = 1.203$; young face stimuli condition: $p = .008$, $d = 1.463$) anger conditions (figure 6.4). Older adults also performed significantly poorer in hard condition of happiness perception using younger face stimuli ($p = .008$, $d = 1.443$), but not in other conditions (figure 6.4). In addition, within-group comparison revealed that younger participants' performance on young and old face stimuli were significantly different in only hard level of anger and happiness perception tasks (anger: $p = .008$, $d = 1.438$; happiness: $p < .001$, $d = 1.512$), with superior performance on younger face stimuli in happiness perceptual tasks and superior performance on older face stimuli in anger perceptual tasks. In contrast, older participants' performances on younger and older face stimuli were not significantly different in both easy and hard levels of anger and happiness perception tasks.

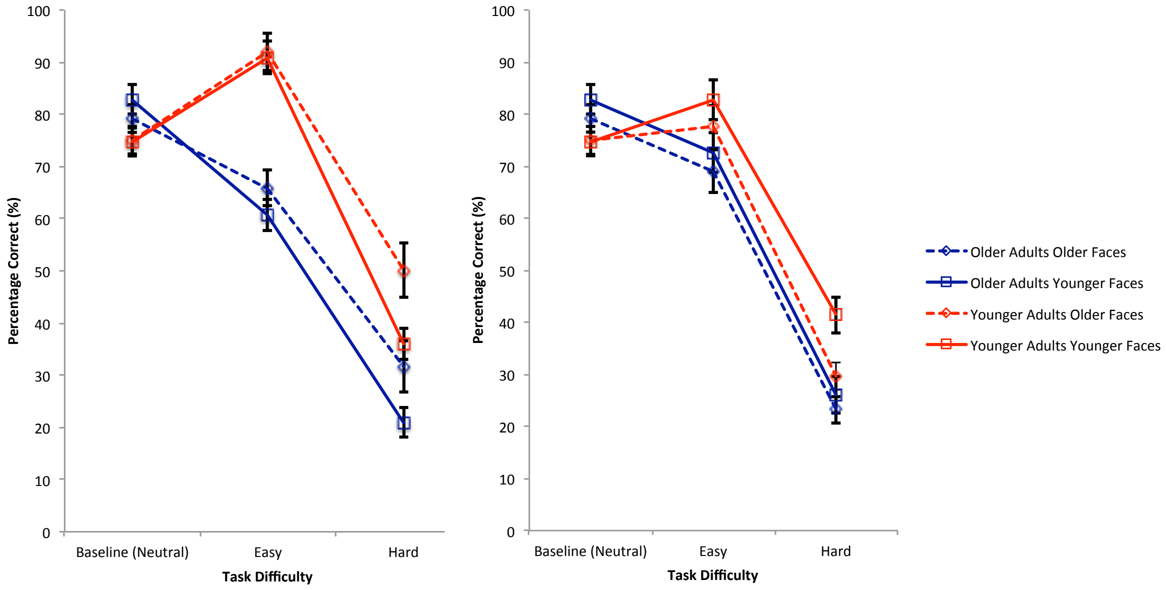


Figure 6.4. Older (lines in blue) and younger (lines in red) participants' perceptual performance (accuracy) in anger (left graph) and happiness (right graph) experimental trials at different task difficulties [neutral (baseline), easy and hard]. Straight lines represent trials with younger face stimuli, dotted lines represent trials with older face stimuli. Error bars represents S.E.

Reaction Times (RTs)

Perception of neutral facial expression

No significant group difference was found for the RTs on neutral perception trials, and there was no other significant main effects or interaction.

Perception of anger and happiness facial expressions

A 2 (emotion type) × 2 (task difficulty) × 2 (face stimuli age) × 2 (group) mixed ANOVAs on the RTs of anger and happiness perception tasks revealed significant main effect of difficulty [$F\ (1,\ 29) = 12.308,\ p = .001,\ \eta^2 = .298$], which was due to participants performing significantly faster in easy tasks compared to hard tasks (figure 6.5). Main effects of group, emotion type and stimuli age were not significant.

The interaction of stimuli age and difficulty was significant, which was due the RT of easy and hard conditions were significantly different in older face stimuli condition (*p* < *.001, d = 1.490*), but not in younger face stimuli condition.

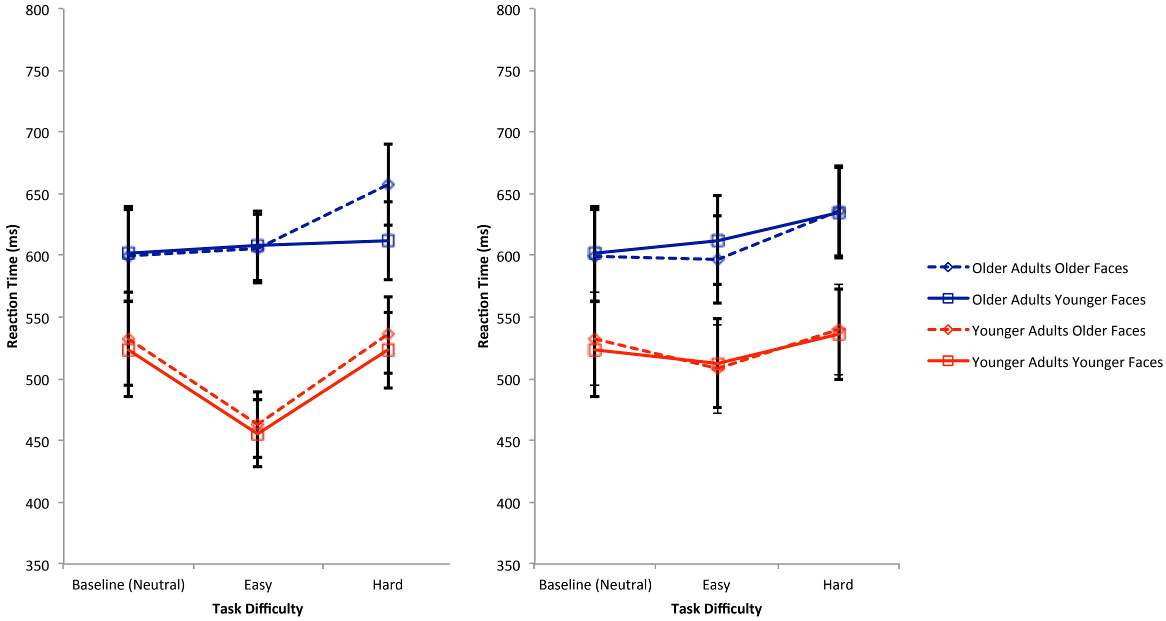


Figure 6.5. Older (lines in blue) and younger (lines in red) participants' RTs in anger (left graph) and happiness (right graph) experimental trials at different task difficulties [neutral (baseline), easy and hard]. Straight lines represent trials with younger face stimuli, dotted lines represent trials with older face stimuli. Error bars represents S.E.

Age-related emotion perceptual bias (from behavioural response results)

Given that older people showed significantly higher accuracy in the neutral emotion perceptual task, it is not certain if this reflects older people's actual ability to recognise 'neutral' facial emotions, or whether it could be due to age-related behavioual response preference in choosing 'neutral' emotion across all emotion perceptual tasks. To investigate this question, further analysis was performed to clarify the group difference in perceiving low- and high- intensities of emotions. Firstly, each participant's proportion of choosing 'neural' emotion for each type of emotion stimuli (anger and happiness with 15%, 30%, 60%, 75% intensities) were calculated, regardless of age of face stimuli. Then, a series of separate independent t-tests were performed between younger and older groups to investigate if there was a group difference in making 'neutral' responses across different emotion stimuli.

The results (see figure 6.6, left graph) showed that in low emotional intensity (15% and 30%) anger conditions, there was a trend that older adult participants were more likely to rate the emotion stimuli as neutral emotion compared to younger adult participants. In other words, older adult participants' mean proportion of making 'neutral' emotion response was higher than younger adult participants in both 15% and 30% anger conditions. [*15% anger*: older group: mean = 61.78%, SE = 4.31%; younger group: mean = 51.56%, SE = 4.46%; $t = 1.64$, $p = 0.111$; *30% anger*: older group: mean = 41.56%, SE = 4.57%; younger group: mean = 32.11%, SE = 4.30%; $t = 1.50$, $p = 0.144$]. In high emotional intensity (60%) anger condition, older adult participants showed significantly higher overall mean proportion (mean = 17.05%, SE = 3.91%) of making 'neutral' emotion responses compared to younger adult participants (mean = 5.45%, SE = 1.17%) ($t = 2.63$, $p = .015$). In another high emotional intensity (75%) anger condition, older adult participants (mean = 10.59%, SE = 2.52%) also showed greater overall mean proportion of choosing 'neutral' emotion than younger adult participants (mean = 5.57%, SE = 1.76%), the group difference was close to significance ($t = 1.87$, $p = .075$).

For happiness emotion (figure 6.6, right graph), older adult participants showed significantly higher overall mean proportion (mean = 56.43%, SE = 4.53%) in making 'neutral' emotion responses compared to younger adult participants in 30% emotion intensity condition (mean = 42.14%, SE = 4.55%) ($t = 2.22$, $p = .035$). For 75% and 15% happiness trials, older people (*15% happiness:* mean = 71.07%, SE =4.32%; *75% happiness:* mean = 16.34%, SE =3.66%) had higher chance of perceiving the stimuli as 'neutral' condition compared to younger adult participants (15% happiness: mean = 60.51%, SE = 4.03%; *75% happiness:* mean = 8.33%, SE =1.42%) (15% happiness: $t = 1.79$, $p = .086$; 75% happiness: $t = 1.98$, $p = .061$). However, for happiness trials with 60% emotion intensity, no group difference was found in making 'neutral' responses.

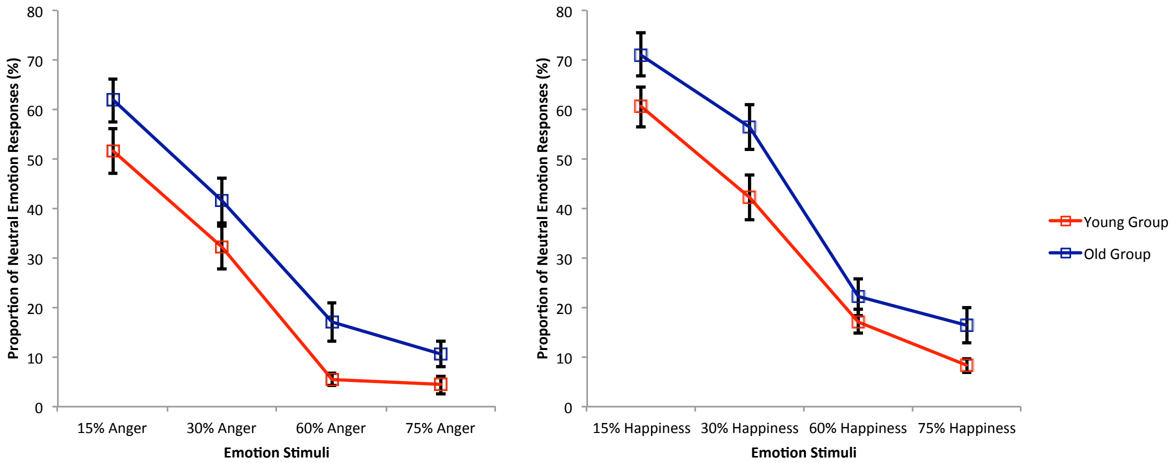


Figure 6.6. Older (lines in blue) and younger (lines in red) groups' overall mean proportion of making neutral emotion responses (%) on anger (left graph) and happiness (right graph) emotion trials with different emotional intensities (15%, 30%, 60%, and 75%).

6.3.2 ERP Analysis

Old-young group ERP cluster difference on each emotion condition

Firstly, older and younger participants' mean grand averaged ERPs on neutral task were used to define significant age-related ERP difference clusters (time windows and electrodes) by using the nonparametric cluster permutation tests (see figure 6.7 for results). Figure 6.7 (a) shows the topographies of the young-old ERPs differences over time on neutral emotion condition. For *neutral* condition, two clusters were found, the first cluster was a frontal cluster between 250–850ms and the second cluster was a left-frontal and centromedial cluster between 100-200ms [figure 6.7 (b)].

The neutral condition clusters (the electrodes and time windows) were chosen to extract the mean ERP amplitudes from other emotion conditions (all anger and happiness conditions) to permit further statistical analysis to test the effect of emotion type, task difficulty and facial stimuli age in modulating participants' ERPs. The neutral condition clusters were chosen as one important goal of the present study is to explore older adults' neural activity patterns from baseline to easy and hard emotion tasks in comparison to younger adults. The neutral condition can represent the baseline of each emotion type (anger, happiness) and therefore they are treated as default clusters[3].

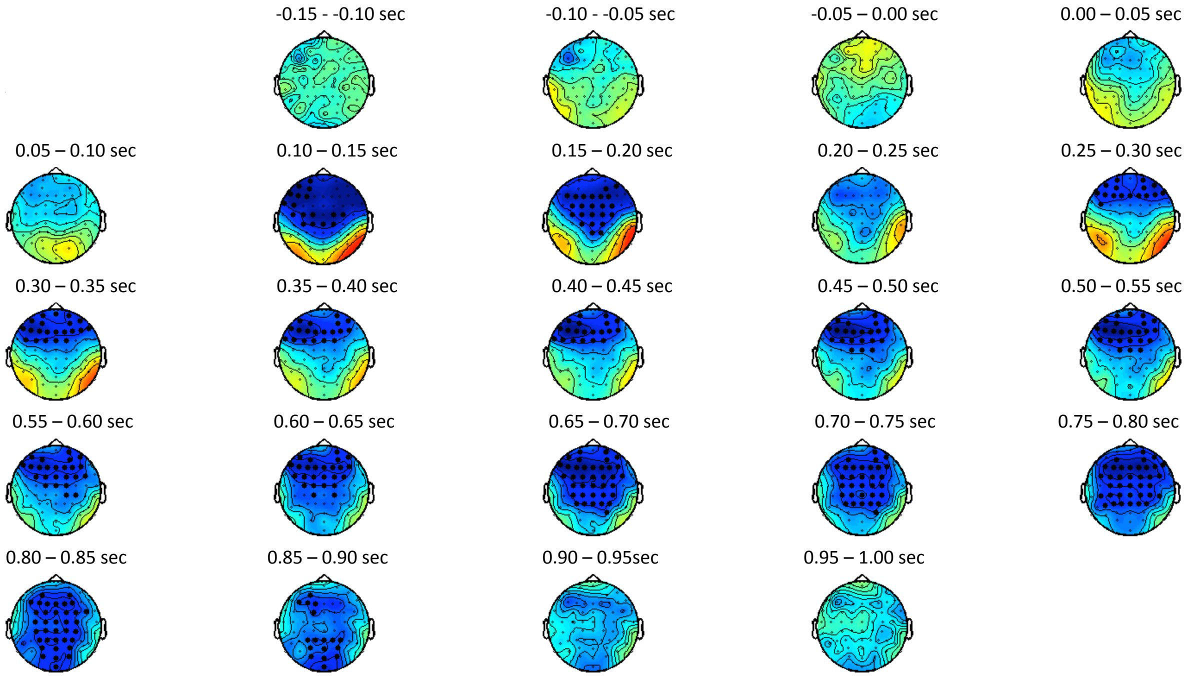
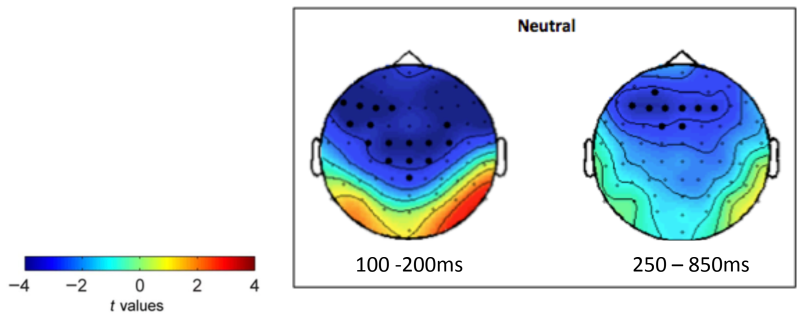


Figure 6.7. (a) shows the topographies of the young-old ERPs differences over time (on neutral condition).



3 Using group difference clusters (time window and electrode) on baseline condition (neutral emotion) to extract and analyse the ERPs of other emotion conditions can help to reveal the age-related compensatory neural pattern. However, this method has an important caveat as the emotion-specific neural differences between groups might be ignored. See *Discussion* for more details.

Figure 6.7. (b) Significant clusters of the nonparametric cluster randomization test comparing the two groups on neutral condition. First cluster: 100 – 200ms, left-frontal and centromedial area (F1, F3, F5, F7, Fc5, Fc5, C1, C3, Cp1, Pz, Cpz, Fc4, Cz, C2, C4); second cluster - time window: 250 – 850ms; frontal area (AF3 F1, F3, F5, Fc1, Fz, F2, F4, Fcz).

The effect of emotion, face stimuli age and task difficulty in modulating ERPs

Participants mean ERP amplitudes of two clusters (neutral emotion condition) were extracted from anger and happiness recognitions, separately. Then participants' mean ERP amplitudes for anger and happiness were analysed using 2 (emotion type) × 2 (task difficulty) × 2 (face stimuli age) × 2 (group) mixed ANOVAs with the between-participants factor of group (young and old), within-participants factor of emotion type (anger and happiness), face stimuli age (young and old) and another within-participants factor of task difficulty (easy and hard).

Cluster one

A 2 (emotion type) × 2 (task difficulty) × 2 (face stimuli age) × 2 (group) mixed ANOVAs on the left frontal and centromedial mean ERP amplitudes (100-200ms) of anger and happiness perception tasks revealed significant main effect of group [$F\ (1, 26) = 20.273,\ p < .001,\ \eta^2 = .438$], which was due to older participants exhibiting significantly higher overall mean ERP amplitudes than younger group (see figure 6.8 and figure 6.9). The main effect of task difficulty was also significant [$F\ (1, 26) = 4.974,\ p = .035,\ \eta^2 = .161$], which was due to easy condition (high-intensity facial expressions) eliciting significantly higher overall mean ERP amplitudes in left frontal and centromedial regions (100-200ms) than hard condition (low-intensity facial expression). Main effects of emotion and stimuli age were not significant.

The interaction of stimuli age × group was significant [$F\ (1, 26) = 5.775,\ p = .024,\ \eta^2 = .182$], pairwise comparison (with Bonferroni correction) revealed that older participants exhibited significantly higher mean ERP amplitudes in left frontal and centromedial regions (100-

200ms) than younger participants in both older and younger face stimuli conditions (older face stimuli, $p < .001, d = 1.764$; younger face stimuli, $p < .001, d = 1.583$) (see figure 6.8). The interaction of emotion type × difficulty was significant [$F\ (1, 26) = 6.632, p = .017, \eta^2 = .201$], pairwise comparison revealed that the mean left-frontal and centromedial ERP amplitude (100-200ms) of easy condition was significantly higher than hard condition in anger task ($p < .001, d = 1.537$) (see figure 6.8).

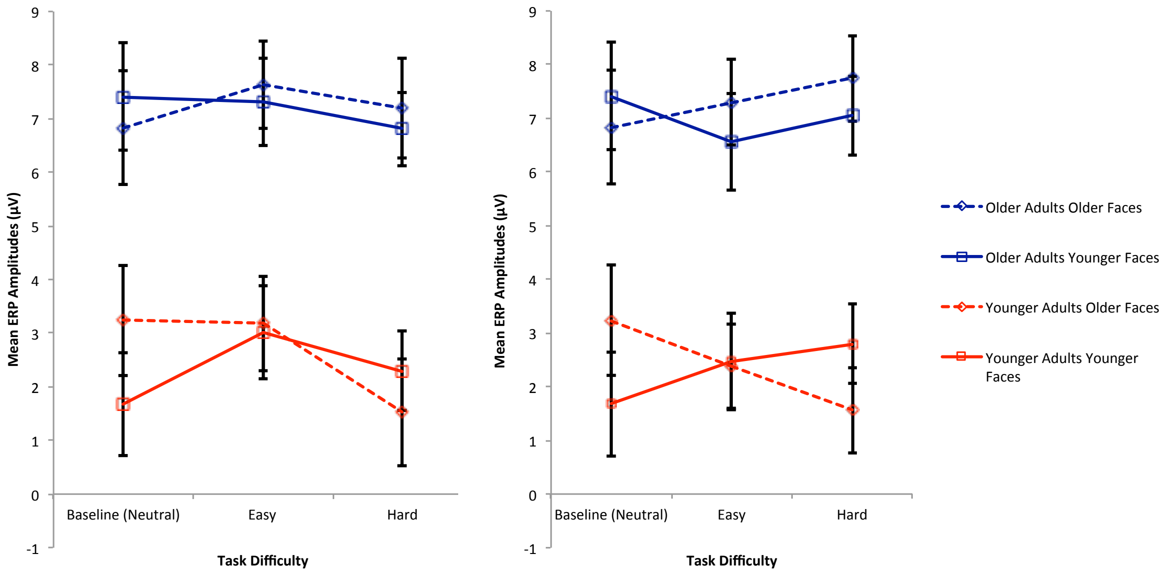
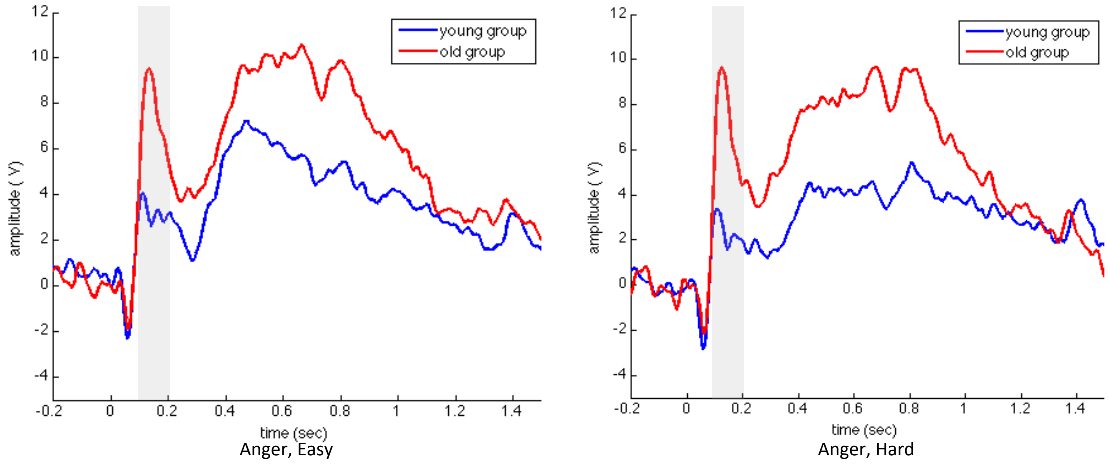
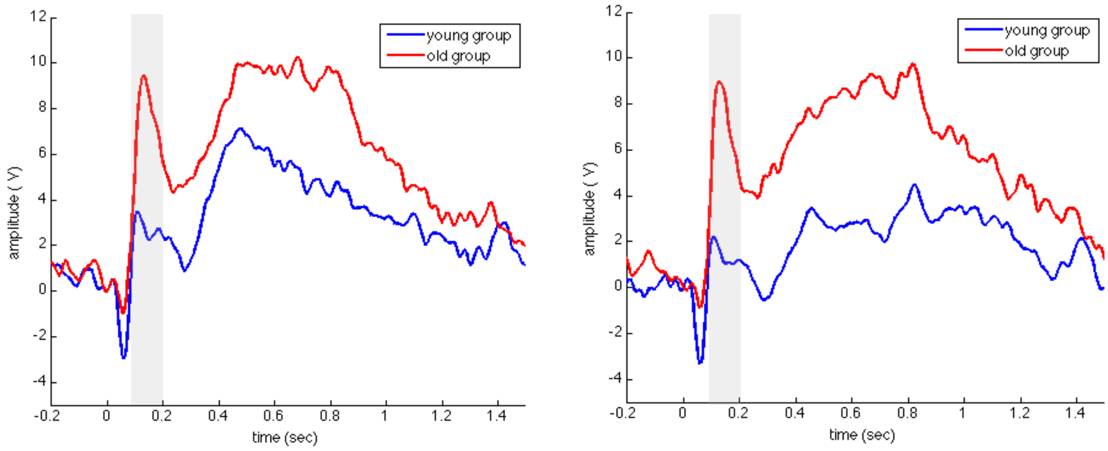


Figure 6.8. Older (lines in blue) and younger (lines in red) participants' cluster one mean ERP amplitude for anger (left graph) and happiness (right graph) experimental trials at different task difficulties [neutral (baseline), easy and hard]. Straight lines represent trials with younger face stimuli, dotted lines represent trials with older face stimuli. Error bars represents S.E.



a. Anger, Easy Anger, Hard

Younger Faces



Anger, Easy Anger, Hard

Older Faces

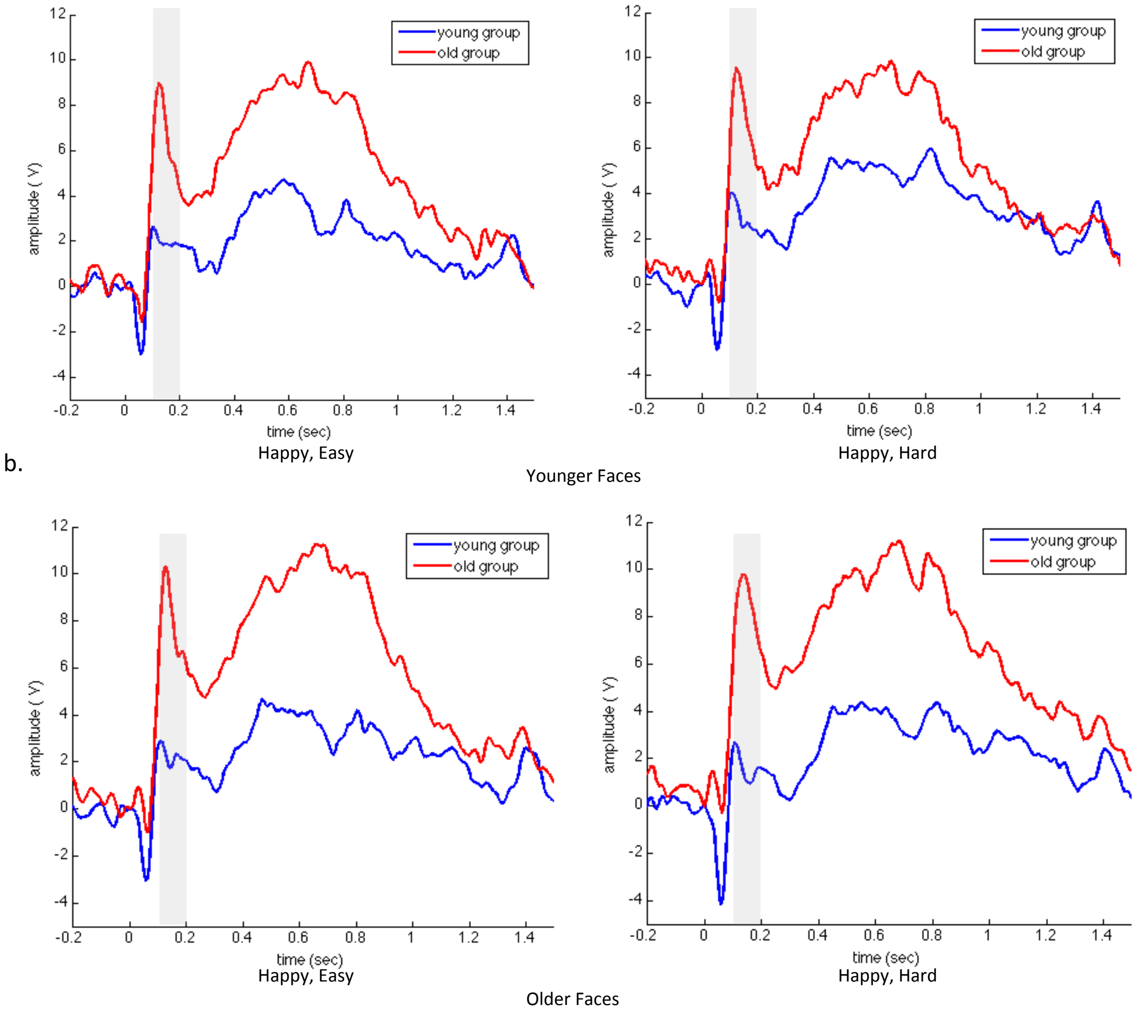


Figure 6.9. Younger (lines in blue) and older (lines in red) participants' cluster one mean ERP waveforms (100-200ms) during anger (a) and happiness (b) perceptual tasks. The time window (100-200ms) used for subsequent statistical analysis are highlighted in grey.

Cluster two

A 2 (emotion type) × 2 (task difficulty) × 2 (face stimuli age) × 2 (group) mixed ANOVAs on the frontal mean ERP amplitudes (250-850ms) of anger and happiness perception tasks revealed significant main effect of group [$F\ (1, 26) = 17.051, p < .001, \eta^2 = .396$], which was due to older participants exhibiting significantly higher overall mean ERP amplitudes than younger group (see figure 6.10 and figure 6.11). The main effect of difficulty was significant [$F\ (1, 26) = 6.813, p = .015, \eta^2 = .208$], which was due to the easy condition (high-intensity facial expressions) eliciting significantly higher overall mean ERP amplitudes in frontal regions (250-850ms) than the hard condition (low-intensity facial expression) (figure 6.10). Main effects of emotion and stimuli age were not significant.

The interaction of stimuli age × group was significant, $F (1, 26) =5.468, p = .027, \eta^2 = .174$, which was due to older adults exhibiting significantly higher ERPs than younger adults in both older ($p < .001, d = 1.641$) and younger ($p = .008, d =1.428$, Bonferroni corrected) face stimuli tasks (see figure 6.10 and figure 6.11).

The interaction of emotion type × task difficulty × group was significant [$F (1, 26) =5.781, p = .024, \eta^2 = .182$], pairwise comparison (with Bonferroni correction) revealed that older participants exhibited significantly higher frontal ERP amplitudes (250-850ms) in both easy and hard levels of anger (easy: $p = .048, d = 1.367$; hard: $p < .001, d = 1.766$) and happiness (easy: $p < .001, d = 1.540$; hard: $p < .001, d = 1.511$) perceptual tasks (see figure 6.10). In addition, the within-group comparison revealed that younger participants' mean frontal ERP amplitudes (250-850ms) for the easy condition was significantly higher than the hard condition in anger perception ($p = .008, d = 1.487$), but not significantly different in the happiness perceptual tasks; whereas older participants did not show significant different ERPs across easy and hard task conditions in both the happiness and anger perceptual tasks (figure 6.10).

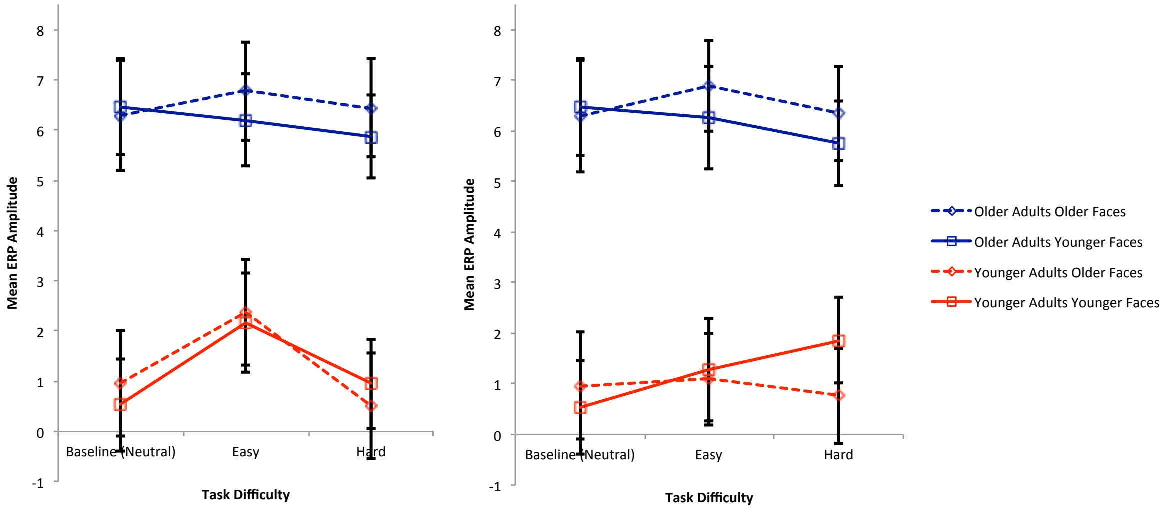
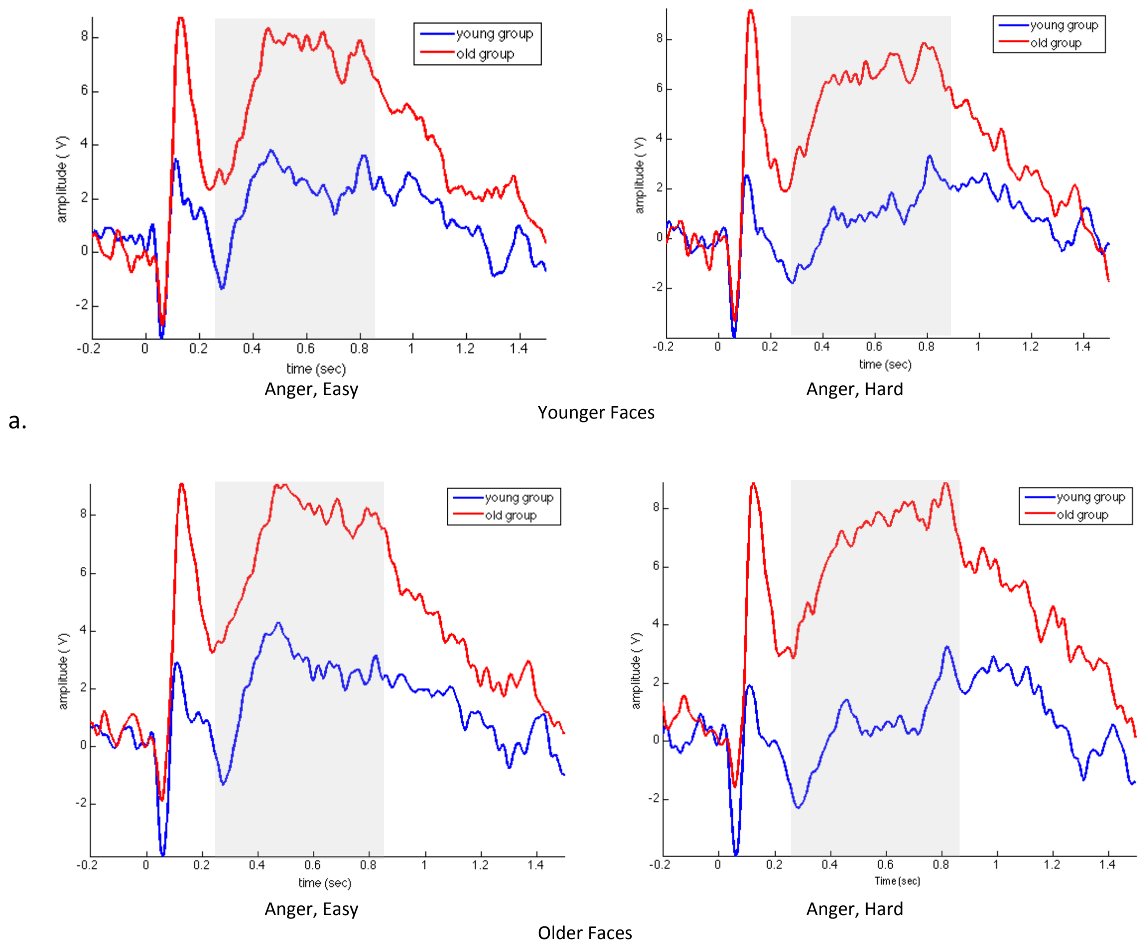


Figure 6.10. Older (lines in blue) and younger (lines in red) participants' cluster two mean ERP amplitude for anger (left graph) and happiness (right graph) experimental trials at different task difficulties [neutral (baseline), easy and hard]. Straight lines represent trials with younger face stimuli, dotted lines represent trials with older face stimuli. Error bars represents S.E.



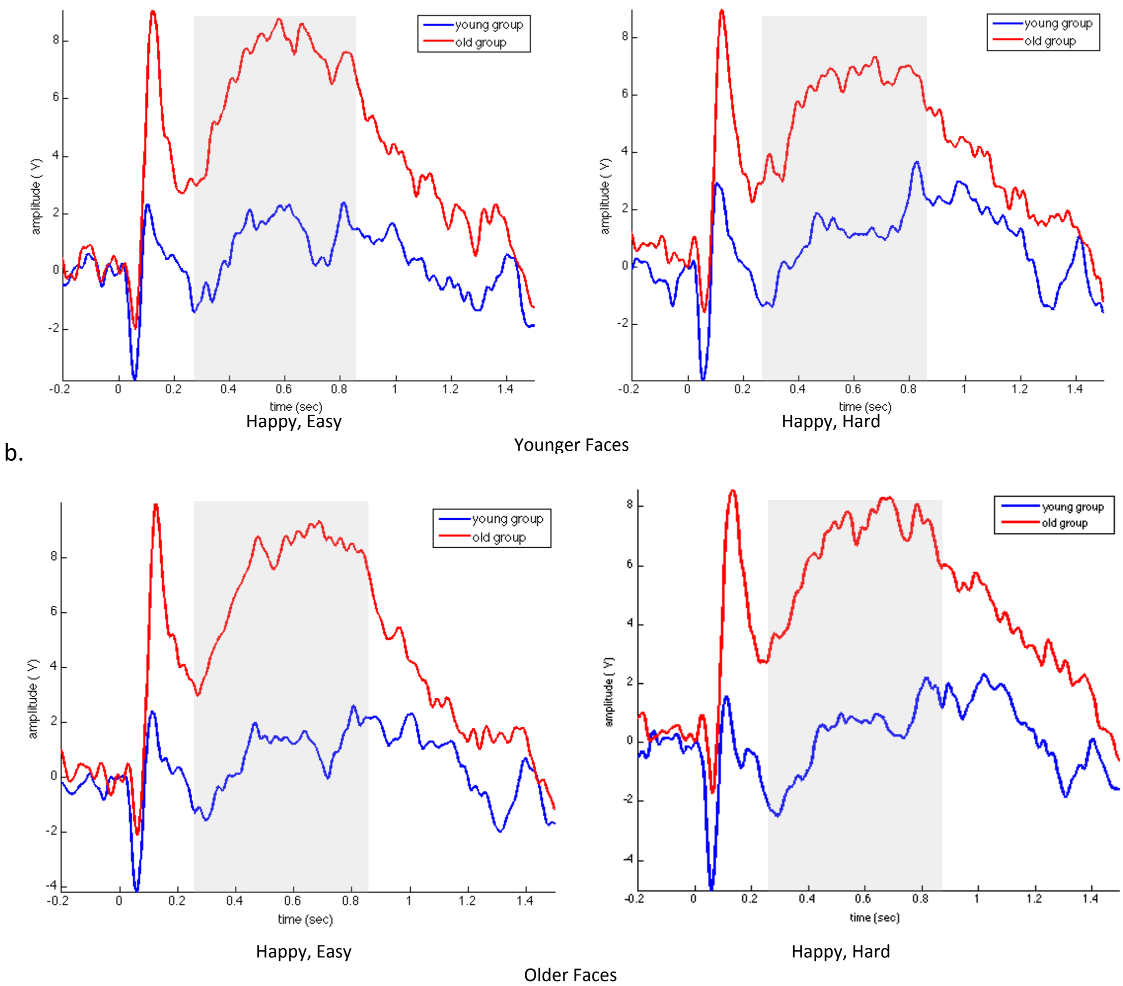


Figure 6.11. Younger (lines in blue) and older (lines in red) participants' mean cluster two ERP waveforms (250-850ms) during anger (a) and happiness (b) perceptual tasks. The time window (250-850ms) used for subsequent statistical analysis are highlighted in grey.

6.4 Discussion

The aim of the present study was to study age-related changes in emotion recognition by using behavioural and EEG measures. I also investigated how 'emotion type', 'age of face stimuli' and 'emotion intensity' would affect both younger and older participants' emotion perception by using both younger and older faces displaying happiness and anger emotions with both high- and low- emotion intensities.

6.4.1 Age-related behavioural perceptual performance differences

For perception of anger, older participants' mean accuracy was significantly lower than younger group in both hard condition and easy conditions. This finding confirmed that older people have declined perceptual performance on both low- and high- intensities of anger facial expressions. This finding is consistent with my finding from chapter 1, and therefore adds strength to confirm older participants' declined perceptual ability in perceiving both subtle and expressive anger from faces. For perception of happiness, older participants showed significantly poorer performance than younger participants in recognising happiness from younger faces in hard condition, but not in easy condition. This finding suggested that older participants have intact perception of expressive (high-intensity) happiness, but they have declined ability in perceiving subtle happiness facial expression from younger faces. This pattern was not found in the neutral (baseline) condition, where no significant group differences were found.

That older adults show impaired happiness perception for low intensity expression challenges most prior studies proposing that older people have intact perception of happiness, and suggests that the incomplete conclusion proposed by previous researchers was drawn from studies where only young face stimuli with considerably high emotional intensities were used. This finding also confirmed my results from experiment 1 where older participants exhibited significantly poorer performance in perception of low-intensity happiness.

Age-related emotion perception response bias

The behavioural accuracy results revealed that the older group showed significantly higher accuracy in the neutral emotion perceptual task compared to younger adult participants. This result is quite novel as few previous studies have investigated young-old group difference in perceiving neutral emotion. Given that older adult participants in this study only showed superior performance in the neutral emotion condition but not on other emotion types, it is not clear whether the results could reflect older people's actual ability in recognising 'neutral' facial emotions, or it is due to older people's behavioural response bias in choosing 'neutral' emotion across all emotion perceptual tasks. The results of the response bias analysis showed that older adult participants' mean proportion (%) of making 'neutral' emotion response was higher than younger adult participants in 15%, 30% and 75% anger conditions. In 60% anger condition, older adult participants showed significantly higher overall mean proportion (%) of making 'neutral' emotion responses compared to younger adult participants. In sum, these results revealed a general pattern that older adult participants showed a preference in labeling anger facial expression stimuli as neutral emotion. As mentioned in chapter one, older people have 'positivity bias' in perceiving facial emotions – they tend to shift towards positive information and avoid negative information, which might help them to maintain their emotional balance and wellbeing. The present finding is in line with the age-related 'positivity bias' proposal as older people might have ignoreed the negative emotional signals exhibited by angry face stimuli to facilitate their attentional shift from negative facial emotion to neutral facial emotion.

For the perception of happiness, older people had higher chance (%) of perceiving the happy facial stimuli as 'neutral' facial expression compared to younger adult participants on 75% and 15% happiness trials. Furthermore, on the 30% happiness trials, older adult participants exhibited significantly higher overall mean proportion (%) of making 'neutral' emotion responses compared to younger adult participants. The overall pattern of happiness trials indicates that older people also have a higher tendency in perceiving happiness as neutral emotion compared to younger people (except the 60% happiness trials). However, this finding does not agree with the age-related ‘positivity bias’ in perceiving facial emotions, which is contradictory to the anger perception results described above. The overall anger and happiness trials might indicate that older people are more likely to perceive anger and happiness facial expressions as neutral compared to younger adults, which reflects their insensitivity of detecting positive and negative facial emotional cues.

In summary, the overall pattern of results suggests that older groups have a tendency to perceive both happiness and anger facial emotions as neutral emotion. Therefore, older group’s higher accuracy on the neutral emotion condition might not reflect their real superior ability in correctly labeling neutral facial expressions compared to younger group. As older people showed a tendency or preference in choosing ‘neutral emotion’ as their perceived emotion in both anger and happiness emotion trials. Therefore, this age-related response bias may systematically distort assessments of age differences on neutral emotion perceptual ability.

6.4.2 Effect of stimuli age on behavioural perceptual performance

For recognition of anger, younger participants’ accuracy of recognising anger from old face stimuli was significantly higher than from younger faces in hard condition. In other words, subtle facial expression of anger was easier to detect from older faces than from younger faces. It might suggest that some facial features (e.g. winkles around eyes and mouths) of older faces may exaggerate fine and subtle anger. However, the superior performance in perceiving subtle anger from older faces was not found in older participants, as their performances on younger and older face stimuli were not significantly different in neither easy or hard levels of anger.

For happiness, within-group comparison revealed that the younger participants' accuracy on younger faces was significantly better than older faces in hard condition; whereas older participants' accuracy on younger and older faces did not significantly differ in either hard or easy conditions. Younger participants' superior performance on younger faces (in hard condition) might reflect 'own-age bias' where people are better at perceiving faces of their own ages (Bäckman, 1991; Lamont, Stewart-Williams, & Podd, 2005). However, this 'own-age bias' was not shown in older participants, which is consistent with my findings from Chapter 3 where older adults showed impairment relative to young adults in the perception of subtle emotional expressions displayed by old adult actors. Younger participants' superior performance in perceiving subtle happiness from younger faces might partially account for the perceptual performance gap between younger and older participants. In other words, older participants' poorer performance might not be entirely due to their perception decline, but younger participants' superior perception of their own age faces.

6.4.3 Facial emotion perception and neural compensation in older people

Prior ERP studies on younger adults have revealed three major facial emotion-related components, which are early frontocentral positivity (around 120ms stimulus onset), later broadly distributed sustained positivity beyond 250ms post-stimulus, and an enhanced negativity at lateral posterior sites (EPN) (Eimer and Holmes, 2002; Eimer, Holmes, and McGlone, 2003, Balconi, Pozzoli, and Possoli, 2003). The present results have revealed that older participants showed significantly higher early frontal and centromedial ERP positivity (100-200ms) and later sustained positivity beyond 250ms post stimulus across all facial emotions types including neutral emotion. However, older participants did not show significantly ERP amplitudes difference in negativity at lateral posterior sites (EPN), which is different from the finding of Wieser et al. (2006).

Based on prior studies of Eimer et al. (2003, 2007), the early and late frontal and centromedial positivity can be interpreted to reflect non-automatic and attentive approach of emotion processing, and they are not modulated by emotion type. Older people's significantly higher early (100-200ms) and late (250-850ms) frontal and centromedial positivities compared to younger participants during emotion processing might suggest that they input more attention regulated cortical neural resources than younger people in all types of emotion perception, this could reflect their compensation for their less activations in subcortical regions (e.g. amygdala) (Fischer, Sandblom, and Gavazzeni, 2005). This additional recruitment of frontal regions during processing facial emotional expression is in parallel with previous fMRI studies which also found that older people showed significantly higher frontal neural activations compared to younger adults during emotion perception tasks (e.g. Tessitore, Hariri, and Fera et al., 2005; Fischer et al., 2010).

However, most previous studies have only used negative facial emotion tasks (e.g. Tessitore, Hariri, and Fera et al., 2005; Fischer, Sandblom, and Gavazzeni, 2005; Iidaka, Okada, & Murata, 2002). In contrast, the present study has used additional happiness and neutral facial expression in the perception task. Consistent with Keightley et al. (2007)'s finding, older adults also showed significantly higher frontal cortical neural activations while processing neutral facial expressions. The finding showing older adults also rely on higher frontal centromedial cortical processing for perceiving happiness awaits confirmation from future studies.

One aim of the present study was to examine the relationship between emotion task difficulty (emotional intensity) and older participants' neural compensation. One interesting pattern of results exhibited in this study is that older people showed similar level of ERP activations across different task difficulty [neutral (baseline), easy and hard] whereas their behavioural performance varied on these tasks. According to the CRUNCH model (Reuter-Lorenz and Cappell (2008), at lower level of task demand, older participants exhibit a region-specific neural overactivation pattern but they can achieve similar or equivalent behavioural as younger participants (successful neural compensation). However, beyond a certain level of task demand, older people's brain falls short of sufficient neural activation and their behavioural performance declines compared to the young people (neural compensation failure). The findings of the present study fit with the CRUNCH model, during anger perception tasks, older participants exhibited similar degrees of ERP amplitudes for three task difficulty [Neutral (baseline), easy and hard] conditions. Older people showed similar performance as younger participants in baseline condition (neutral), but they had significantly poorer performance than younger participants in both easy and hard anger perception trials. It seems that at neutral (baseline) level, the neural overactivation of older participants enable them to compensate neural inefficiency and provide enough neural recourses in processing neutral emotion, however, the similar level of neural overactivation was not enough for older participants to process easy and hard level of anger emotions.

For happiness perception, older participants also displayed significant neutral overactivation in left frontal and centromedial (100-200ms stimuli onset) and frontomedial region (250-850ms stimuli onset) compared to younger participants, and ERP amplitude of three task difficulty conditions (baseline, easy and hard) of older groups were also similar. However, older people showed intact performance in both the baseline and easy conditions, but exhibited significantly declined performance in hard condition (young face stimuli). It seems that older people's overactivation in happiness perception successfully compensate in easy condition, but not enough for them to process subtle happiness facial expression.

It should be noted that the neural overactivation in left frontal and central regions (100-200ms stimuli onset) and frontal region (250-850ms stimuli onset) might not reflect emotion-specific neural compensation, as the neural overactivation patterns was not only shown in anger and happiness trials, but also in neutral (baseline) trials. In addition, other aging studies have also shown that older people tend to recruit more frontal cortical regions than younger people when performing identical cognitive tasks, especially when performing effortful tasks (Grady, 2000; Raz, 2000), it has been proved in other brain imaging studies of attention (Johannsen, Jakobsen, & Bruhn, 1997; Madden, Turkington, & Provenzale, 1997; Anderson, Iidaka, & Cabeza, 2000), working memory (Hartley, Speer, & Jonides et al., 2001; Mitchell, Johnson, & Raye et al., 2000) and executive functioning (Smith, Geva, & Jonides, 2001). Therefore, the neural overactivation in frontal-centro regions might reflect a general neural compensation for different cognitive functions.

6.4.4 Effect of 'emotion type', 'task difficulty' and 'face stimuli age' on ERPs

The results showed that the effect of emotion type (happiness and anger) and face stimuli age (young and old) did not significantly modulate younger and older participants' early (100-200ms) or late (250-850ms) positivities during facial emotion perceptual tasks. This finding confirmed previous studies that claimed the early and late positivities are not modulated by emotion type (Eimer, 2003, 2007; Schupp, Cuthbert, & Bradley, 2000).

In contrast, the effect of task difficulty (or facial emotional intensities) significantly modulated the overall ERP amplitudes of both early (100-200ms) frontal and centromedial and late (250-850ms) frontal brain regions in anger tasks, but not in happiness tasks.

Specifically, the overall mean left-frontal and centromedial ERP amplitudes (100-200ms) of easy condition (high emotion intensity) was significantly higher than hard condition (low emotion intensity) in anger task, regardless of group and face stimuli age. In other words, higher intensities of anger elicited significantly higher early (100-200ms) frontal and centromedial positivities in participants, regardless of group and face stimuli age. Furthermore, younger participants' mean frontal ERP amplitudes (250-850ms) for the easy condition was significantly higher than the hard condition (low emotion intensity) in anger perception, but this pattern was not shown in the happiness condition; whereas older participants did not show significant different ERPs across easy and hard conditions in both happiness and anger perceptual tasks. In other words, higher intensities of anger elicited significantly higher late (250-850ms) frontal positivities in only younger participants. These findings suggest that higher intensities of anger can trigger higher early (100-200ms) frontal and centromedial positivities and late (250-850ms, only in younger participants) frontal positivities. These findings seem consistent with Eimer et al.'s (2003, 2007) interpretation of these two positivity components as attention-regulated emotional processing, as higher intensities of anger signal potential threat and they are normally associated with higher level devotion of attention (Phelps, Ling, & Carrasco, 2006). Furthermore, this finding partially agrees a previous proposal suggesting high intensities of emotional images elicited larger late positive potentials than lower intensities of emotional images (Schupp, Cuthbert, & Bradley, 2000), as it is not the case for happiness perception in present study.

6.4.5 Methodology issues

In the present study, the group difference clusters (time window and electrode) on neutral condition were to used to extract the ERPs of other emotion conditions as the neutral emotion condition was treated as the baseline condition. This method can help to investigate the role of emotion type, task difficulty and face stimuli age in modulating the same neural regions. Specifically, it can help to reveal the participants' neural changes from baseline to easy and hard emotion conditions, which provides the evidence to demonstrate the age-related neural compensation hypothesis. However, this method might have ignored the group ERP differences on specific emotions, as prior studies have suggested that neutral, anger and happiness facial emotions are processed by different neural regions (e.g. Fusar-Poli, Placentino, & Carletti et al., 2009; Kesler, Andersen, & Smiths, 2001).

6.6 Summary

In summary, the older group showed declined ability in recognising anger in both hard and easy conditions. For happiness recognition, the older group only showed degeneration in perceiving low-intensity happiness from younger faces. In addition, the overall pattern of results suggests that older groups have a to perceive both happiness and anger facial emotions as neutral emotion, which reflects older adults' insensitivity to detecting positive and negative facial emotional cues.

Stimuli age plays an important role in modulating younger participants' performance in low-intensity emotion perception. In low-intensity anger recognition, their accuracy of perceiving anger from older stimuli faces was significantly higher than accuracy of perceiving anger from younger stimuli faces. Whereas in low-intensity happiness perceptual task, younger participants' accuracy of perceiving happiness from younger stimuli face were significantly higher than from old stimuli faces, which reflects 'own-age bias' in face perception. The effect of 'face stimuli age' did not significantly modulate older participants' performance.

In terms of ERPs, older participants showed neural overactivation in the left frontal and centromedial region (100-200ms stimuli onset) and frontal region (250-850ms stimuli onset) at neutral condition, which suggests that older people’s neural compensation starts at the neutral (baseline) condition. Older participants also exhibited similar neural overactivations during anger and happiness emotion perception tasks to compensate their inefficiency in cortical processing. However, older people’s neural compensation was efficient in neutral emotion perception as they exhibited similar performance as younger participants, but the similar level of neural resources was not enough for them to apply the compensation strategy in perception of anger (both easy and hard conditions) and happiness (hard condition).

CHAPTER 7: CONCLUSIONS

This chapter provides a summary of the empirical findings reported in this thesis. It discusses findings from behavioural, brain stimulation (high-frequency tRNS) and brain imaging (EEG) research approaches, and provides an overview of the effect of normal aging on facial identity and facial emotion perceptual abilities from both behavioural and neurological perspectives. In addition, it will discuss the limitations involved in my PhD research and possible future research directions of this research field.

7.1 Introduction

As mentioned in chapter 1, prior behavioural studies suggested that normal aging is associated with declined perception of anger, sadness and fear, while the perception of happiness showed inconsistent results. The general limitations involved in both behavioural and neuroimaging studies were that 1) only one (mostly high-) emotion intensity, and 2) only young face stimuli were used in those studies. Therefore, previous findings might not reflect a comprehensive account of older people's facial emotion perception, and own-age bias may have been involved in previous research. In addition, most behavioural investigations on aging and face perception have agreed that older people have a declined ability in face identity perception. General limitations of most previous studies were that they contained only comparisons of young-old behavioural performance on a single task that only had one level of task complexity (mostly low task difficulty). In addition, these studies only used young facial stimuli in facial identity perceptual tasks, which might bias the performance results due to 'other-age bias'. In addition, the underlying mechanism of the age-related decline in facial identity are still in debate. In my PhD research both younger (*chapter 2*) and older (*chapter 3*) face stimuli were used in face perception tasks to clarify the effect of normal aging on facial perception. I also explored what underlying mechanisms contribute to the face identity decline in older people, and whether the age-related face perception decline extends to non-social object perception *(chapter 3)*.

Several non-invasive brain stimulation studies on memory have proved the effectiveness of brain stimulation in enhancing older people's behavioural performance by boosting their cortical activations. The evidence suggested that the older people's neural resource ceiling can be altered by boosting the cortical neural activation and recruiting additional neural regions. This type of study has not been done in face perception studies with the older population. One of my research aims is to use non-invasive method to enhance older people's facial emotional perception (*chapter 5*). This can help to understand the age-related neural changes in facial emotion perception.

In chapter 1, neuroimaging studies proposed two age-related brain activation models for face perception, both of which have suggested that older adults exhibited different brain activation patterns from younger adults. The general limitations in previous neuroimaging studies supporting these accounts are that 1) they only used facial displays of negative emotions, while few have compared the young-old neural activations during the perception of happiness and neutral emotions, 2) only one (mostly high-) emotion intensity and 3) only young face stimuli were used in those studies. Therefore, one of my research aims was to demonstrate whether older people rely on any compensatory strategies in their face emotion perception by comparing younger and older adults' perceptual performance and ERPs on tasks that comprise different emotion types (anger, happiness and neutral) with both low- and high-emotional intensities. I addressed this question in my EEG study (*chapter 6*).

7.2. Conclusions of Chapter 2

As discussed in chapter 1, a general limitation involved in most previous research is that only high-intensity prototypes of facial expression images have been used. In chapter 2, I compared younger and older participants' perceptual performance on lower-intensity facial emotional expressions and facial identity with subtle differences. Secondly, in order to demonstrate whether older adults have a domain-specific deficit in emotion perception or more domain-general declines in the ability to make fine-grained visual discrimination, I compared older and younger subjects' perception of facial emotions and identities using same experimental paradigm. Thirdly, behavioural and neuroimaging evidence has shown that facial trait perceptual abilities are closely related to the perception of facial expressions and facial identities. However, whether the facial emotion and identity perceptual decline in older adults extend to such trait judgements remains unknown. Therefore, I also examined two age group's perceptual performance on facial traits judgement and demonstrated the relationship between facial trait perceptual performance and other two facial perceptual performances (facial emotional expression and facial identity).

The results showed that older participants showed declined performance in the perception of subtle facial expressions of anger. Combining with previous literature, this finding adds strength in confirming that normal aging is associated with decay in perceiving anger, in both low- and high- emotional intensities. Older people's perceptual performance of happiness did not show a significant difference from younger people at a group level, however, it should be noted that there is a trend that older people might have age-related difference in perception of happiness from low-intensity facial expressions. Older adult participants' perceptual performance on both upright- and inverted- facial identities were significantly lower than younger adult participants. This result is in line with prior findings (Boutet and Faubert, 2006;

Meinhardt-Injac & Meinhardt, 2014) that there are reliable age-related differences for both upright- and inverted- face perception. No group difference was found in perception of facial trait trustworthiness or aggressiveness. Given that this experiment has shown older adults' significant age-related decline in both anger and facial identity perception, this facial trait perception result does not fit the model proposed by Oosterhof and Todorov (2008). This finding suggests that the age-related decline in anger and facial identity perception did not extend to facial trait perception.

In addition, the relationship between age and each face perceptual performance were explored using regression model fitting. Polynomial regression revealed a significant quadratic relationship between age and performance on the CFPT-Happy task, suggesting that normal aging affects the perception of facial happiness in an inverted-U curve with a potential peak in middle age. In contrast, normal aging affects anger, facial identity and facial trait aggressiveness perception in a linear fashion.

7.3. Conclusions of Chapter 3

In chapter 3 I sought to examine how typical aging is associated with the perception of subtle changes in facial emotional and facial identity with older adult faces, and whether the age-related facial identity perceptual decline is a face-specific decline or extended to the perception of complex objects. I developed novel tasks that permitted the ability to assess facial emotion (happiness perception), facial identity, and non-social perception (object perception) across similar task parameters. I observed that normal aging is linked with decreased ability to make fine-grained judgements in the perception of facial happiness and facial identity (from older adult faces), but not for non-social perception. This pattern agreed with some previous findings claiming that aging is associated with declined face identity perception, while non-social object perception remains intact (Boutet and Faubert, 2006) or is less affected by aging (Meinhardt-Injac, Persike & Meinhardt, 2014).

The object control (cars) has very similar configurations of individual features as with faces, and the main difference between faces and cars are the individual features and fine spatial relationships between these features. In addition, previous studies proposed that visual cues used for face and object discrimination might be associated with distinct spatial frequencies (Morrison and Schyns, 2001). It seems that older people's intact performance on object perception but significantly declined perceptual performance for both upright and inverted faces might be due to their deficits in handling fine internal features that involve perception of fine spatial frequencies (e.g. Meinhardt-Injac, Persike & Meinhardt, 2014). This finding will be an interesting avenue to explore with future work.

In addition, I observed that declined face perception of subtle facial emotion and facial identity in older adults is evident for older face stimuli, implying that declines in social perception associated with aging are not fully accounted for by an other-age bias. Furthermore, the pattern of change in social perception abilities across the lifespan differed for facial happiness and facial identity. Facial happiness was associated with increases in performance in young adulthood, but declines in older adulthood. Facial identity was associated with linear declines from young to old adulthood. These findings seem consistent from the findings reported in chapter 1. However, due to the lack of middle aged participants in both experiments illustrated in chapter 2 and chapter 3, these findings need to be confirmed by further investigations.

7.4. Behavioural investigations: Implications and future research avenues

There are implications of my findings in relation to prior work comparing older and younger adults in the ability to perceive facial emotion displayed by younger and older adult faces. In addition by ensuring similar task demands for identity, happiness, and non-face perceptual tasks I am able to ensure that differences in the pattern of relationship between aging and performance is not due to specific task demands (e.g. working memory, emotional vocabulary). This is an important addition to prior work that has compared older and younger adults in the ability to perceive facial emotion displayed by younger and older adult actors because much of that work has used prototypical emotions in labelling based tasks. Theoretically these measures might tap additional processes alongside perceptually driven performance factors (Phillips, Channon, Tunstall, Hedenstrom, & Lyons, 2008). My findings suggest that older adults display difficulties in social perception even when additional constraints on performance (e.g. emotional vocabulary, cognitive load, working memory) are low.

The reasons for reductions in social perception throughout aging remain a topic of debate. Explanations include socio-emotional selectivity theory (SST; Carstensen & Charles, 1998), which suggests that older adults may show deficits compared to younger adults in the perception of negative emotions due a preference to engage / encode signals that promote positivity, emotional balance, and well-being. My findings conflict with this account since I observe declines in the perception of positive emotions in older compared to younger adults. This is in line with criticisms of SST arguing that prior work indicating that older adults show deficits in the perception of negative, but not positive, emotions may relate to the ease of tasks involving positive emotions in past research (Isaacowitz & Stanley, 2011).

Alternative explanations of age-related changes in social perception include accounts based on perceptual strategies employed by older compared to younger adults. Prior work has suggested that older adults tend to use perceptual information from upper parts of the face (e.g. eye region) less often and less efficiently (i.e. they are worse at detecting changes in this region) than young adult participants (Circelli et al., 2013; Murphy and Isaacowitz, 2010; Sullivan et al., 2007; Slessor et al., 2013; Chaby et al., 2011; Wong et al., 2005). This has been used to explain why older adults tend to show more consistent impairment in the perception of some negative emotions (anger, sadness, and fear) than positive emotion since the upper part of the face plays a more important role in the expression of anger, fear and sadness (Calder et al., 2000). Based on prior work one would expect that happiness perception should rely more heavily on the lower part of the face (Calder et al., 2000), thus to some degree our findings of impaired happiness may be considered to conflict with this account. However, it is worth noting that there are other reasons why visual scan patterns may not fully account for age-related declines in social perception. For example, these declines also exist for the perception of vocal cues (Ruffman, Halberstadt, & Murray, 2009; Paulmann, Pell, & Kotz, 2008) and data on differences in eye-movements between younger and older adults when perceiving emotional faces is also mixed (e.g. see Ebner et al., 2011). With that being said, it is possible, however, that the use of subtle shifts in facial emotion in the current investigation may require additional perceptual information to be used (e.g. use of upper as opposed to lower parts of the face), which may contribute to the age-related impairments that we observe. As I did not measure eye-movement in my investigation I cannot be sure whether my findings of impaired happiness and identity perception are related to inefficient eye-movement patterns. Moving forward, investigating eye-movements in the perception of subtle differences in social cues in younger and older adults will be an important extension of the current work.

Another important consideration for future work is to address a caveat of our study - namely that the behavioural investigations lack data from participants in the middle adulthood range (from 40 years to 60 years). While my results are indicative that subtle facial happiness and facial identity perception change throughout adulthood, examining the trajectory of this change requires future work. There is some evidence to suggest that facial identity processing (particular face recognition memory) peaks in middle adulthood, before declining into and throughout older adulthood (Germine, Duchaine, & Nakayama, 2011). Whether a similar pattern holds for facial identity and emotion perception remains an important question for future studies. In addition it will be important to examine the extent to which age-related differences in facial emotion perception that we observe here for happiness perception hold for other emotion types.

7.4. Brain stimulation (tRNS) study and its implications, limitations and future avenues

Chapter 1 and 2 have shown that older adults are associated with declined abilities in perceiving subtle facial expressions of anger and happiness. Previous findings suggest that older people show impairments in facial emotion perception. High-frequency transcranial random noise stimulation (tRNS) is a neuromodulation technique that has previously been shown to improve cognitive and perceptual performance. However, few researches have focused on the effects of high-frequency tRNS as a tool to modulate emotion perception in older adults. Here I assessed whether high frequency tRNS applied to the inferior frontal cortex would enhance facial expression perception in older adults, given that normal aging is associated with decline in frontal lobe and inferior frontal gyrus (involved in emotion processing, especially anger). The results showed that active tRNS enhanced anger perception but the same tRNS stimulation did not significantly change the performance on two other face perception tasks assessing facial identity and facial happiness perception.

Examination of how inter-individual variability related to changes in anger perception following tRNS indicating that the degree of performance change in anger perception following active tRNS to inferior frontal cortex was predicted by baseline ability and gender of older adult participants.

These findings are important as they help to increase our understanding of the neural plasticity in older people and the underlying neural mechanism of emotion perception, and highlights high frequency tRNS as a potential tool to aid anger perception in typical aging. It also showed the importance to consider individual baseline performance in brain stimulation studies with older subjects, as the efficiency of brain stimulation may vary between high- and low- performing older adults. In addition, gender is also a significant predictor stimulation efficacy, future studies will need to assess whether and how gender is likely to act as a moderator of performance change following non-invasive brain stimulation in older adults. These factors are relatively ignored in current field of brain stimulation research that use older adults as target cohorts and future studies should consider these factors prior to application. In addition, as I only tested older adult participants in the current investigation it remains important for future work to consider whether the pattern of effects is specific to older adults or evident across different age groups.

7.5 Brain imaging study (ERPs) and its implications, limitations and future avenues

In chapter 6, behavioural results showed that the older group showed declined ability in perceiving both low- and high- intensities of anger, and low-intensity happiness (only with younger faces). This older people's deficits in perceiving subtle anger and happiness facial expression are consistent with my findings of other behavioural studies (chapter 2 and chapter 3). Stimuli age plays an important role in modulating younger participants' performance in low-intensity emotion perception. Specifically, their accuracy of perceiving anger from older stimuli faces was significantly higher than perceiving anger from younger stimuli faces; whereas their accuracy of perceiving happiness from younger stimuli faces were significantly higher than perceiving happiness from old stimuli faces, which reflects 'own-age bias' in face perception. However, the effect of 'face stimuli age' did not significantly modulate older participants' behavioural performance.

7.5.1. Older people's emotion perceptual bias

The results showed that older people consistently showed higher mean proportions of making neutral emotion response in anger and happiness trials. It is interesting to see that older people had higher chances in making neutral emotion response on happiness trials compared to younger adults, which is contradictory to the 'positivity bias' proposal. In sum, older group's higher accuracy on the neutral emotion condition might not reflect their actual superior ability in encoding neutral facial expressions compared to younger group. This finding suggests that older people have declined ability in perceiving both anger and happiness facial clues therefore they persistently perceived angry and happy facial expressions as neutral facial expression.

7.5.2. Effect of 'emotion type', 'task difficulty' and 'face stimuli age' on ERPs

The results showed that the effect of emotion type (happiness and anger) and face stimuli age (young and old) did not significantly modulate younger and older participants' early (100-200ms) or late (250-850ms) positivities during facial emotion perceptual tasks. This finding confirmed previous studies that claimed the early and late positivities are not modulated by emotion type (Eimer, 2003, 2007; Schupp, Cuthbert, & Bradley, 2000).

The effect of task difficulty (or facial emotional intensities) significantly modulated the overall ERP amplitudes of both early (100-200ms) frontal and centromedial regions and late (250-850ms) frontal brain regions in anger tasks, but not in happiness tasks. Specifically, higher intensities of anger elicited significantly higher early (100-200ms) frontal and centromedial positivities in participants, regardless of group and face stimuli age; and it also elicited significantly higher later (250-850ms) frontal positivities in younger participants. These findings seem consistent with Eimer et al.'s (2003, 2007) interpretation of these two positivity components as attention-regulated emotional processing, as higher intensities of anger signal potential threat and they are normally associated with higher level devotion of attention (Phelps, Ling, & Carrasco, 2006). Furthermore, this finding partially agrees with a previous proposal suggesting high intensities of emotional images elicited larger late positive potentials than lower intensities of emotional images (Schupp, Cuthbert, & Bradley, 2000), as it is not the case for happiness perception in the present study.

7.5.3. Older people's neural activity pattern and their neural compensation strategy

In terms of ERPs, older participants showed neural overactivation in the left frontal and centromedial region (100-200ms stimuli onset) and frontal region (250-850ms stimuli onset) at neutral condition, which suggests that older people's neural compensation starts at the neutral (baseline) condition. Older participants also exhibited similar neural overactivations during anger and happiness emotion perception tasks to compensate for their inefficiency in cortical processing. However, older people's neural compensation was efficient in neutral emotion perception as they exhibited similar performance as younger participants, but the similar level of neural resources was not enough for them to apply the compensation strategy in perception of anger (both easy and hard conditions) and happiness (hard condition).

Based on prior studies of Eimer et al. (2003, 2007), the early and late frontal and centromedial positivity reflects non-automatic and attentive approach of emotion processing, therefore older people's significantly higher early (100-200ms) and late (250-850ms) frontal and centromedial positivities compared to younger participants during emotion processing might suggest that they input more attention regulated cortical neural resources than younger people in all types of emotion perception, this reflects their compensation for their less activations in subcortical regions (e.g. amygdala) (Fischer, Sandblom, and Gavazzeni, 2005). This additional recruitment of frontal regions during emotion processing is in parallel with previous fMRI studies which also found that older people showed significantly higher frontal neural activations compared to younger adults during emotion perception tasks (e.g. Tessitore, Hariri, and Fera et al., 2005; Fischer et al., 2010).

It is worthy noting that the neutral overactivation in left frontal and centromedial regions (100-200ms stimuli onset) and frontal region (250-850ms stimuli onset) might not reflect emotion-specific neural compensation, as the neural overactivation patterns was not only shown in anger and happiness trials, but also in neutral (baseline) trials. Other aging studies have also shown that older people tend to recruit more frontal cortical regions than younger people when performing identical cognitive tasks, especially when performing effortful tasks (e.g. Grady, 2000; Raz, 2000), as proven in other brain imaging studies of attention (Johannsen, Jakobsen, & Bruhn, 1997; Madden, Turkington, & Provenzale, 1997; Anderson, Iidaka, & Cabeza, 2000), working memory (Hartley, Speer, & Jonides et al., 2001; Mitchell, Johnson, & Raye et al., 2000) and executive functioning (Smith, Geva, & Jonides, 2001). Therefore, the neural overactivation in frontal-centro regions might reflect older people's general neural compensation for different cognitive functions and inputting more attentional load across different cognitive tasks in order to achieve better behavioural performance.

This ERP study shows an attempt in demonstrating the age-related Compensation-Related Utilization of Neural Circuits Hypothesis (Reuter-Lorenz and Cappell, 2008) by comparing older and young adults' behavioural performance and ERPs, and the results have revealed some important findings. However, a methodology limitation involved in the ERP analysis is that the default clusters are defined by comparing young-old group ERP differences on neutral condition, then the anger and happiness ERPs are extracted from these clusters for further analysis. This method might fail to capture certain emotion-specific neutral activation differences between young and older adults as the processing of anger and happiness rely on different regions of the brain.

7.6 General Summary

In summary, this thesis investigated the effect of advancing age on social perception, and explored the underlying neural mechanism of facial emotion perception in older adults. Current findings show that healthy aged adults have declined perception of facial emotion and facial identity. Specifically, older adults have declined ability in perceiving both upright- and inverted- facial identities, but they have intact ability in perceiving fine-detailed non-face objects. This might be due their deficits in handling fine internal features that involve perception of fine spatial frequencies (e.g. Meinhardt-Injac, Persike & Meinhardt, 2014). For facial emotion perception, older adults have deficits in encoding both low- and high-intensities of anger, and low-intensities of happiness. Using non-invasive brain stimulation, high frequency tRNS targeted to older adults' inferior frontal cortex enhanced their perception of anger, especially with low-performing older adults. This finding seems compatible with the CRUNCH model, in which low-performing older adults (i.e. those that are inefficient in recruiting additional/bilateral neural regions) have more available neural resources for stimulation to induce additional benefits. In terms of ERPs, older participants showed neural overactivation in the left frontal and centromedial regions (100-200ms stimuli onset) and frontal region (250-850ms stimuli onset) not only in anger and happiness perception, but also in neutral emotion perception. This suggested that older people's neural compensation starts at the neutral (baseline) condition. Combining with their behavioural performance on each face perception task, the results might suggest that older people's neural compensation was efficient in neutral emotion perception as they exhibited similar performance as younger participants, but the similar level of neural resources was not enough for them to apply the compensation strategy in perception of anger (both easy and hard conditions) and happiness (hard condition) and lead to their declined perceptual performance compared to younger participants. The findings of ERP study suggest that older people's neural overactivation in frontal-centro regions reflects older people's neutral compensation strategy: inputting increased attention and mental effect across different cognitive tasks in order to achieve better behavioural performance.

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