

Synaesthesia: mechanisms and broader traits.

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I, Agnieszka Barbara Janik, 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

Synaesthesia is a condition in which perceptual or conceptual stimulation in one modality leads to additional experiences within the same or different modality. In grapheme-colour synaesthesia achromatic letters or numbers elicit secondary synaesthetic colour experiences while in mirror-touch synaesthesia observing touch to another person results in tactile sensations on a synaesthete's own body. This thesis examines broader differences in personality and social perception associated with synaesthesia and investigates neural mechanisms underlying social perception in typical adults. Firstly, an association between grapheme-colour synaesthesia and personality traits was examined which revealed an altered personality profile in this group. Additionally grapheme-colour synaesthesia showed typical and (in some cases) superior social perception abilities relative to typical adults which most likely reflects wider perceptual differences related to sensitivity to high spatial frequency information previously found in this group. Secondly, an investigation into the wider consequences of mirror-touch synaesthesia revealed that the presence of this form of synaesthesia is linked with lower levels of alexithymia relative to typical adults and lower interoceptive sensitivity relative to grapheme-colour synaesthetes and controls. This thesis also explored the neural mechanisms underlying social perception in typical adults using non-invasive transcranial alternating current stimulation. This revealed that enhancing occipital gamma oscillations facilitates facial anger perception offering a new avenue to examine the neural mechanisms underlying social perception advantage in synaesthesia. Current findings are discussed in the context of existing literature on synaesthesia and social perception.

TABLE OF CONTENTS

List of figures	7
Publications arising from thesis	9
Chapter 1: Introduction	10
1.1 Definition and origins of synaesthesia	10
1.2 Tests of authenticity	11
1.3 Prevalence and classification	14
1.4 Theories of synaesthesia and supporting evidence	16
1.5 Grapheme-colour synaesthesia	22
1.5.1 Prevalence and classification	22
1.5.2 Characteristics	23
1.5.3 To what extent is the synaesthetic colour like real colour perception	26
1.5.4 To what extent is the synaesthetic colour like imagined colour	29
1.5.5 Broader traits associated with grapheme-colour synaesthesia	29
1.5.5.1 Imagery	29
1.5.5.2 Memory	31
1.5.5.3 Perceptual differences	32
1.5.5.4 Personality	35
1.6 Mirror-touch synaesthesia	35
1.6.1 Prevalence and classification	35
1.6.2 Tests of authenticity	37
1.6.3 Theories of mirror-touch synaesthesia and supporting evidence	39
1.6.4 Broader traits associated with mirror-touch synaesthesia	42
1.7 Aims of thesis	43

Chapter 2: Synaesthesia and personality traits	45
2.1 Introduction	46
2.2. Study 1: Imagery and schizotypy	49
2.3 Study 2: Sensation seeking and Self-monitoring	55
2.4 General Discussion	58
Chapter 3: Social perception in grapheme-colour synaesthesia	64
3.1 Introduction	64
3.2 Experiment 1: Processing of facial expressions of emotion and identity using the Cambridge Face Perception Tests	67
3.3 Experiment 2: Processing of facial information using the face composite task	74
3.4 General Discussion	80
Chapter 4: Relationship between synaesthesia and alexithymia	84
4.1 Introduction	84
4.2 Experiment 3: Synaesthesia and alexithymia	88
4.3 Discussion	91
Chapter 5: Interoceptive sensitivity in synaesthesia	96
5.1 Introduction	97
5.2 Experiment 4: Interoceptive sensitivity in mirror-touch synaesthetes, grapheme-colour synaesthetes and controls	102
5.3 Experiment 5: Interoceptive sensitivity and emotion recognition	106
5.4 Discussion	107
Chapter 6: Methodological introduction to transcranial current stimulation	111
6.1 Introduction	111
6.2 Transcranial direct current stimulation (tDCS)	112

6.3 Transcranial random noise stimulation (tRNS)	112
6.4 Transcranial alternating current stimulation (tACS)	113
Chapter 7: Mechanisms of facial expressions of affect	122
7.1 Introduction	122
7.2 Experiment 6: The role of occipital gamma and occipital alpha in anger perception	125
7.3 Experiment 7: The role of occipital gamma in anger and facial identity Perception	128
7.4 Experiment 8: The role of occipital gamma at 40 Hz and 100 Hz in anger perception	131
7.5 General Discussion	133
Chapter 8: Conclusions	137
References	147

LIST OF FIGURES

Figure 1.1 Examples of Eagleman Synaesthesia Test Battery results.	12
Figure 1.2. Example of the classic and synaesthetic Stroop Effect.	13
Figure 1.3 Specular and anatomical frames of reference present in MTS.	37
Figure 1.4 Synaesthetic Stroop task	39
Figure 2.1 Mean scores on the Unusual Experiences subscale of O-Life in grapheme-colour synaesthetes and controls.	52
Figure 2.2 Mean total scores on the Vividness of Visual Imagery Questionnaire in grapheme-colour and controls.	52
Figure 2.3. Regression coefficients for the relationship between group and UE (schizotypy) are not mediated by TVVIQ (imagery).	54
Figure 2.4. Regression coefficients for the relationship between group and TVVIQ (imagery) are not mediated by UE (schizotypy).	55
Figure 3.1 Examples of trials of a) CFPT-Identity and b) CFPT-Angry	69
Figure 3.2 Mean percentage of correct responses for synaesthetes and controls on the Cambridge Face Perception Task-Identity upright and inverted trials	71
Figure 3.3 Mean percentage of correct responses for synaesthetes and controls on the Cambridge Face Percentage Task-Angry and Cambridge Face Percentage Task -Happy.	72
Figure 3.4 Example of stimuli used in the face composite task.	76
Figure 3.5 Mean accuracy scores for synaesthetes and controls on the face composite task including upright aligned, upright misaligned, inverted aligned and inverted misaligned trials.	77
Figure 3.6 Mean reaction times for synaesthetes and controls on the face composite task including upright aligned, upright misaligned, inverted aligned and inverted misaligned trials.	78
Figure 3.7 Face composite effect computed on accuracy data for synaesthetes and controls on upright and inverted trials.	79
Figure 3.8 Face composite effect computed on reaction times data for synaesthetes and controls on upright and inverted trials.	80

Figure 4.1 Mean total scores on Toronto Alexithymia Scale for grapheme-colour synaesthetes, mirror-touch synaesthetes and control participants.	90
Figure 5.1 Diagram showing existing findings on the association between interoceptive sensitivity, body representation, imitation inhibition, alexithymia, sensitivity to emotions of others and mirror-touch synaesthesia.	102
Figure 5.2 Mean scores on interoceptive sensitivity for mirror-touch synaesthetes, grapheme-colour synaesthetes and controls.	105
Figure 6.1 tACS devise manufactured by Neuroconn.	116
Figure 7.1 Mean percentage of correct responses on the Cambridge Face Perception Task-Angry when delivering transcranial alternating current stimulation to the primary visual cortex in the gamma and alpha band.	127
Figure 7.2 Mean percentage of correct responses following occipital gamma or sham transcranial alternating current stimulation on the Cambridge Face Perception Task-Angry, Cambridge Face Perception Task - Identity upright trials, and Cambridge Face Perception Task -Identity inverted trials.	131
Figure 7.3 Mean percentage of correct responses following occipital gamma transcranial alternating current stimulation at 40 Hz and 100 Hz on the Cambridge Face Perception Task-Angry.	133

PUBLICATIONS ARISING FROM THESIS

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CHAPTER 1: INTRODUCTION

This introduction provides a review of the existing scientific literature on synaesthesia. It discusses prevalence, authenticity and characteristics of this condition. It also provides a summary of dominant theories of synaesthesia as well as an overview of psychophysical, neuroimaging and non-invasive brain stimulation studies which shed light on its underlying neurocognitive mechanisms. This chapter also provides a summary of wider traits associated with synaesthesia. This thesis focuses on two forms of this condition: grapheme-colour synaesthesia and mirror-touch synaesthesia. The primary aims of this thesis are to elucidate broader personality traits and differences in social perception linked to these two forms of synaesthesia and to investigate neural mechanisms underlying social perception in typical adults.

1.1 Definition and origins of synaesthesia

Synaesthesia (Greek: syn – union, aesthesis – sensation) is a rare condition where one attribute of a stimulus (e.g. its shape or meaning) triggers an involuntary and automatic conscious experience of another attribute, which may be within the same or different modality (Sagiv, 2004; Grossenbacher and Lovelance, 2001; Ward, 2013). For instance, in grapheme – colour synaesthesia, letters or numbers printed in black ink (the inducers) elicit secondary synaesthetic colour experiences (the concurrents). More than 60 different types of this condition have been documented so far (Cytowic and Eagleman, 2009). They include, for instance, tone-colour synaesthesia where sounds trigger colour experiences (Ward, Huckstep, and

Tsakanikos, 2006), lexical-gustatory synaesthesia where words elicit taste sensations (e.g. Ward and Simner, 2003) or time-space synaesthesia where days and months are represented in a spatial arrangement (Simner, Mayo, and Spiller, 2009).

Although first documented cases of synaesthesia date back to the beginning of the 19th century (Jewanski, Day, and Ward, 2009) it was not until the end of the 20th century when new objective tests were developed that synaesthesia became recognized as a legitimate phenomenon. Since then scientific investigation of synaesthesia has extended beyond merely examining the nature of the synaesthetic experience and focused on broader differences including multisensory processing (Sagiv and Ward, 2006), imagery (Barnett and Newell, 2008; Spiller and Jansari, 2008), or attention (Treisman, 2004; Sagiv, Heer, and Robertson, 2006). In this chapter, I will review the existing literature on prevalence, authenticity, theories and characteristics of synaesthesia. I will then discuss these in the context of grapheme-colour and mirror-touch synaesthesia. The aim of this thesis is to investigate broader differences associated with these two variants of synaesthesia and their underlying mechanisms.

1.2 Tests of authenticity

The authenticity of synaesthesia is typically established by means of consistency tests where synaesthetes show greater consistency of inducer-concurrent pairings (as much as 80-100%) relative to controls (30-50%) (Mattingley, Rich, Yelland, and Bradshaw, 2001). Originally, the tests would be repeated after some time has elapsed (e.g. several weeks) in order to calculate the consistency score (Baron-Cohen and Wyke, 1987). However, nowadays they are typically done within the same session using, for example, the online Eagleman Synaesthesia Test Battery

(Eagleman, Kagan, Nelson, Sagaram, and Sarma, 2007) where inducers are paired with concurrents using a colour picker and where a score below 1 indicates a presence of synaesthesia (Figure 1.1). Although this form of verification has received some criticism for being too strict and not sensitive enough to detect synaesthetes with less fixed inducer-concurrent pairings (Simner, 2012), consistency tests are widely used in synaesthesia research. In addition to grapheme-colour synaesthesia other forms of this condition including emotion-colour (Ward, 2004) or lexical-gustatory synaesthesia (Ward and Simner, 2003; Ward, Simner, and Auyeung, 2005) have been associated with similar consistency levels.

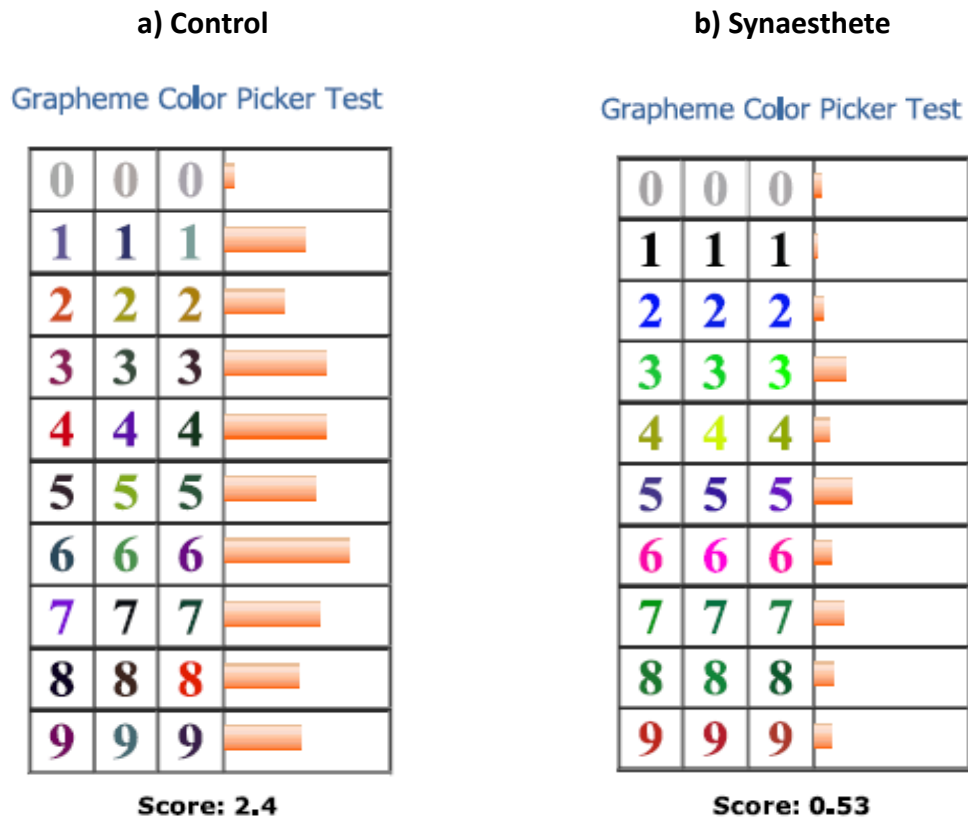


Figure 1.1 Examples of Eagleman Synaesthesia Test Battery results. In this consistency test participants are asked to pick a colour from a colour palette that best matches their synaesthetic colour of that grapheme. Graphemes are ordered randomly and each of them appears three times. Synaesthetes are more consistent with their matching than controls: a) Test results of a control participant b) Test results indicating presence of synaesthesia. These screenshots were taken from <http://www.synesthete.org>.

Another method to verify synaesthesia is by means of a synaesthetic Stroop test (Mills, Boteler, and Oliver, 1999). In the original Stroop paradigm participants are presented with colour words which are printed in congruent (e.g. word RED is printed in red ink) or incongruent colours (e.g. word RED is printed in blue ink). The Stroop effect relates to an interference manifested in reduced accuracy and slower reaction times when participants need to name the ink colour of incongruently coloured words (Stroop, 1935). In the synaesthetic version of this classic paradigm synaesthetes are asked to name the real colour of the inducers i.e. letters which are printed either in colours which are congruent or incongruent with their synaesthetic experiences (Figure 1.2). While for controls there is no interference, synaesthetes are faster at naming the colours which are in line with their synaesthesia and slower when the two colours do not match (Mills et al., 1999). The same pattern of results was found for other forms of synaesthesia including sound-colour (Ward et al., 2006) or music-taste synaesthesia (Beeli, Esslen, and Jäncke, 2005).

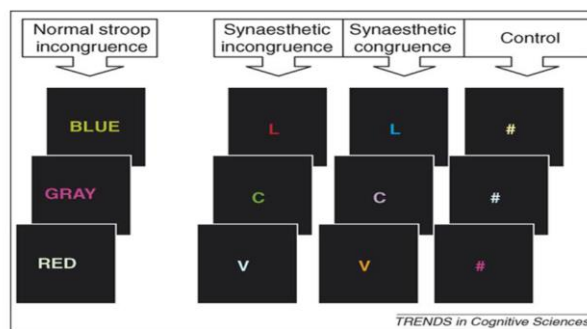


Figure 1.2. The classic Stroop Effect causes interference when naming the ink colour of incongruently coloured words (e.g. when word 'blue' is printed in green). Synaesthetic Stroop effect consists in reduced performance when naming the real colour of graphemes which are incongruent with the synaesthetic experiences (e.g. when letter L is printed in red and its synaesthetic colour is blue) but not when the real and synaesthetic colours are congruent (e.g. when letter L is printed in blue and its synaesthetic colour is also blue) or when control symbols that do not induce synaesthetic experiences (e.g. hashtag) are used. Taken from Mulvenna and Walsh (2006).

1.3 Prevalence and classification

Although earlier reports speculated that approximately 1 in 2000 people experience synaesthesia and that the female to male ratio is 5:1 (e.g. Baron-Cohen, Burt, Smith-Laittan, Harrison, and Bolton, 1996; Rich, Bradshaw, and Mattingley, 2005) the current estimate suggests that synaesthesia is present in about 4% of the population and that equally as many men and women experience this condition (Simner et al., 2006; Ward and Simner, 2005). The possible explanation behind this discrepancy might be that earlier studies relied on self-referrals (Baron-Cohen et al 1996; Rich et al 2005), while later estimates were based on objective tests verifying authenticity of synaesthesia (e.g. Simner et al., 2006).

Synaesthesia can be both developmental and acquired. Developmental cases are not a results of neurological damage but rather are present from birth and tend to run in families (Jewanski, Day, Simner, and Ward, 2011), although individual family members may experience different forms of synaesthesia and their inducer-concurrent pairings are often not the same (Barnett et al., 2008). Additionally, having one type of synaesthesia increases the likelihood of experiencing another form of this condition (Sagiv, Simner, Collins, Butterworth, and Ward, 2006). There is evidence that synaesthesia can skip generations (Hubbard and Ramachandran, 2003) and of monozygotic twins being discordant for synaesthesia (Smilek, Mofatt, Pasternak, White, Dixon, and Merilke, 2002) suggesting that while a susceptibility for developing synaesthesia might have its roots in genetics it is by no means deterministic (Asher et al., 2009).

Acquired cases are typically brought on by a traumatic head injury or a stroke (Ro et al., 2007) as well as a loss of sensory input (e.g. blindness; Afra, Funke, and Matsuo, 2009). There have also been attempts to induce synaesthesia with drugs

(Sinke, Halpern, Zedler, Neufeld, Emrich, and Passie, 2012), hypnosis (Cohen Kadosh, Henik, Catena, Walsh, and Fuentes, 2009; Anderson, Seth, Dienes, and Ward, 2014) or by establishing inducer-concurrent associations through training (e.g. Rothen and Meier, 2014; Bor, Rothen, Schwartzman, Clayton, and Seth, 2014). It has been suggested that artificially induced synaesthesia is not in fact synaesthesia but rather an example of cross-modal correspondences or imagery due to a lack of reported synaesthetic phenomenology as well as the fact that the effects of training disappear with time whereas developmental synaesthesia tends to persist throughout a lifetime (Deroy and Spence, 2013). However, recently Bor and colleagues (2014) reported that they were able to induce synaesthesia with training which they assessed with various tests of authenticity, and that their participants reported phenomenological experiences which resembled those of genuine grapheme-colour synaesthetes (GCS). However, although their participants still showed synaesthetic Stroop effect after 3 months from training, their phenomenological experiences largely disappeared thus putting in question the genuineness of their synaesthesia.

Synaesthetes can also be classified as high or low depending on the level of their synaesthetic triggers. While low synaesthetes might be sensitive to the physical characteristics of an inducer such that e.g. upper case letters or high frequency fonts would produce more vivid colour experiences than those printed in lower case or in low frequency fonts (Ramachandran and Hubbard, 2003; Witthoft and Winawer, 2006). On the other hand for high synaesthetes it is the higher level conceptual properties of an inducer that elicit synaesthetic experiences rather than its low level features. For instance, different physical variants of the same letter (e.g. printed in different fonts) would consistently induce the same synaesthetic concurrent for high level synaesthetes (Grossenbacher and Lovelace, 2001).

1.4 Theories of synaesthesia and supporting evidence

Three influential hypotheses of the mechanisms underlying synaesthesia are the cross-activation (Ramachandran and Hubbard, 2001a), cortical disinhibition (Grossenbacher and Lovelace, 2001; Cohen Kadosh and Walsh, 2008) and the re-entrant feedback theory (Smilek, Dixon, Cudahy and Merikle, 2001).

The cross-activation model states that increased connections between neighbouring brain areas such as the visual word form area (VWFA) and colour sensitive regions of the brain (e.g. hV4) provide the basis for synaesthetic experiences. Recent cross-activation accounts also highlight an important role of attentional processes located in the parietal lobe, which allow for binding information from these two areas into one coherent percept (Hubbard, Brang, and Ramachandran, 2011).

Disinhibition accounts advocate that a lack of inhibition from multisensory (Grossenbacher and Lovelace, 2001) or executive control regions (Cohen Kadosh et al., 2009) to unisensory brain areas is the source of synaesthesia. In a related context it has also been suggested that synaesthesia arises as a consequence of local differences in cortical excitation through mechanisms akin to perceptual unmasking (Cohen Kadosh and Henik, 2007; Cohen Kadosh and Walsh, 2008).

The re-entrant feedback model (Smilek et al., 2001) suggests a crosstalk between form and colour sensitive brain regions but at the same time highlights the importance of top-down processes exerted by feedback connections from brain regions involved in conceptual representation to those involved in colour processing, thus emphasizing the essential role of the activation of the conceptual representation of the inducer (e.g. grapheme) in the elicitation of the synaesthetic experience of colour concurrent.

While these different theoretical models can explain the mechanisms underlying synaesthesia construed as a perceptual condition, their ability to account for the conceptual phenomena of synaesthetic experiences is not uniform. The cross-activation theory (Ramachandran and Hubbard, 2001a) acknowledges the involvement of top down mechanisms in the binding of the inducer and concurrent, however it does not regard this process to play a role in evoking synaesthetic experiences. Similarly, the disinhibited feedback theory does not consider the possibility of purely concept driven synaesthetic concurrents (Grossenbacher and Lovelace, 2001). On the other hand, the re-entrant model postulates that top down processes such as categorization of an inducer play an essential part in the elicitation of the synaesthetic experiences (Smilek et al., 2001) and as such can accommodate the findings of conceptually induced synaesthesia.

To examine these models, one stream of research has investigated if synaesthesia is associated with structural brain differences in colour relevant brain areas. Using diffusion tensor imaging technique (DTI) Rouw and Scholte (2007) found synaesthesia to be linked with increased structural connectivity in the right inferior temporal cortex. Others, however, failed to find similar results (e.g. Jancke, Beeli, Eulig, and Hanggi, 2009; Hupé, Bordier, and Dojat, 2012). A similar pattern has emerged from studies using voxel-based-morphometry (VBM) to examine grey matter differences between synaesthetes who experience colour as their evoked sensation; with some (Jancke et al., 2009; Weiss and Fink, 2009; Banissy et al., 2012), but not all (e.g. Hupé et al., 2012; Rouw and Scholte, 2010) studies reporting synaesthesia to be associated with increased grey matter volume in brain areas linked to veridical colour processing in typical adults. Notably, in the studies that do report grey matter differences in neural regions close to those previously associated with

veridical colour processing, the regions responding to colour were not functionally localized in their subjects; given inter-individual variability in cortical colour responsiveness it is therefore difficult to disentangle the exact relationship between brain structure and function.

A number of studies have also used non-invasive brain stimulation methods to elucidate neural mechanisms underlying synaesthetic experiences. Such techniques allow for establishing whether specific cortical regions are necessary for particular functions and as such they permit inferences about the causal involvement of specific brain areas in cognition (e.g. the role of the right occipital face area in face processing; Pitcher, Walsh, Yovel, and Duchaine, 2007). However, non-invasive brain stimulation methods cannot reach deep brain structures and therefore they can only be used to examine the functional contribution of superficial brain areas (Chen and Rothwell, 2012).

Esterman, Verstynen, Ivry, and Robertson (2006) delivered repetitive transcranial magnetic stimulation (rTMS) over right parieto-occipital region, left parieto-occipital region and V1 of two projector GCS in order to examine the role of these regions in synaesthesia. TMS uses electromagnetic induction to depolarize or hyperpolarize a target area of the cortex depending on the setup leading to a transient and reversible modulation of neural activity in this area (Walsh and Rushworth, 1999). rTMS allows for delivering repeated single magnetic pulses of the same intensity to a target brain region (e.g. Wassermann et al., 1996). The authors of this study concluded that delivering rTMS to right parieto-occipital region, previously linked to feature binding in typical individuals (Freidman-Hill, Robertson, and Treisman, 1995; Donner, Kettermann, Diesch, Ostendorf, Villringer, and Brandt,

2002), but not other two areas disrupts synaesthesia measured by diminished interference on a synaesthetic Stroop task.

Muggleton, Tsakanikos, Walsh, and Ward, (2007) extended these findings by examining the effect of TMS on synaesthetic experience measured with a synaesthetic Stroop test in a group of four associator synaesthetes and one projector synaesthete. In line with Esterman et al., (2006) study, Muggleton and colleagues also concluded that delivering TMS to the right parieto-occipital area leads to a reduction in interference, highlighting a key role of this region in spatial binding of graphemes and colours both in associator and projector synaesthetes. Further, Rothen, Nyffeler, von Wartburg, Müri and Meier (2010) demonstrated that both right and left parieto-occipital areas are involved not only in explicit but also implicit binding of inducer and concurrent in synaesthesia as suppressing these regions with TMS disrupts implicit biderctionality.

TMS has also been employed by Terhune, Tai, Cowey, Popescu and Cohen Kadosh, (2011) who delivered it over primary visual and motor cortices to establish whether grapheme-colour synaesthesia is associated with enhanced cortical excitability. Their results indicated that synaesthetes had substantially lower phosphene thresholds, which is a measure of cortical excitability, compared to controls but there was no group difference in terms of motor excitability, suggesting a modality-specific cortical hyperexcitability in synaesthesia. To further elucidate underlying neural mechanisms Terhune and colleagues delivered transcranial direct current stimulation (tDCS) over V1 while participants completed a synaesthetic digit-colour priming task and a control task. tDCS is a non-invasive transcranial current stimulation (tCS) technique which involves applying low intensity direct constant current via external electrodes placed on scalp in order to increase (anodal

stimulation) or decrease (cathodal stimulation) cortical excitability in the area beneath the electrodes (Costa, Lapenta, Boggio, and Ventura, 2015). The results of this study revealed that delivering cathodal (inhibitory) tDCS over V1 increases the magnitude of synaesthetic interference relative to sham condition, while anodal stimulation (excitatory) produces the opposite effect, suggesting that hyperexcitability within V1 generates excess noise resulting in diminished synaesthesia. The authors speculated that this enhanced cortical excitability might have promoted atypical binding of graphemes and colours in the early stages of development leading to the emergence of synaesthesia, but that with maturation this hyperexcitability has become a source of cortical noise.

In a recent study Terhune, Song and Cohen Kadosh (2015) found projector synaesthetes (who report their synaesthetic photisms to occur externally on the surface of the inducers) to have reduced phosphene thresholds relative to associator synaesthetes (who experience their synaesthetic concurrents internally in their mind's eye) and controls when delivering transcranial alternating current stimulation (tACS) at 40Hz to V1. tACS is another form of tCS which is able to interact with and align neural oscillations within a target brain area to the frequency of stimulation (Antal and Paulus, 2013). The results of this study are in line with previous findings suggesting a crucial role of oscillatory activity in this frequency band in perceptual binding (Boudreau, 1964; Freeman, 1975; Singer, 2001). This was interpreted by Terhune et al. (2014) as evidence for increased visuospatial binding underpinning co-localization of inducers and concurrents in the external space in projector synaesthetes (Ward, Li, Salih, and Sagiv, 2007).

Further Terhune, Murray, Near, Stagg, Cowey and Cohen Kadosh (2015) examined whether previously identified differences in phosphene thresholds found in

synaesthesia (Terhune et al., 2015) have neurochemical basis. In this new study they again delivered TMS over V1 and M1 to establish phosphene and motor thresholds in synaesthetes and controls. Additionally, using magnetic resonance spectroscopy, which is a non-invasive analytical technique conducted on the same scanner as magnetic resonance imaging which allows for examining the chemical composition of brain tissue (Frangou and Williams, 1996), the authors measured the concentration of basal GABA and glutamate in V1 and M1. They focused on these neurotransmitters as previous work has shown that glutamate level in M1 correlates with motor cortex excitability (Stagg et al., 2011) while other strand of research suggests that phosphene thresholds may rely on local GABA concentration (Brigo et al., 2013). This led the authors to hypothesise that similar mechanisms may underly enhanced V1 excitability in synaesthetes. Their findings indicated that phosphene thresholds negatively correlated with glutamate levels in visual cortex and that projector synaesthetes had lower phosphene thresholds compared to associator synaesthetes. Additionally, both synaesthetic subgroups had lower phosphene thresholds relative to controls, thus replicating and extending their previous findings. While glutamate level was associated with individual differences in synaesthetic experience, with projectors having elevated glutamate in the visual cortex relative to associators, no difference was found in terms of concentration of this neurochemical between synaesthetes and controls. Additionally, synaesthetes did not differ from controls in terms of visual cortex GABA concentration. As in their previous study Terhune et al., (2015) suggest that heightened glutamate might have contributed to the development of synaesthesia in the initial stages but that with time concentration of this neurochemical returned to a normal level. They also hypothesise that atypical

glutamate receptor activity, rather than its levels, might account for elevated phosphene thresholds found in this group.

1.5 Grapheme – colour synaesthesia

1.5.1 Prevalence and classification

Grapheme-colour synaesthesia is a type of synaesthesia where achromatic letters or numbers trigger secondary synaesthetic colour experiences e.g. the letter A is perceived as red or the number 8 as green (Ward, 2013). It is estimated that the prevalence of this variant of synaesthesia is 1.4 % (Simner et al. 2006). The authenticity of this form of synaesthesia is typically verified with consistency tests such as the previously described online Eagleman synaesthesia test (Eagleman, et al., 2007) or with a synaesthetic Stroop test (Mills et al., 1999).

Synaesthesia is a highly heterogeneous condition and as many as five different spatial reference frames have been identified (Ward, 2013). However, grapheme – colour synaesthetes are usually classified either as projectors or associators based on the locus of their synaesthetic experiences (Ward, Li, Salih, and Sagiv, 2007). Projectors report experiencing their concurrents in the external space, often superimposed on the inducers but without obstructing them so that the real and synaesthetic colour of a grapheme co-exist. Associators, on the other hand, describe their synaesthetic experiences to be located in their mind's eye. Neuroimaging studies have demonstrated that these two groups of synaesthetes are linked to distinctive structural and functional brain differences. For instance associator synaesthetes have been shown to have greater grey matter volume and increased activity in the hippocampus and parahippocampal gyri, while projector synaesthetes

have been linked to increased grey matter volume in the primary visual cortex (e.g. Rouw and Scholte, 2010).

1.5.2 Characteristics

A number of studies reported that low-level physical features of inducers can influence synaesthetic colour experiences. For instance, high frequency fonts give rise to greater intensity of synaesthetic colours compared to low frequency fonts (Ramachandran and Hubbard, 2003; Witthoft and Winawer, 2006). Similarly, upper case letters can produce more vivid colour experiences than those printed in lower case (A vs a) (Witthoft and Winawer, 2006). It has also been shown that graphemes that are similar in shape (e.g., E, 3) compared to those which are not (e.g., E, X) can be coloured in a similar fashion (Eagleman, 2010; Brang, Rouw, Ramachandran, and Coulson, 2011).

Although these reports suggest that visual properties of inducers might influence synaesthetic experiences, other findings indicate that the appearance of inducers has little impact on synaesthetic colours. For instance, an inducer would typically elicit different synaesthetic colours depending on its context, which has been demonstrated with a version of a synaesthetic Stroop paradigm (Dixon, Smilek, Duffy, Zanna, and Merikle, 2006). The authors of this study reported that for a projector synaesthete naming the colour of an unambiguous grapheme, which could be interpreted either as a letter or a number depending on whether it was embedded in a digit or letter string, led to faster responses when that grapheme was coloured congruently with her interpretation of that grapheme than when the grapheme was coloured incongruently. Similarly, different physical variants of the same letter (e.g., a, A, **a**) tend to consistently produce the same synaesthetic colour (Grossenbacher

and Lovelace, 2001). Additionally, although in some cases the modality of an inducer plays an important role (e.g. see Arnold, Wegener, Brown, and Mattingley, 2012; Simner, 2012; Jansari, Spiller and Redfern, 2006) for other synaesthetes colour concurrents are elicited irrespective of whether the inducer is heard, read, or merely thought about (Rich, Bradshaw, and Mattingley, 2005).

These findings demonstrate that while occasionally purely perceptual features of an inducer might influence concurrents, for a number of synaesthetes it is higher level cognitive constructs that elicit colour experiences. This has led some to suggest that synaesthesia is in fact a form of 'ideasthesia' (Jürgens and Nikolic, 2012). This idea has been addressed in a number of different studies that sought to determine if it is necessary for the inducer to be physically present in order to produce synaesthetic experiences. For example, in a study carried out by Dixon, Smilek, Cudahya and Merikle (2000) a synaesthete was visually presented with a simple arithmetic task such as e.g. '2+5 =' followed by a colour patch. The task was to first name the colour patch and to subsequently give a solution to the problem. The authors reported that the synaesthete was quicker at naming the colour patch when it was congruent with the synaesthetic colour of the solution and slower when these colours did not match. These results have been subsequently replicated in the auditory domain in a study carried out by Jansari and colleagues (2006), where participants heard rather than saw examples such as '2+5 = yellow'. These findings suggest that it is the concept of the inducer rather than physical properties that triggers synaesthetic experiences of colour.

Additionally, implicit bidirectionality has been demonstrated in many studies. For instance, Brugger et al., (2004) reported that digit-colour synaesthetes compared to controls had faster left-hand responses to colours associated with small digits and

faster right-hand responses for colours representing large numbers, suggesting that these synaesthetes could access numerical magnitude information through their colour associations. Similar results have been found in the domain of lexical processing. For example, Weiss et al. (2009) asked GCS and controls to perform a word completion task where either high or low-frequency words could be generated by inserting a different first letter. A colour patch consistent with the individual synaesthetes' colour concurrents replaced the space where first letter would appear, biasing them to generate low-frequency words significantly more often than the control participants. This was interpreted as evidence for implicit bidirectional priming. Behavioral data demonstrating the bidirectional nature of synaesthetic experience has also been supported by neuroimaging evidence which suggested that colour can activate the number form area of the fusiform gyrus in a grapheme-colour synaesthete, for whom synaesthesia typically manifests itself in a uni-directional fashion i.e. digits elicit colour concurrents (Cohen Kadosh, Cohen Kadosh, and Henik, 2007). Recently bidirectional priming in synaesthesia has also been demonstrated across different sensory modalities (vision and audition; Paffen, Van der Smagt, and Nijboer, 2015), further supporting the claim that although subjective synaesthetic experiences are typically reported to follow the unidirectional path from the inducer to the concurrent, it is possible to induce priming in the opposite direction. More importantly, these findings suggest that synaesthesia relies on higher-order representations rather than low-level sensory processing.

Further evidence in support of the idea that it is possible to elicit synaesthetic concurrents in the absence of a sensory inducer has been provided by Nikolić Juergens, Rothen, Meier, and Mroczko (2011), and Rothen et al. (2013), who reported a new form of synaesthesia where swimming styles evoke colour

concurrents. Their findings suggest that the proprioceptive input associated with different swimming styles is not essential to elicit synaesthetic colours, instead the mere concept of it, induced with photographs (Nikolić et al., 2011) or pictograms of different swimming styles (Rothen et al., 2013) is sufficient to evoke colour concurrents.

Grapheme-colour synaesthesia might also be elicited in even more extreme circumstances. For instance, synaesthetes who have lost their sight and thus have no means of visually processing the graphemes still report very vivid colour experiences triggered by letters, numbers, words or Braille characters (Steven and Blakemore, 2004). Neuroimaging studies using fMRI have further validated these subjective reports by demonstrating that listening to words inducing synaesthetic colour experiences in blind synaesthetes is associated with activity in colour sensitive brain areas (Steven, Hansen, and Blakemore, 2006; Niccolai, van Leeuwen, Blakemore, and Stoerig, 2012). However, as the experimenters were not able to localize these brain regions there is no guarantee that the reported activation in colour areas is actually related to veridical colour processing.

1.5.3 To what extent is the synaesthetic colour like real colour perception?

The findings of functional neuroimaging studies are inconsistent. Some fMRI studies report hV4 activation in response to both chromatic and achromatic stimuli inducing synaesthetic colour experiences (Hubbard, Arman, Ramachandran, and Boynton, 2005; Sperling, Prvulovic, Linden, Singer, and Stirn, 2006). Hubbard and colleagues (2005) also found that the strength of hV4 activation to achromatic inducers in GCS was mediated by their performance on a visual crowding task, which required identifying an achromatic target grapheme presented in the visual

periphery and surrounded by other graphemes printed in black ink. Greater activation in hV4 was linked to better performance on this task suggesting that real and synaesthetic colour processing might be driven by the same mechanisms. However, other studies failed to replicate these findings, putting in question the idea that these processes are analogous (Sinke et al., 2012; Hupe et al., 2012; Rouw and Scholte, 2010). Indeed, recently the reliability of the findings suggesting that synaesthetic colour is handled by colour-sensitive brain regions has been further undermined by Hupe and colleagues (2012) who pointed out that studies reporting functional neural activity in regions of the brain linked to colour processing during the experience of synaesthesia tended to apply liberal statistical thresholds. In their own fMRI study, Hupe and colleagues (2012) investigated whether the brain regions responsive to real colour and those activated by synaesthetic colour overlapped in a group of GCS. Their findings indicated that none of the areas recruited in veridical colour processing, which were individually identified for each of the participants by means of full retinotopic mapping, were activated by a synaesthetic colour; suggesting that it is unlikely that synaesthetic and real colour share identical neural mechanisms. In this regard, neuroimaging has struggled to clarify the extent to which synaesthetic and veridical colour processing rely on common or distinct mechanisms.

Aside from neuroimaging, psychophysical studies have also been employed to investigate whether synaesthetic colour has the properties of the real colour. For instance, Erskine, Mattingley, and Arnold (2012) demonstrated that synaesthetic colour does not produce the colour constancy effect, which characterizes real colour perception and reflects the fact that the perceived colour of objects remains constant despite variations in illumination, which helps to identify objects such as a red apple to be recognized in different lighting conditions. Moreover, it has been reported that

synaesthetic colour is not susceptible to simultaneous colour contrast (Nijboer, Gebuis, Te Pas, and Van Der Smagt, 2011) or chromatic adaptation (Hong and Blake, 2008) all of which are produced by veridical colour. Some reports have, however, indicated that synaesthetic colour and real colour share common characteristics such as the ability to produce the watercolour illusion (Kim and Blake, 2005) or to influence bistable apparent motion (Kim, Blake, and Palmeri, 2006). Nevertheless, these results have been questioned on their methodological basis as well as the fact that the authors used a very small sample size of only two synaesthetes (Chiou and Rich, 2014) and thus need to be treated with caution.

Similarly, although initial reports suggested that synaesthetic colour might pop-out of a display of achromatic graphemes and facilitate the visual search just like real colour does (Ramachandran and Hubbard, 2001b), subsequent studies failed to replicate this finding. While some found synaesthetes to be better than controls on the visual search tasks (Palmeri, Blake, Marois, Flanery, and Whetsell, 2002; Laeng, Svartdal, and Oelmann, 2004; Ward, Jonas, Dienes, and Seth, 2010; Rich and Kartstoft, 2013), their results indicated an involvement of attentional resources in this process thus refuting the possibility that synaesthetic colour is a result of low-level, pre-attentive processes and can pop-out like real colour (Treisman and Gelade, 1980). It has also been suggested that implicit processing of visual stimuli is not sufficient for synaesthetic concurrents to occur, and that only by consciously identifying the inducers it is possible to elicit them (Mattingley, Rich, Yelland, and Bradshaw, 2001). Based on these findings it appears that the mechanisms underlying synaesthetic and real colour are not identical thus putting in question the perceptual nature of synaesthetic experiences.

1.5.4 To what extent is the synaesthetic colour like imagined colour?

In a neuroimaging study conducted by Rich and colleagues (2006) GCS and controls were asked to perform a voluntary colour imagery task which required participants to make colour judgements about objects in grey scale photographs. Participants were also shown letters inducing synaesthetic colours and asked to perform a localization task. The aim of this study was to examine neural mechanisms underlying colour experiences arising in the absence of veridical colour input. Their results indicated that voluntary colour imagery was associated with hV4 activation both in synaesthetes and controls, while synaesthetic colour was linked to neural activity in the left medial lingual gyrus. These findings suggest that synaesthetic and imagined colour may be supported by different brain structures. Interestingly, in view of this others (e.g. Mattingley, 2009; Chiou and Rich, 2014) have suggested that previous reports of enhanced hV4 activation in synaesthesia might in fact reflect mental imagery rather than a perceptual process. Further support for the idea of V4 activity being linked to imagery was provided by Sinke and colleagues (2012) who found no difference between synaesthetes and controls in hV4 activation in response to coloured and black letters and pseudo-letters, when both groups were matched in terms of scores on VVIQ. These findings suggest that synaesthetic colour is a separate phenomenon from real colour perception, although it probably entails much more than mere imagination.

1.5.5 Broader traits associated with grapheme – colour synaesthesia

1.5.5.1 Imagery

Synaesthetes have been found to show enhanced self-reported imagery vividness measured with the Vividness of Visual Imagery Questionnaire (VVIQ)

(Barnett and Newell, 2008; Spiller, Jonas, Simner, & Jansari, 2015). They have also reported increased imagery across other sensory modalities, including audition, gustation, olfaction and tactile modality, and reported to often use imagery in their daily lives (Spiller et al., 2015). Interestingly Spiller and colleagues (2015) also found that greater number of synaesthetic modalities was positively related to greater vividness of imagery. Other forms of synaesthesia have also been associated with enhanced imagery. For instance, sequence-space synaesthetes who experience letters, numbers or months in specific spatial arrangements (Sagiv et al., 2006) showed increased self-reported imagery measured with Object-Spatial Imagery Questionnaire (Price 2009).

GCS have also been found to have enhanced imagery relative to controls on an objective experimental paradigm (Spiller and Jansari, 2008). In this experiment participants heard a grapheme and were required to imagine an upper-case mental representation of that grapheme in a circle presented in the middle of a screen in front of them. They then had to inspect the graphemes and make size-based decisions. Importantly, the background colour was neutral, congruent or incongruent with the synaesthetic colour of the imagined graphemes, which were individually determined prior to the experimental session. The authors of this study found that GCS were faster on this visual imagery task, and that there were important individual differences among synaesthetes. Namely, for some of them background colour which was congruent with their synaesthetic colour of a grapheme facilitated their imagery, for others this resulted in an interference and yet for another group colour congruency did not play a role in their ability to generate a mental image of a grapheme, suggesting a great deal of heterogeneity among GCS.

1.5.5.2 Memory

Synaesthetes have also been found to be better than controls on tests of colour recognition memory as well as memory tests inducing synaesthetic experiences (Yaro and Ward, 2007; Mills, Innis, Westendorf, Owsianiecki, and McDonald, 2006; Rothen and Meier, 2010). There is also some evidence suggesting that GCS have enhanced memory for stimuli that do not trigger their synaesthesia (Ward, Hovard, Jones, and Rothen, 2013; Rothen, Meier, and Ward, 2012).

Results of structural neuroimaging studies using voxel-based morphometry also suggest that GCS, at least those classified as associators, have greater grey matter volume in the hippocampus and parahippocampal gyri, which are brain regions involved in memory processes. Functional imaging results confirmed these results by showing increased activity in these areas in the same group of synaesthetes (Rouw and Scholte, 2010).

Rouw and Scholte (2010) found projector synaesthetes to have structural differences in other brain regions (e.g. increased grey matter volume in V1) than those classified as associators, suggesting that experiencing internal vs external concurrents differs in terms of underlying neural substrates. Van Leeuwen, den Ouden and Hagoort (2011) reported bottom-up activation in projector synaesthetes and top-down influences in associators determined using dynamic causal modelling, providing further evidence for the claim that differences in phenomenal experiences between projector and associator synaesthetes are reflected in different neural mechanisms. Taking into account these individual differences, it is possible that the potential involvement of memory would appear more crucial to associator synaesthetes.

The hypothesis that synaesthesia involves recollection of colour rather than actual colour perception was directly tested in a study carried out by Arnold and colleagues (2012). The authors recruited grapheme—colour synaesthetes who only experienced colours for read, but not heard inducers. In this experiment participants were presented both with printed and spoken graphemes. Using a colour picker they adjusted the colour of the graphemes that triggered, or in case of the auditory condition, that would normally trigger synaesthetic experiences if seen. Their results indicated no difference in the precision of the colour matching between the two conditions, which was interpreted by the authors as evidence for the idea that automatically induced synaesthetic colour resembles colour recalled from memory. In addition, they ran a control experiment which indicated that the precision of matching real visible colours was much greater to recollected colours. Their findings are consistent with previous reports indicating that the precision of colour memory is much lower compared to real-time colour perception (Krill and Richards, 1996). Taken together these results suggest that if triggered in real time or recalled from memory synaesthetic colour is subject to greater variability and less precision than real colour perception suggesting that synaesthetic colour appears to behave more like colour memory than real colour perception.

1.5.5.3 Perceptual differences

While synaesthetic experiences might involve visual imagery or colour memory, grapheme-colour synaesthesia has been shown to be linked to broader differences in perceptual processing. For instance, psychophysical studies examining colour processing of stimuli that do not evoke synaesthesia have reported superior processing of colour in synaesthetes who experience colour concurrents (Banissy,

Walsh, and Ward, 2009; Banissy et al., 2013; Yaro and Ward 2007; Arnold et al., 2012). For example, it has been shown that colour synaesthetes outperform controls on a visual search paradigm in which targets and distractors differ in a single colour dimension (hue, saturation, or luminance), but do not differ when discriminating line orientation (Banissy et al., 2013).

Further, EEG findings suggest that synaesthetes who experience colour as their evoked sensation show perceptual processing differences to stimuli that bias parvocellular pathways (Barnett et al., 2008). In that study, Barnett and colleagues examined neural responses of linguistic-colour synaesthetes to Gabor patches varying in spatial frequency and stimuli of various luminance contrasts. Their results indicated that high spatial frequency stimuli which do not induce synaesthesia and selectively bias parvocellular pathways of the visual system (Derrington and Lennie, 1984; Kaplan, 1991), were associated with enhanced cortical responsiveness in synaesthetes relative to controls. These findings would appear to fit with evidence that synaesthetes who experience colour show heightened perceptual processing of colour. However, it is of note that the perceptual advantage in colour processing shown by colour synaesthetes has been shown to be present for dimensions of hue, luminance, and saturation (Banissy et al., 2013). This, in turn, implies that synaesthetes show perceptual processing advantages for stimuli that do not rely solely upon parvocellular projections (e.g. Lee, Pokorny, Smith, Martin, and Valberg, 1990).

Another broader perceptual difference that has been recently observed in synaesthetes who experience colour as their evoked sensation are elevated motion coherence thresholds (i.e. a reduction in motion processing abilities; Banissy et al., 2013). Colour synaesthetes' and controls' abilities to detect global motion direction

were tested with random-dot kinematograms, which revealed reduced performance in synaesthetes relative to controls. These findings were interpreted in the context of principles that govern interactions between colour and motion in controls. Moreover, non-invasive brain stimulation experiments suggest that brain regions involved in motion and colour processing (e.g. hV5 / MT and hV4) can mutually inhibit one another (Ellison, Battelli, Cowey, and Walsh, 2003; Walsh, Ellison, Battelli, and Cowey, 1998). For example, transcranial magnetic stimulation (TMS) to hV5 / MT results in enhanced colour and form perception and simultaneous suppression of motion processing (Ellison et al., 2003; Walsh et al., 1998). This has been interpreted in the context of a competition for resources between motion and colour areas in the visual system (Ellison et al., 2003; Walsh et al., 1998). It has been suggested that a bias towards colour processing in synaesthesia may mediate this interaction leading to heightened colour, but reduced motion perception in synaesthetes who experience colour as their evoked sensation.

In this context, synaesthesia may be useful to help inform us about principles that govern typical perceptual interactions. For example, the findings of increased colour, but reduced motion processing in synaesthetes who experience colour as their evoked sensation raises the question of the extent to which the perceptual profile that is observed in synaesthetes is present in controls. That is to say, if an individual has elevated colour processing does this come at a cost for motion processing or vice versa. If so, this would suggest a clear way in which synaesthesia may help to inform studies on typical visual processing (see McCarthy and Caplovitz, 2014 for a similar discussion).

1.5.5.4 Personality

Grapheme - colour synaesthesia has also been linked to differences in personality. For instance, it has been linked to greater Openness to Experience, and reduced Agreeableness, which are two subscales of the Big Five Inventory (John, Donahue, and Kentle, 1991; Banissy et al., 2013). GCS have also been associated with increased Fantasizing dimension of the Interpersonal Reactivity Index (Davies, 1980; Banissy et al., 2013). Interestingly, visual artists have also been linked to a similar personality profile (Burch, Pavelis, Hemsley, and Corr, 2006), which is line with previous findings showing a high prevalence of synaesthetes in creative professions (Ward et al., 2008; Rothen and Maier, 2010). This form of synaesthesia has also been associated with positive and disorganized schizotypy (Banissy et al., 2012). Again, similar findings have been reported in non-synaesthetic artistic individuals (Nelson and Rawlings, 2010). Recent findings of Ward et al., (2008) suggest that grapheme-colour synaesthesia might also be linked to greater creativity (Ward et al., 2008) and as mentioned before to possess enhanced imagery vividness (Spiller, Jonas, Simner, and Jansari, 2015; Barnett and Newell, 2008). Interestingly both creativity and imagery have been associated with schizotypy in controls (Oertel et al., 2009).

1.6 Mirror-touch synaesthesia

1.6.1 Prevalence and classification

Mirror-touch synaesthesia is a condition characterized by experiencing tactile sensations on one's own body when observing touch applied to another person. The first documented case of this form of synaesthesia was reported by Blakemore, Bristow, Bird, Frith and Ward (2005). The prevalence of people who meet objective

requirements for mirror–touch synaesthesia is estimated to be 1.6 % of the population (Banissy, Kadosh, Maus, Walsh, and Ward, 2009). Mirror–touch synaesthesia can be divided into two groups based on the spatial mapping of their synaesthetic tactile sensations relative to observed touch (Figure 1.3). Specular type entails experiencing synaesthetic touch on the opposite side to the observed touch. For instance, watching another person being touched on a left cheek will result in a synaesthetic touch on the right side of the face as if looking into a mirror. On the other hand, the anatomical type involves experiencing tactile synaesthetic sensation in the same location where the observed person is being touched, as if a synaesthete mentally rotated him/herself to the position of the observed person. For instance, a synaesthete would experience touch on his/her left cheek when seeing another person being touched on the left cheek. Banissy and colleagues (2009b) report that specular subtype is much more prevalent than the anatomical, with approximately 80% of synaesthetes falling under the former category. The spatial frame of reference extends to other body parts such that e.g. a specular synaesthete would also experience tactile sensation in a specular fashion in response to touch observed to hands (Banissy and Ward, 2007). Recently, further differentiation within the specular subtype into a body-centred and viewer-centered frame of reference has been put forward by White and Aimola Davies (2012) based on the direction of touch.

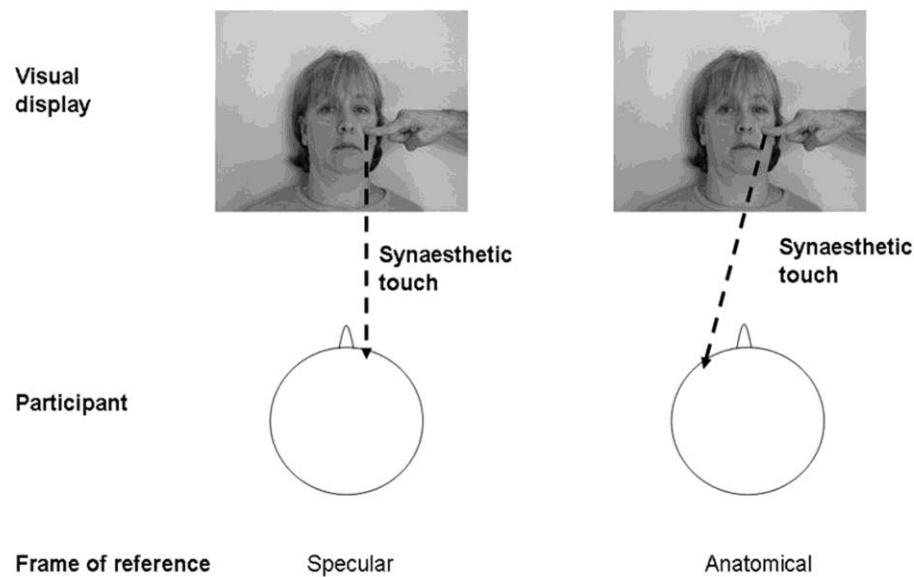


Figure 1.3 Specular and anatomical frames of reference present in mirror-touch synaesthesia. Specular mapping entails experiencing tactile sensation in contralateral fashion i.e. as if looking in a mirror, while anatomical mapping entails feeling touch in the same location as the observed person. Taken with permission from Banissy and Ward (2007).

1.6.2 Tests of authenticity

The authenticity of mirror-touch synaesthesia can be established by means of a mirror-touch Stroop test developed by Banissy and Ward (2007). In this test participants are required to report the location of the felt touch (left, right, both sides, no touch) delivered through tappers secured to the face while watching a series of videos showing a person or an object also being touched (on the left, right, both sides or none). For mirror-touch synaesthetes (MTS) the synaesthetic touch could either be congruent or incongruent with the real touch. For instance, if the participant is a specular mirror-touch synaesthete and the person in the video is touched on the right cheek, he/she will experience synaesthetic touch on the left side of the face (Figure

1.4). Therefore if he/she is also touched on the left cheek it will be congruent with his/her synaesthesia. If, however, the real touch is applied to the right cheek, then the actual and synaesthetic touch will be incongruent. MTS for whom real and synaesthetic touch are phenomenologically similar have been shown to be faster on congruent relative to incongruent trials. They have also been found to make mirror-touch errors e.g. reporting real touch in response to videos where a person was touched but when no real touch was applied to them. Further research has shown that in order for a synaesthetic experience of touch to occur, the stimulus needs to be able to elicit tactile sensations and so e.g. a flash of light is not sufficient to induce mirror-touch synaesthesia (Banissy et al., 2009).

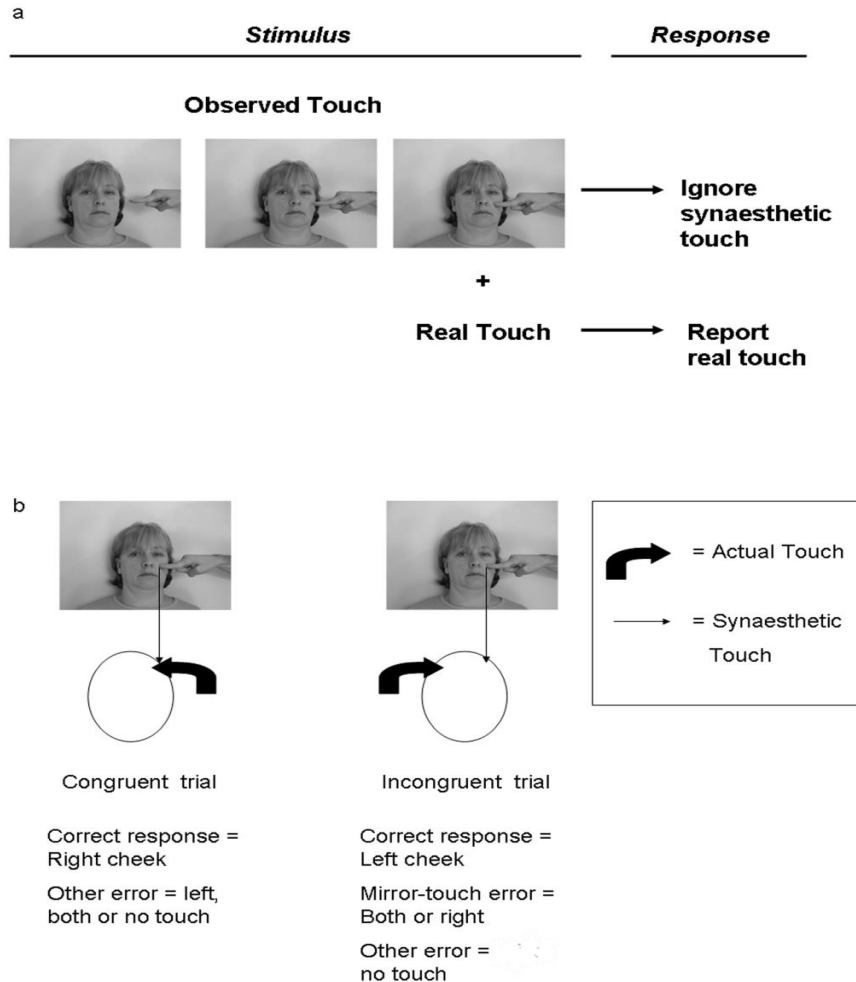


Figure 1.4 Synaesthetic Stroop task a) Participants are asked to indicate the location where they experience real touch while observing touch to another person. b) Example of congruent and incongruent trials for a mirror-touch synaesthete with a specular spatial mapping. For this type of reference frame congruent trials constitute applying real touch to the same side of the face where synaesthetic tactile sensation occurs. Mirror-touch synaesthetes are faster on this type of trials. Incongruent trials involve experiencing real touch and synaesthetic touch on opposite sides of the face. Synaesthetes are prone to mirror-touch errors on incongruent trials. In this case reporting the site of a synaesthetic touch or real touch to both cheeks would constitute such an error. Errors not associated with mirror-touch synaesthesia are referred to as ‘other errors’. Taken with permission from Banissy et al., (2009).

1.6.3 Theories of mirror-touch synaesthesia and supporting evidence

The first documented case of mirror-touch synaesthesia was reported by Blakemore et al., (2005). This single MTS reported experiencing tactile sensations on her body when observing touch to others. Her self-report was then corroborated

using functional magnetic resonance imaging (fMRI) which revealed that in response to videos where a person (but not an object) was touched she showed hyper-activity within the neural network typically recruited when observing touch to others (the primary and secondary somatosensory cortex, premotor area and the superior temporal sulcus). Similar brain regions were activated by a group of control participants, although to a lesser degree and during actual touch, suggesting that observing touch to someone else and experiencing real touch relies on a similar neural circuitry. This atypical cortical excitability was proposed to be the neural signature of mirror–touch synaesthesia.

In a recent study by Holle, Banissy and Ward (2013) further support was provided for the presence of cortical hyperactivity in mirror–touch synaesthesia. In this fMRI study a group of MTS and a group of controls were presented with a series of videos showing touch or no-touch to a face, a dummy or an object. The authors report mirror–touch synaesthesia to be associated with hyper-excitability both within primary (SI) and secondary somatosensory cortex (SII) in response to videos showing touch to a real face but they suggest SII to play a key role in this form of synaesthesia as this region was activated by actual touch, which also correlated with tactile intensity ratings and also showed increased grey matter density in MTS.

Additionally, voxel based morphometry (VBM) analysis employed by Holle et al., (2013) revealed structural differences associated with mirror–touch synaesthesia in brain regions extending beyond the somatosensory cortices. They also found reduced grey matter volume in the right temporo-parietal junction (rTPJ), the medial prefrontal cortex (mPFC), as well as increased grey and white matter density in the right temporal pole. These regions have been previously implicated in self-other monitoring (Santiesteban, Banissy, Catmur, and Bird, 2012) and perspective taking

(Arzy, Thut, Mohr, Michel, and Blanke, 2006) leading Banissy and Ward (2013) to form a hypothesis that hyper-excitability within the mirror neuron network system observed in mirror-touch synaesthesia may be mediated by atypical self-other distinction reflected in the aforementioned differences in rTPJ and mPFC found in MTS.

Interestingly, mirror-touch synaesthesia has been associated with deficits related to inhibiting the perspective of another person. In a recent study Santiesteban, Bird, Tew, Cioffi and Banissy (2015) employed a finger lifting paradigm (Brass et al., 2005), which requires lifting the index or middle finger which is either congruent or incongruent with the action of the stimulus hand presented on screen. Performance on this task is measured with a congruency effect whereby participants are usually faster and more accurate on congruent trials than compared to the incongruent ones. The authors of this study reported that MTS have deficits in suppressing the representation of the other person, which is manifested in a tendency to over-imitate observed actions. These results are consistent with the hypothesis that atypical self-other processing may underpin the actual experience of mirror-touch synaesthesia (Banissy and Ward, 2013; Ward and Banissy, 2015) as well as with prior work showing a reduction in grey matter volume in brain areas linked to self-other representation in MTS (Holle, Banissy and Ward, 2013).

Recent work by Maiester, Banissy and Tsakiris (2013) provides further support for the unusual self-other processing in mirror-touch synaesthesia. In their study MTS were found to possess highly malleable mental representations of the self, indexed by greater susceptibility to the 'enfacement illusion' relative to controls. In this illusion participants view a video where an unfamiliar person's features are gradually morped with their own face. Their task is to pause the video

when the image looks more like their own face than the other person's. This task is performed before and after they observe touch applied to another person's face accompanied by synchronous touch delivered to their own face (Tsakiris, 2008; Tajadura-Jimenez, Grehl, and Tsakiris, 2012). Typical adults tend to judge images, which they had initially perceived as containing equal portions of self and other, to look more like themselves after they have been exposed to the synchronous touch condition. This illusion has been interpreted by the authors in terms of individuals incorporating features of the other's face into their representation of the self, which leads to perceiving another person's face as more similar to their own. For MTS this illusion is even more pronounced as it is enough just to watch videos of another person being touched without experiencing real touch in order to induce this illusion (Maiester et al., 2013). In addition, similar findings have been reported by Aimola-Davies and White (2013) who found that MTS are highly susceptible to the rubber hand illusion. This classic paradigm involves synchronous stroking of a prosthetic hand and participant's own hand hidden from view which leads to an illusion that the dummy hand belongs to the participant (Botvinick and Cohen, 1998). Aimola-Davies and White (2013) found that it was possible to induce the rubber hand illusion in MTS in the absence of real touch, and by merely showing touch to a prosthetic hand, suggesting greater malleability of body representation in this population.

1.6.4 Broader traits associated with mirror-touch synaesthesia

Apart from deficits related to inhibiting the perspective of another person and greater malleability of body representation MTS have been linked to other traits, for instance, greater empathy relative to control participants as well as GCS (Banissy

and Ward, 2007). Specifically, MTS were associated with enhanced emotional reactivity measured with the Empathy Quotient (Baron-Cohen, and Wheelwright, 2004). They were also found to possess superior emotion recognition ability compared to non-synaesthetic individuals on a task which consisted in matching an adjective describing an emotional state with an image showing a person with a facial expression which best represented that label (Banissy et al., 2011). These findings are in line with the simulation accounts of social cognition which suggest that activating common brain areas both when performing and observing actions (the so called ‘mirror-neuron network’) but also when experiencing and observing emotions facilitates our ability to empathise and understand others (Gallese, Keysers, and Rizzolatti, 2004; Gallese, 2006; Keysers and Gazzola, 2006). These results are also consistent with prior work demonstrating heightened activity within the mirror-neuron network in this form of synaesthesia (Holle, Banissy and Ward, 2013; Blakemore et al., 2005).

1.7 Aims of thesis

The primary aims of this thesis are to explore broader differences in personality and social perception associated with synaesthesia and to investigate neural mechanisms underlying social perception in typical adults. Firstly, this thesis will examine whether grapheme-colour synaesthesia is associated with a specific personality profile and whether presence of this form of synaesthesia has consequences for social perception. Specifically, Study 1 will seek to replicate previous findings showing increased schizotypy and imagery in GCS relative to controls. I will also examine whether greater imagery reported in synaesthesia is mediated by elevated schizotypy in this population. Study 2 will investigate whether

GCS differ from controls in terms of sensation seeking and self-monitoring, as these traits are conceptually related to agreeableness and openness to experience and GCS were previously found to differ from typical adults on these personality characteristics.

Based on previous work showing deficits in social perception in individuals who score high on schizotypy, as well as findings of elevated schizotypy in GCS it will be the aim of Chapter 3 (Experiment 1 and 2) to examine whether this form of synaesthesia would also be associated with reduced social perception using facial emotion and facial identity processing tasks.

This thesis (Experiment3) will also explore whether mirror-touch synaesthesia, previously associated with superior emotion recognition and enhanced empathy, is linked to altered levels of alexithymia, which is a personality construct characterized by compromised emotional awareness, reduced emotion recognition and empathy. Subsequently, Experiment 4 will examine whether MTS differ in terms of their interoceptive sensitivity relative to GCS and general population. This ability to monitor internal bodily changes has been linked to alexithymia, malleability of body representation and difficulties in inhibiting imitation, all of which have been found to differ in MTS relative to controls. Additionally, I will also investigate whether interoceptive sensitivity is linked to social perception abilities in typical adults (Experiment 5).

Finally, Experiments 6, 7 and 8 will probe the functional role of neural oscillations within the gamma frequency band on social perception in typical adults using non-invasive transcranial alternating current stimulation in order to open a new avenue for research exploring the mechanisms underlying enhanced social perception in synaesthesia.

CHAPTER 2: SYNAESTHESIA AND PERSONALITY TRAITS

Recently there has been a growing interest in investigating wider traits linked to synaesthesia. One example is in the domain of personality, where higher rates of positive and disorganized schizotypy, openness to experience and lower agreeableness have been reported in synaesthetes who experience colour as their evoked sensation. Additionally, GCS have previously been reported to show elevated mental imagery compared to typical adults. Here, I aimed to further elucidate the relationship between personality, synaesthesia, and other cognitive traits. In Study 1, I examined self-reported schizotypy and self-reported visual imagery vividness in GCS and typical adults. Current results partially replicated previous findings by showing that synaesthesia was associated with greater positive schizotypy and enhanced self-reported imagery vividness. The results also extend previous reports by demonstrating that differences in positive schizotypy and mental imagery vividness are not related in grapheme-colour synaesthesia. In Study 2, I sought to build on prior work showing lower agreeableness and increased openness to experience in synaesthetes by examining whether grapheme-colour synaesthesia is associated with other conceptually related traits; namely lower self-monitoring and increased sensation seeking. I did not find any differences between synaesthetes and controls on either of these traits. These findings are discussed in relation to potential factors that may contribute to the observed personality profile in grapheme-colour synaesthesia.

2.1 Introduction

In recent years there has been growing interest in using synaesthetes as a unique experimental population to investigate wider aspects of perception and cognition that extend beyond the synaesthetic experience itself. For instance, recent work has demonstrated an association between synaesthesia and enhanced memory (Rothen, Meier, & Ward, 2012), sensory perception (Banissy, Walsh, & Ward, 2009; Banissy et al., 2013; Yaro & Ward, 2007), and creativity (Ward, Thompson-Lake, Ely, & Kaminski, 2008).

There is also some evidence suggesting that synaesthesia might be linked to a specific personality profile. For example, colour synaesthesia has been recently associated with positive and disorganized schizotypy (Banissy et al., 2012). Schizotypy is a sub-clinical construct tapping normative dispositions towards characteristics that are associated with schizophrenia (Mason & Claridge, 2006). Non-synaesthetic artistic individuals have also been found to score high on positive schizotypy (Nelson & Rawlings, 2010), which is interesting in the context of reports showing that synaesthetes themselves tend to gravitate towards creative industries (Ward et al., 2008) and art-related university courses (Rothen & Maier, 2010b). There is also some evidence suggesting that compared to controls, synaesthetes score higher on creativity measures (Ward et al., 2008) and show enhanced self-reported imagery vividness (Spiller et al., 2015; Barnett & Newell, 2008). These skills have also been previously linked to schizotypy in the general population (Oertel et al., 2009). With this in mind, one account for why synaesthetes show heightened levels of positive and disorganized schizotypy may be because these traits are part of a broader constellation of characteristics (e.g. increased creativity and mental imagery) associated with synaesthesia (Banissy et al., 2012). An alternative possibility is that

previously reported differences in schizotypy in synaesthesia for colour reflect some degree of similarity in mechanisms that might contribute to synaesthesia and schizotypy. For example, synaesthesia and schizophrenia have both been linked to abnormalities in early stages of visual processing (Banissy et al., 2013; Barnett et al., 2008; Butler et al., 2005). In schizophrenia, these deficits have been associated with NMDAR hypofunction (Butler et al., 2005) and it is feasible that similar signalling deficits may be related to reductions of cortical inhibition in synaesthesia (e.g. Brang & Ramachandran, 2008). A direct examination of the relationship between differences in schizotypy and mental imagery in synaesthesia for colour is lacking, thus investigating this relationship further is important to help constrain our understanding of factors that contribute to synaesthesia.

Synaesthetes who experience colour as their concurrent (i.e. their evoked sensation) have also been found to score higher on the openness to experience, and lower on agreeableness subscales of the Big Five Inventory (John, Donahue, & Kentle, 1991; Banissy et al., 2013). These synaesthetes also showed higher scores on the fantasizing dimension of the Interpersonal Reactivity Index (Davies, 1980; Banissy et al., 2013). Again, a similar personality profile has previously been reported in visual artists (Burch, Pavelis, Hemsley, & Corr, 2006). This finding is consistent with the aforementioned reports of a higher prevalence of synaesthetes in creative professions (Ward et al., 2008) and the possibility that there may be a constellation of personality traits associated with synaesthesia.

In the general population, a number of other traits have been associated with personality dimensions that have been shown to be different in colour synaesthetes (e.g. openness to experience, agreeableness). For example, sensation seeking and openness to experience both relate to the desire to seek novel and exciting sensations

and experiences. Garcia, Aluj, García, and Cuevas (2005) found sensation seeking (in particular experience seeking) to be a good predictor of openness to experience. Sensation seeking has also been found to be positively linked to the novelty seeking subscale of Temperament and Character Inventory (Cloninger, 1994), which has been positively associated with the Five Factor Model trait of openness to experience and inversely associated with conscientiousness (De Fruyt, Van De Wiele, & Van Heeringen, 2000). Further, self-monitoring is a personality trait that has been suggested to relate to the agreeableness subscale of the Big Five Inventory (Keller, 1999). This trait reflects the degree to which a person regulates his/her behaviour in order to adapt to social situations. People who score high on this measure tend to closely monitor their behavior and to be more responsive to various social cues. On the other hand, low self-monitors tend to be more expressive of their own opinions and feelings and less adaptable in a social context. As yet, the question of whether levels of self-monitoring or sensation seeking differ in synaesthetes relative to the general population has not been examined.

With this in mind, the primary objectives of the current study were as follows. Firstly, I aimed to replicate previous findings linking synaesthesia for colour with enhanced self-reported positive and disorganised schizotypy (Banissy et al., 2012), and mental imagery vividness (Barnett & Newell, 2008; Spiller et al., 2015). Secondly, I investigated whether greater self-reported imagery vividness present in synaesthesia for colour mediates elevated levels of schizotypy in this group. Finally, based on previous findings showing lower agreeableness and increased openness to experience in synaesthetes (Banissy et al., 2013) I also aimed to establish if synaesthesia for colour would be associated with other conceptually similar personality characteristics. Specifically, I hypothesized that synaesthesia might be

linked to lower self-monitoring and increased sensation seeking. To do so I conducted two studies, with Study 1 focusing on mental imagery and schizotypy in synaesthesia, and Study 2 investigating self-monitoring and sensation seeking in synaesthesia.

2.2 Study 1: Imagery and schizotypy

Method

Participants

35 grapheme-colour synaesthetes (32 female, 3 male age $M = 38.6$ $SD = 15.05$) and 35 age and gender matched controls (32 female, 3 male age $M = 38.51$ $SD = 17.07$) took part in this study. Some of the synaesthetes also reported spatial forms (7), personification (6), mirror-touch (3) and other forms of synaesthesia involving colour (16). They were recruited from a database of verified synaesthetes. 110 synaesthetes were invited to take part, 11 of whom had previously taken part in the study by Banissy et al. (2012). To preserve anonymity the participants did not provide personal identifying details when completing the questionnaires online. Therefore it is not possible to trace exactly which synaesthetes from the invited sample took part in the study. All synaesthetes had been previously tested either using the online Eagleman Synaesthesia Test Battery (Eagleman, Kagan, Nelson, Sagaram, & Sarma, 2007) where a score below 1 indicates a presence of grapheme-colour synaesthesia (also see Rothen et al., 2013), or using a test-retest consistency over time method (all synaesthetes showing >85% consistency over time). The controls were recruited from the student population and via acquaintances. They were asked whether they had been previously verified as synaesthetes and if not

whether they suspected they might have grapheme-colour synaesthesia (which was explained as a condition where one experiences letters or numbers in particular colours), or whether they thought they might have other forms of this condition. They were also provided with a link to the Eagleman's test which they were asked to do if they suspected they might have synaesthesia. Those who were verified as synaesthetes were excluded from the control group. (Please note that the same screening procedure was used for controls in subsequent chapters). Participants were entered into a prize-draw competition (£50 shopping voucher) as compensation for their time. All participants gave informed consent and the study was approved by the local ethics committee of Goldsmiths (University of London).

Materials

Participants completed two measures online. One was the Oxford-Liverpool Inventory of Feelings and Experiences (O-Life, Mason, & Claridge, 2006). This standardized instrument is designed to measure schizotypal traits in non-clinical groups and has been used previously in the study of synaesthetes by Banissy et al. (2012). It consists of 104 items and has four subscales: Unusual Experiences (30 items), Introvertive Anhedonia (27 items), Cognitive Disorganization (24 items) and Compulsive Non-Conformity (23 items). This measure has a dichotomous response format where 'yes' is scored as 1 and 'no' as 0 except for negatively worded items.

Additionally all subjects completed the Vividness of Visual Imagery Questionnaire VVIQ (Marks, 1973), which is a widely used measure of self-reported imagery and was used in previous studies examining mental imagery in synaesthesia (Barnett & Newell, 2008; Spiller et al., 2015). Participants were required to rate their imagery on a 5 point scale (1 – perfectly clear and as vivid as normal vision, 2 –

clear and reasonably vivid, 3 – moderately clear and vivid, 4 – vague and dim, 5 – no image at all, only ‘knowing’ that you are thinking of the object) with eyes open, then with eyes closed, resulting in two separate scores (maximum 80) which when summed together give a total VVIQ score (maximum 160). The lower the score on this measure the greater the vividness of visual imagery.

Results

Only the Unusual Experiences (UE) subscale of O-Life and Total VVIQ (TVVIQ) scale were normally distributed. Both UE and TVVIQ had high consistency scores with Cronbach's Alpha of .884 and .972, respectively. Both UE and TVVIQ were then analyzed using separate independent samples t-tests. Synaesthetes scored higher on UE subscale compared to controls [$t(68) = 3.697$, $p < .001$, Cohen's $d = 0.88$] (Fig. 2.1), indicating higher levels of positive schizotypy in synaesthetes; therefore replicating one aspect of previous findings (Banissy et al., 2012). Synaesthetes also reported significantly greater self-reported visual imagery than controls [$t(68) = 2.160$, $p = .034$, Cohen's $d = 0.51$] replicating previous findings (Barnett & Newell, 2008; Spiller et al., 2015) (Fig. 2.2).

All other subscales, which were not normally distributed, were analysed with nonparametric independent-samples Mann-Whitney U tests. The only significant difference between synaesthetes and controls was on the VVIQ open eyes subscale of VVIQ measure ($U(70) = 389.500$, $z = 2.622$, $p = .009$, $r = -0.31$) where synaesthetes reported greater imagery than controls. There were no other statistically significant differences (Introvertive Anhedonia: $U(70) = 651.500$, $z = .460$, $p = .646$, $r = 0.05$; Cognitive Dizorganization: $U(70) = 692.000$, $z = .935$, $p = .350$, $r = 0.01$;

Compulsive Non-Conformity: $U(70) = 674.00, z = .726, p = .468, r = 0.08$; VVIQ closed eyes: $U(70) = 497.50, z = -1.352, p = .177, r = -0.16$

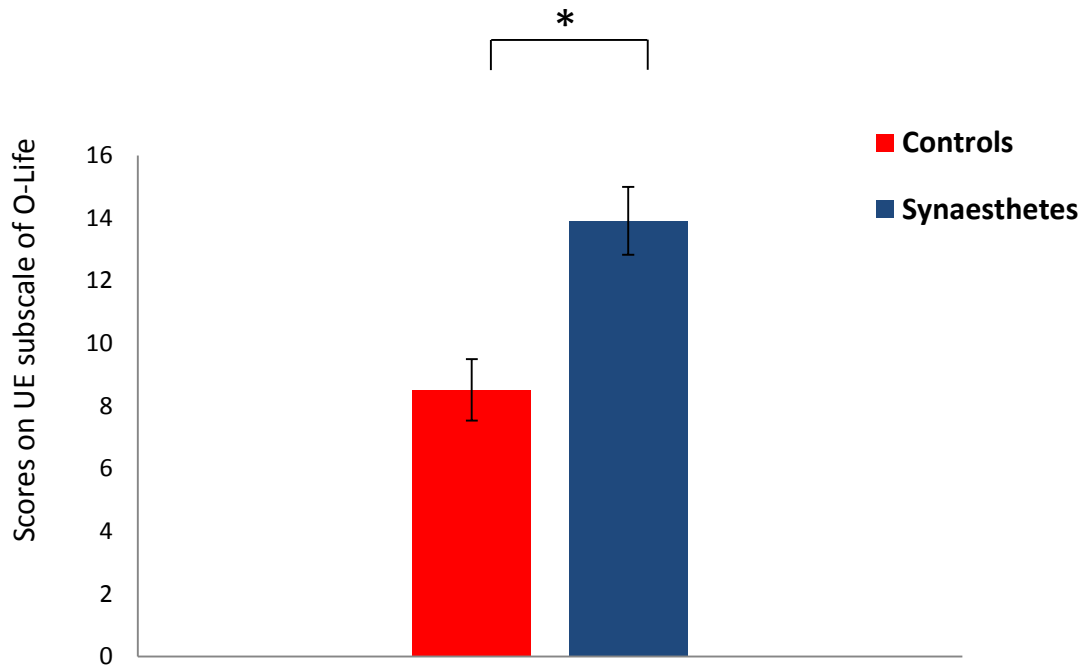


Figure 2.1. Mean scores on the Unusual Experiences subscale of O-Life in grapheme-colour synaesthetes ($N = 35$) and controls ($N = 35$). Error bars show SEM. * $p < .05$

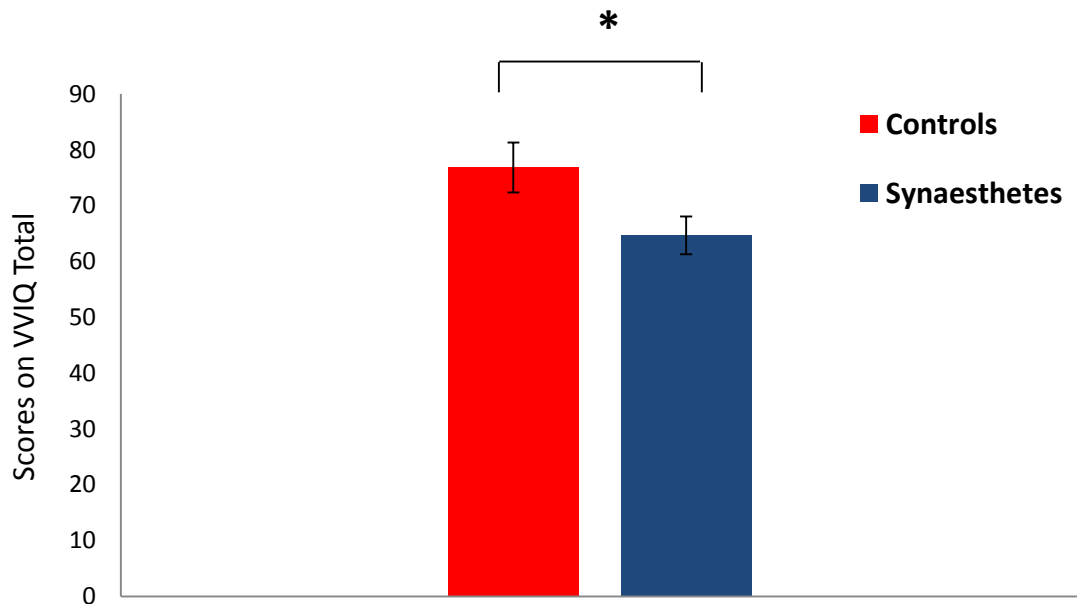


Figure 2.2. Mean total scores on the Vividness of Visual Imagery Questionnaire in grapheme-colour synaesthetes ($N = 35$) and controls ($N = 35$). Error bars show SEM. * $p < .05$

The relationship between elevated schizotypy and visual imagery in synaesthesia.

To examine the relationship between elevated schizotypy and visual imagery scores in synaesthetes, I also calculated Pearson Correlation Coefficients. The correlation between TVVIQ and UE was not significant in either synaesthetes ($r(35) = -.169, p = .330$) or controls ($r(35) = -.081, p = .644$).

Additionally, I ran a mediation analysis using bootstrapping with bias-corrected confidence estimates (Hayes, 2013) to assess the interaction between schizotypy, visual imagery and synaesthesia. 95% confidence interval of the indirect effect was obtained with 1000 bootstrap samples. As Figure 2.3 shows group membership (being a synaesthete as opposed to a control participant) was positively associated with schizotypy ($B = 5.40, t(68) = 3.69, p < .001$) and negatively associated with imagery (as lower scores on TVVIQ indicate greater vividness of visual imagery; $B = -12.14, t(68) = 2.15, p = .034$). The results also showed that the association between imagery and schizotypy was not significant ($B = -.03, t(67) = .98, p = .330$). The mediation analysis did not show a mediating role of imagery on the relationship between group and schizotypy ($B = 3.54, CI [-.19, 1.73], Z = .82, p = .410, \kappa^2 = .03$); model statistics between group and schizotypy when controlling for imagery were $B = 5.02, t(67) = 3.32, p = .001$. In this regard, elevated self-reported visual imagery did not mediate the relationship between increased positive schizotypy and presence of synaesthesia for colour.

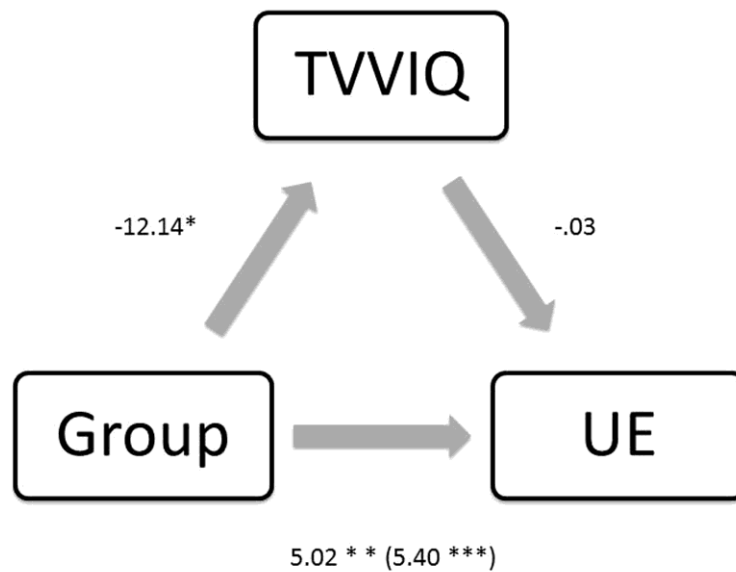


Figure 2.3. Regression coefficients for the relationship between group and UE (schizotypy) are not mediated by TVVIQ (imagery). * $p < .05$, ** $p < .01$, *** $p < .001$

Additional mediation analysis was run in order to determine whether the presence of schizotypy would mediate levels of imagery using the same method as above (Fig. 2.4). Again, there was a negative association between group and TVVIQ ($B = -12.14$, $t(68) = 2.15$, $p = .034$), and a positive association between group and schizotypy ($B = 5.40$, $t(68) = 3.69$, $p < .001$). There was no significant association between schizotypy and imagery ($B = -.45$, $t(67) = .98$, $p = .330$). Although the significance level of the relationship between group and imagery was reduced when controlling for schizotypy ($B = -9.67$, $t(67) = 1.568$, $p = .121$), the mediation effect was not significant suggesting that schizotypy is not a significant mediator of the

relationship between group and imagery ($B = -2.47$, $CI [-8.80, 2.19]$; $Z = -0.91$, $p = .359$, $\kappa^2 = .04$).

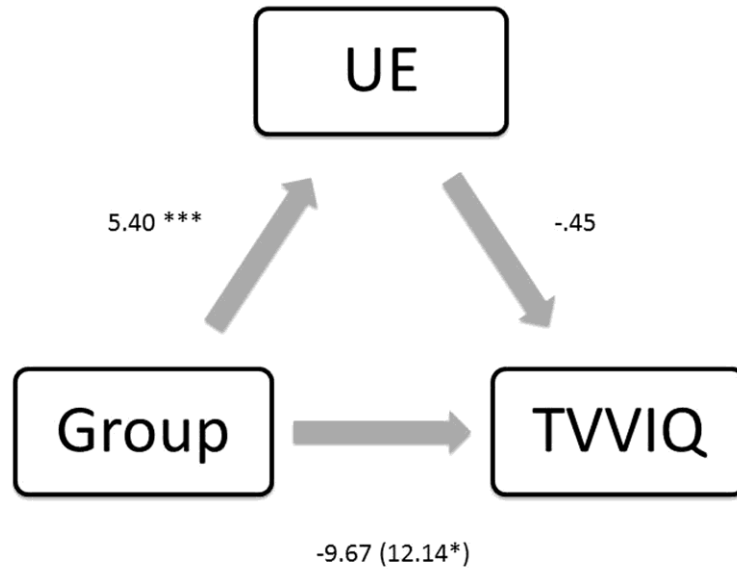


Figure 2.4. Regression coefficients for the relationship between group and TVVIQ (imagery) are not mediated by UE (schizotypy). * $p < .05$, ** $p < .01$, *** $p < .00$

2.3 Study 2: Sensation Seeking and Self-Monitoring

Taking into account recent findings demonstrating that synaesthesia for colour is linked to lower agreeableness as well as increased openness to experience subscales of the Big Five Inventory (Banissy et al., 2013) I sought to determine whether this form of synaesthesia would also be associated with other conceptually related personality characteristics; namely lower self-monitoring and increased sensation seeking.

Material and methods

Participants

The same sample of synaesthetes that were invited to take part in Study 1 (i.e. N = 110 synaesthetes) were invited to take part in this study. From this 37 GCS (34 female, 3 male age M = 41.27 SD = 17.58) and 37 age and gender matched controls (34 female, 3 male age M = 38.70 SD = 17.82) took part. Some of the synaesthetes also reported spatial forms (4), personification (3) and mirror-touch (2) synaesthesia, and other forms of synaesthesia involving colour (9). For all synaesthetic participants, synaesthesia had been confirmed either using an online consistency test (Eagleman et al., 2007), or using a test-retest method carried out on two separate occasions. The controls were recruited from the student population via Mahara (an online platform used for advertising experiments) and via acquaintances. Participants were screened for synaesthesia and entered into a prize-draw competition (£50 shopping voucher) as payment for their time. All participants gave informed consent and the study was approved by the local ethics committee of Goldsmiths (University of London).

Materials

Participants completed two measures online. One was the Sensation Seeking Scale (SSS-V) (Zuckerman, 1979; Zuckerman, 1995), which measures a person's need to experience new and stimulating experiences and sensations. This widely used instrument has a dichotomous response format where participants must choose one of two statements which best describes their likes and feelings (e.g. A: 'I get bored seeing the same old faces', B: 'I like the comfortable familiarity of everyday friends'). SSS-V has four underlying dimensions each containing 10 items: thrill

and adventure seeking (TAS), experience seeking (ES), disinhibition (D) and boredom susceptibility (BS), which summed together give a total sensation seeking score (maximum 40).

Participants also completed the Self-Monitoring scale (Snyder & Gangestad, 1986). Self-monitoring (SM) is a personality trait whereby a person adapts his/her behaviour in order to fit into a social context. Participants who score high are classified as high self-monitors. These individuals tend to be concerned about their social desirability and thus regulate their behavior in order to adapt to the social situations. On the other hand, low self-monitors are less concerned with the judgment or opinion of others, are more expressive of their own views and tend to be less socially adaptable (Flynn, Reagans, Amanatullah & Ames, 2006; Friedman & Miller-Herringer, 1991). Self-Monitoring scale (Snyder & Gangestad, 1986) consists of 18 statements such as e.g. 'I would not change my opinions (or the way I do things) in order to please someone or win their favour'. Participants need to indicate if the statements in relation to their own feelings and experiences are true or false. Each item is keyed such that high-self monitors tend to indicate answers in the keyed direction, while low-self monitors tend to opt for the alternative answer. The maximum possible score on this measure is 18.

Results

Only the Self-Monitoring scale was normally distributed. Cronbach's alpha for this measure was .771. Independent samples t-test revealed that the difference in SM between synaesthetes and controls was not significant [$t(61,116) = 1.268, p = .209$, Cohen's $d = -0.29$]. Similarly, no significant differences were found between the groups on the Sensation Seeking subscales using Independent-Samples Mann-

Whitney U tests (TAS: $U(74) = 677, p = .935, r = <0.001$; ES: $U(74) = 636, p = .596, r = 0.06$; D: $U(74) = 638, p = .617, r = 0.05$; BS: $U(74) = 624, p = .512, r = 0.07$; TOTAL: $U(74) = 623.50, p = .509, r = 0.07$).

2.4 General Discussion

This study examined the relationship between increased self-reported mental imagery and schizotypy in grapheme-colour synaesthesia. Building on prior work indicating greater positive and disorganized schizotypal traits amongst individuals with synaesthesia for colour (Banissy et al., 2012) and increased self-reported mental imagery vividness in synaesthesia for colour (Barnett & Newell, 2008; Spiller et al., 2015) it was expected that GCS would differ on these measures relative to controls. Further given prior suggestions that differences in schizotypy levels found between synaesthetes and controls may be related to comorbidity between schizotypy and mental imagery vividness, I sought to examine the relationship between visual imagery and schizotypy in the same sample of synaesthetes.

Current findings partially replicate Banissy et al.'s (2012) results by showing that synaesthetes who experience colour as their evoked sensation score higher on positive schizotypy, but not other aspects of schizotypy. It is of note that I did not replicate the Banissy et al (2012) finding of differences between GCS and controls in terms of disorganised schizotypy. Consistent with previous findings, I also found synaesthesia for colour to be linked with greater self-reported imagery vividness compared to controls (Barnett & Newell, 2008; Spiller et al., 2015). By comparing levels of self-reported mental imagery vividness and schizotypy in the same sample of synaesthetes, I was also able to determine that elevated schizotypal traits present in GCS were not related to self-reported imagery vividness. This suggests that

increased levels of these traits in GCS may be independent of each other, and constrains explanations of why GCS may have heightened positive schizotypy. Moreover, prior accounts have suggested that heightened levels of positive and disorganized schizotypy in synaesthesia for colour may be because these traits are part of broader constellation of characteristics (e.g. increased mental imagery) that have been associated with the presence of synaesthesia (Banissy et al., 2012). That GCS did not show a relationship between positive schizotypy and self-reported mental imagery vividness in the current study argues against this possibility. This pattern of data is also consistent with previous findings demonstrating that while non-synaesthetic individuals with increased schizotypal traits score higher on vividness of mental imagery, these two constructs appear to be independent of each other (Oertel et al. 2009). It will therefore be important for future work to determine factors contributing to elevated positive schizotypy and self-reported vividness of mental imagery in synaesthesia for colour.

One possible reason for elevated positive schizotypy in synaesthesia for colour may be that there is some degree of similarity in mechanisms contributing to synaesthetic, and the unusual visual experiences associated with positive schizotypy. For example, synaesthesia and schizophrenia have both been linked to abnormalities in early stages of visual processing (e.g. Barnett et al., 2008; Butler et al., 2005). In schizophrenia, these deficits have been associated with NMDAR hypofunction (Butler et al., 2005) and it is feasible that similar mechanisms may be related to reductions of cortical inhibition in synaesthesia (e.g. Brang & Ramachandran, 2008). Understanding factors that contribute to the relationship between elevated positive schizotypy and grapheme-colour synaesthesia will therefore be an important line of future study in order to constrain our understanding of mechanisms that are linked to

both synaesthesia and schizotypy. Further, it will be important for future work to extend the mediation analysis conducted here to a larger sample. Interpreting null results is always a challenge, and in the context of mediation analyses GCS sample size used in this study was relatively modest. The results found here therefore require future replication. I note, however, that prior work in non-synaesthetic participants using the same measures and a larger sample than mine found similar results on the relationship between schizotypy and imagery in non-synaesthetes (Oertel et al., 2009; Bell & Halligan, 2010).

Additionally, as this study GCS (some of whom also reported other forms of synaesthesia) on vividness of visual imagery I can only make inferences about visual forms of synaesthesia and imagery within the visual domain. Spiller and colleagues (2015) found that while synaesthetes tend to show heightened imagery in the modality of their synaesthetic experiences relative to controls and other synaesthetes (i.e. those that experience synaesthesia in a different modality), synaesthetes also showed a general enhancement of imagery across various modalities in which they do not experience synaesthesia relative to non-synaesthetes. In this context, one may expect some difference in visual imagery irrespective of the modality of synaesthesia, but predictions regarding differences in positive schizotypy are less clear. While theories of synaesthesia (e.g. in relation to cortical inhibition) tend to take a one size fits all approach, in practice our knowledge of factors that contribute to synaesthetic experience are largely restricted to studies of grapheme-colour synaesthesia. Therefore the extent to which grapheme-colour synaesthesia is a consequence of domain-general (i.e. common to all types of synaesthesia) or domain-specific (i.e. specific to grapheme-colour) factors is unclear. Understanding domain-general and domain-specific factors that contribute to grapheme-colour

synaesthesia (and other variants of synaesthesia), and how these factors are associated with broader traits (e.g. schizotypy) will help to constrain predictions on putative relationships between different variants of synaesthesia and wider aspects of perception and cognition that extend beyond the synaesthetic experience itself.

Another question is whether the number of synaesthesia forms could influence current results. Based on prior findings suggesting an association between the number of synaesthetic modalities and vividness of reported imagery (Spiller et al., 2015) it could be hypothesised that individuals with multiple forms of synaesthesia stretching across different modalities would report elevated levels of visual imagery relative to those with fewer synaesthetic modalities. However, greater vividness of visual imagery should not influence the findings on schizotypy, as enhanced imagery and schizotypy appear to be independent of each other (Oertel et al. 2009; Bell & Halligan, 2010; current study), and thus greater intensity of imagery in individuals with different synaesthetic forms would not be expected to alter this relationship.

Based on previous findings demonstrating an association between synaesthesia and greater openness to experience (Banissy et al., 2013), and studies showing that openness to experience and sensation seeking are conceptually related (Garcia et al., 2005), I also investigated if grapheme-colour synaesthesia would be linked to greater sensation seeking and lower self-monitoring. However, I did not find this. One reason for this might be due to methodological weaknesses of the SSS-V. For example, the SSS-V requires participants to make forced-choice answers, (e.g. between options such as A: 'I am not interested in experience for its own sake' or B: 'I like to have new and exciting experiences and sensations even if they are a little frightening, unconventional or illegal') and, although some of the items have been

revised, it is still sometimes considered to be a dated measure (Gray & Wilson, 2007). In this regard, a questionnaire using a Likert-type format may have been more sensitive. That being said, prior work linking openness to experience with sensation seeking in the general population (Garcia et al., 2005) administered the same questionnaire as used here, thus the measure can be considered reliable. A further possibility is that as synaesthesia results in very rich sensory experiences, which at times might be overwhelming, synaesthetes may not actively seek situations that would provide even more sensory stimulation.

In light of previous research showing an association between synaesthesia and decreased agreeableness (Banissy et al., 2013), it was also hypothesised that grapheme-colour synaesthesia would be linked to low self-monitoring because both constructs relate to a person's ability and desire to cooperate, and adjust their behaviour to a social context (Keller, 1999). Nevertheless, I found no difference in behaviour monitoring between synaesthetes and controls. In conjunction with the findings of Banissy et al. (2012; 2013) and the findings from Study 1 of differences between synaesthetes and controls on specific trait dimensions (e.g. positive schizotypy, but not other traits), the lack of a difference in sensation seeking and self-monitoring in synaesthetes implies that grapheme-colour synaesthesia is linked to a specific personality profile and that these differences are not due to a general self-report bias in synaesthetes.

Summary

In sum, I demonstrated that GCS show greater positive schizotypy and self-reported visual imagery vividness compared to controls. By examining these two constructs in one sample of synaesthetes, I also found that heightened positive

schizotypy is not a result of a relationship between schizotypy and mental imagery vividness. Finally, synaesthetes did not differ from controls in terms of levels of self-monitoring or sensation seeking despite previous work reporting that colour synaesthetes differ from controls on agreeableness and openness to experience (Banissy et al., 2013), suggesting a specific personality profile difference in synaesthesia for colour.

CHAPTER 3: SOCIAL PERCEPTION IN GRAPHEME – COLOUR

SYNAESTHESIA

The results presented in Chapter 2 confirmed that synaesthesia for colour is linked to an atypical personality profile. Specifically I partially replicated previous findings by showing that synaesthetes who experience colour as their evoked synaesthetic sensation score high on positive schizotypy and increased imagery. Based on these findings and prior work linking synaesthesia to neurodevelopmental conditions characterized by deficits in social perception such as Autism Spectrum Disorder, this study sought to examine social perception abilities in synaesthesia for colour by examining facial affect and facial identity perception in GCS and controls. Current findings suggest that individuals who experience grapheme-colour synaesthesia outperformed controls on upright facial identity, but not inverted identity perception, emotion perception or the face composite task. These findings are discussed in the context of broader perceptual and cognitive traits previously associated with synaesthesia for colour, including putative relationships between synaesthesia and autistic spectrum disorder.

3.1 Introduction

Building on the findings from Chapter 2 showing that GCS report greater positive schizotypy compared to control participants and prior work linking grapheme-colour synaesthesia to broader differences in schizotypal personality traits (Banissy et al., 2012), which, in turn, have been associated with deficits in emotion recognition in controls (Abott and Byrne, 2013; Morrison, Brown and Cohen, 2013)

the purpose of this chapter was to elucidate if this form of synaesthesia would be associated with deficits in social perception.

In the study conducted by Abbott and Byrne (2013) an association between global and positive schizotypy and poor emotion recognition was found, and deficits in recognizing positive emotions have been linked to negative schizotypal traits. Similarly, Morrison and colleagues (2013) found that individuals who score high on schizotypy compared to controls perform worse on a facial affect recognition task. When coupled with my findings of enhanced positive schizotypy in grapheme-colour synaesthesia one may suspect that GCS may show some levels of impairment in social processing relative to controls.

There are other reasons why studying social perception in synaesthetes who experience colour as their evoked sensation is interesting. For instance, there are reports suggesting links between synaesthesia and other neurodevelopmental conditions, including Autism Spectrum Disorder (ASD; Neufeld et al., 2013; Asher et al., 2009; Bouvet et al., 2014). For example, in a recent study Baron-Cohen and colleagues (2013) report that synaesthesia is more common among individuals diagnosed with ASD. They speculate that similar biological mechanisms may underlie these conditions (e.g. increased neural connections between neighbouring brain areas). ASD is also associated with a range of behavioural characteristics, including but not limited to atypical social and sensory processing (Uljarevic and Hamilton, 2012; Lane, Molloy, and Bishop, 2014; Weigelt, Koldewyn, and Kanwisher, 2012). For example, individuals with ASD have shown impairments in the perception of facial identity and emotion (Hedley, Brewer and Young, 2014; Uljarevic and Hamilton, 2012; Weigelt et al., 2012).

While basic sensory processing in synaesthetes has received some attention (e.g. Yaro and Ward, 2007; Barnett et al., 2008; Banissy et al., 2009; Banissy et al., 2013; Terhune et al., 2015) there is little work examining whether synaesthetes show differences in processing social cues. One exception to this is the case of mirror-touch synaesthesia, where individuals experience tactile sensations on their own body when observing pain or touch to other people (see Banissy (2013); Ward and Banissy (2015) for review). Recent findings have linked mirror-touch synaesthesia to heightened emotional empathy relative to controls and GCS (Banissy and Ward, 2007; Goller, Richards, Novak, and Ward, 2013), and enhanced emotion perception relative to controls (Banissy et al., 2011). It is of note, however, that while labelled as synaesthesia the notion that mirror-touch synaesthesia relies upon similar mechanisms as more traditional forms of synaesthesia (e.g. grapheme-colour synaesthesia) is somewhat controversial (e.g. Rothen and Meier, 2013). In this regard a systematic investigation of social perception abilities in synaesthesia is lacking.

With the above in mind, here I sought to elucidate if grapheme-colour synaesthesia would be associated with broader differences in social perception. To do so I compared a group of GCS to a matched control group on their abilities to perceive facial identity and facial emotion.

3.2 Experiment 1: Processing of facial expressions of emotion and identity using the Cambridge Face Perception Tests.

Methods and Materials

Participants

34 control participants (21 female, 13 male, age $M = 24.11$, $SD = 5.54$) and 12 GCS (11 female, 1 male, age $M = 26$, $SD = 6.52$) took part in this experiment. The groups did not significantly differ in terms of age [$t(44) = .965$, $p = .340$] or gender [$\chi^2(1, N = 46) = 3.746$, $p = .053$]. Additionally six of the synaesthetes reported weekday-colour and month-colour synaesthesia. Synaesthetes had been previously verified using the online Eagleman Synaesthesia Test Battery (Eagleman et al., 2007) where a score below 1 indicates a presence of synaesthesia. The controls were recruited from the student population via posters displayed at the university buildings or via acquaintances. Participants received £10 for their participation.

Task

Facial Identity Perception

To measure facial identity perception abilities, the Cambridge Face Perception Test (CFPT-Identity; note prior studies refer to this as CFPT) was employed (Duchaine, Yovel, and Nakayama, 2007). Participants were simultaneously presented with a target image on top of the screen consisting of a male face shown at a three quarter angle, and six male, test faces shown at a frontal view underneath (Figure 1a). These images were constructed by morphing different degrees of the frontal view of the target face at 88, 76, 64, 52, 40 and 28% with another face thus representing a gradual variation in similarity to the target face. Test faces were

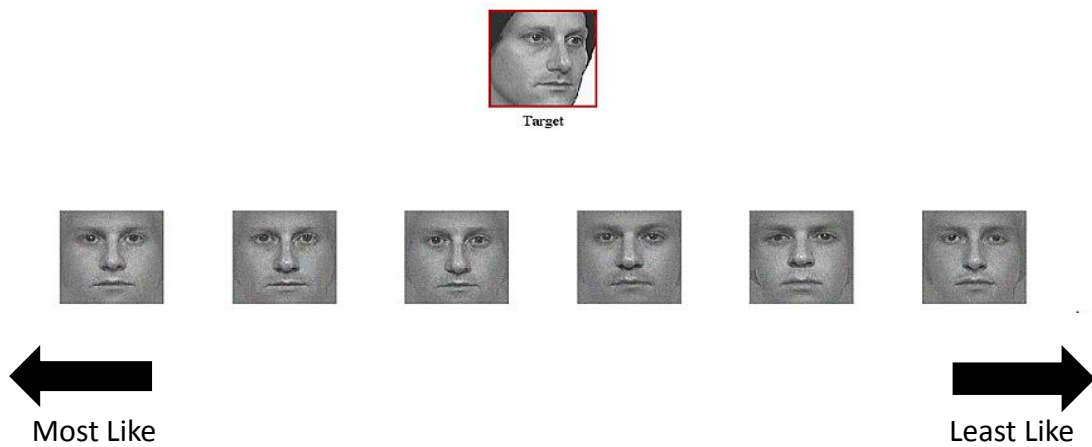
presented in random order and participants were required to sort them in order of least to most like the target face. Participants had one minute to complete each trial. There were sixteen test trials, eight using upright images, and eight using inverted pictures of faces, preceded by two practice trials. Performance on this task was measured using an error score calculated by summing the deviations of each image from its correct location. For instance if the picture was three spaces from its correct position the error score for that trial would be three. Error score was then converted into percentage of correct responses. Chance performance is 36%.

Facial Emotion Perception

The Cambridge Face Perception Angry Expression (CFPT-Angry) and Cambridge Face Perception Happy Expression (CFPT-Happy) were used in order to evaluate participants' facial emotion perception abilities. These two emotions were chosen as examples of positive and negative valence. In each trial, a row of six frontal view images of a model showing different degrees of emotion was displayed. For CFPT-Happy, the images were morphed from a neutral facial expression to contain 0, 3, 6, 9, 12 and 15% happiness and for CFPT-Angry the images were morphed from a neutral face to contain 0, 8, 16, 24, 32 and 40% anger. Due to the fact that positive affect is easier to detect than negative emotions (Jansari, Tranel, and Adolphs, 2000; Leppanen and Hietanen, 2004; Jansari, Rodway, and Goncalves, 2011) stimuli comprising CFPT-Happy contained lower intensities of emotion than CFPT-Angry to aid comparability of the tasks and avoid a ceiling effect when processing facial expressions of happiness. The stimuli were generated using male and female pictures from the Radboud Faces Database (Langner, et al., 2010). Participants were required to order the faces from the most to the least intense

expression of the given emotion (Figure 1b). Each of the two tasks consisted of ten test trials preceded by two practice trials. Participants had one minute to complete each trial. Performance on these tasks was measured using percentage of correct responses calculated in the same way as for CFPT-Identity. Chance performance is 36%.

a) CFPT - Identity



b) CFPT- Emotions (Angry/Happy)



Figure 3.1. Examples of trials of a) CFPT-Identity (note that while upright faces are shown, half of the trials were inverted) and b) CFPT-Angry (note that the same format was used for CFPT-Happy, but the expression type differed).

Results

Facial Identity Perception

One control participant's score was removed from this analysis as they performed below chance (31.94%) on inverted CFPT-identity trials: their inclusion does not qualitatively change the pattern of data. Performance on CFPT-Identity was analysed using a 2 (Trial Type [upright, inverted]) x 2 (Group [synaesthetes, controls]) ANOVA, which yielded a significant main effect of trial type [$F(1, 43) = 258.351, p < .001, \eta^2 = .85$], due to participants performing better overall on upright than inverted faces (i.e. the face inversion effect; Yin, 1969). There was also a significant interaction between task and group [$F(1, 43) = 4.313, p = 0.044, \eta^2 = .09$]. Two post hoc independent samples t-tests were performed on CFPT-Identity upright and inverted faces. This revealed a significant difference between groups on CFPT-Identity upright trials ($p = 0.01, \text{Cohen's } d = 0.827, \text{GCS: } M = 80.20, SD = 5.95; \text{controls: } M = 73.81, SD = 9.15$), with synaesthetes out-performing controls (Fig 3.2), but no difference in performance between the groups on CFPT-Identity inverted trials ($p = .961; \text{GCS} = M 53.35, SD = 8.81; \text{controls: } M = 53.49, SD = 7.91; \text{Fig 3.2}$).

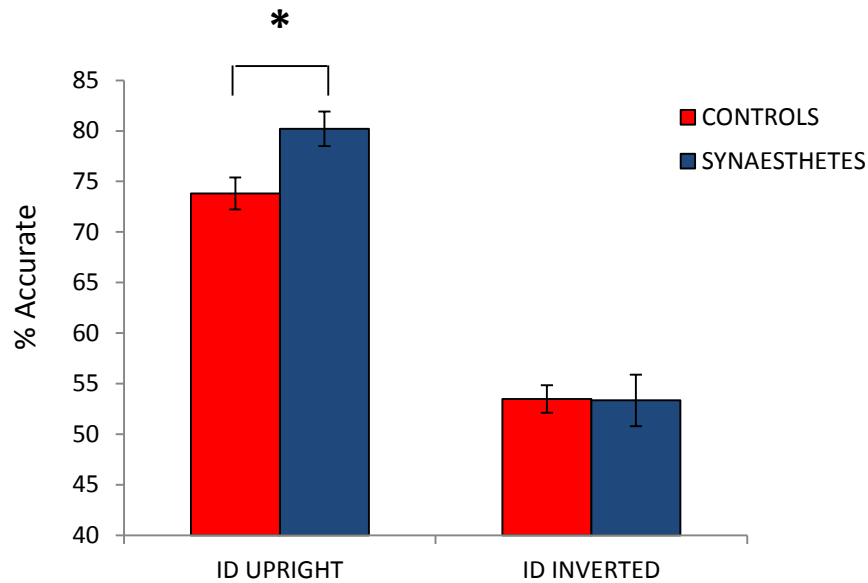


Figure 3.2 Mean percentage of correct responses for synaesthetes (N = 12) and controls (N = 34) on the Cambridge Face Perception Task-Identity upright and inverted trials. Error bars show SEM. * $p < .05$

Emotion Perception

Performance on emotion perception was measured with the CFPT-Happy and CFPT-Angry tasks. A 2 (Task [angry / happy]) x 2 (Group [synaesthetes, controls]) ANOVA was conducted, which yielded a significant main effect of task [$F(1, 44) = 15.738, p < .001, \eta^2 = .263$], due to participants performing better overall on CFPT-Angry. While there was a trend for GCS to outperform controls on both tasks (CFPT-Happy: GCS $M = 76.29, SD = 10.30$; controls $M = 70.75, SD = 12.14$, CFPT-Angry: GCS $M = 81.85, SD = 10.29$; controls $M = 77.67, SD = 9.05$; Fig 3.3), there was no significant main effect of group [$F(1, 44) = 2.309, p = .136, \eta^2 = .050$] or a significant interaction [$F(1, 44) = .190, p = .665, \eta^2 = .004$].

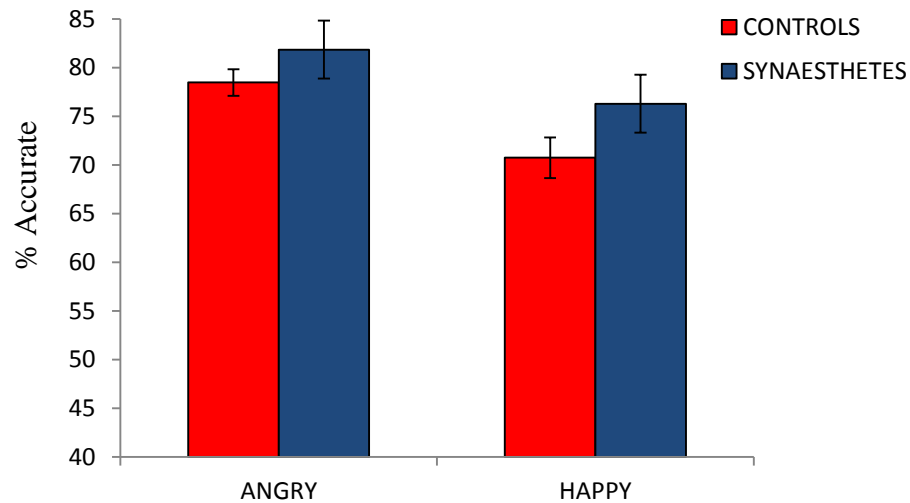


Figure 3.3 Mean percentage of correct responses for synaesthetes (N = 12) and controls (N = 34) on the Cambridge Face Percentage Task-Angry and Cambridge Face Percentage Task -Happy. Error bars show SEM.

Experiment 1 Discussion

Building on my findings of increased positive schizotypy in GCS relative to controls (Chapter 2) and prior studies suggesting a link between synaesthesia and other traits (e.g. Banissy et al., 2012) and conditions (Neufeld, et al., 2013; Baron-Cohen et al., 2013) linked with atypical social perception abilities, this study sought to examine whether GCS differed to controls in their social perception abilities. GCS were compared to control participants in their ability to perceive facial identity and facial emotion (happiness and anger perception). Current findings show that GCS outperformed control participants in their ability to perform upright facial perception but did not differ in their ability to perceive inverted faces, implying a degree of task specific performance advantage shown by synaesthetes. Despite having higher accuracy scores on facial anger and happiness perception relative to controls that difference was not statistically significant.

While these findings could reflect some level of domain-specific processing of facial cues in grapheme-colour synaesthesia, a more likely explanation is that the data are related to broader perceptual differences that have been reported in this cohort. For example, Barnett and colleagues (2008) report that synaesthetes who experience colour as their evoked sensation show enhanced sensitivity to high spatial frequency Gabor patches that bias parvocellular channels, but not low spatial frequency stimuli processed via magnocellular streams. Prior work suggests that such high spatial frequency information may be important for face perception by conveying fine-grained featural information (Vuilleumier, Armony, Driver, and Dolan, 2003). In the context of the tasks used here, this information may be of particular utility in the CFPT-Identity and to some extent in the CFPT-Emotion tasks given that these tasks require participants to make fine-grained visual judgments regarding how well each image matches a target face or in order to detect small featural differences between images. In this regard, performance differences on the CFPT tasks may relate to a domain general advantage for synaesthetes in processing high spatial frequency cues that aid fine-grained visual discrimination rather than a domain-specific advantage in face perception. The fact that this effect was not observed for inverted trials which contained the same spatial frequency information as upright trials is most likely due to increased task difficulty in this orientation (Rossion, 2008). On the other hand, no significant difference between GCS and controls on CFPT-Emotion tasks is likely to be due to the fact that high spatial frequency visual information is of particular relevance when processing facial identity but to a lesser degree when processing facial affect (Vuilleumier et al., 2003).

To address the question of a domain general enhancement in synaesthesia, a second study was conducted which compared the performance of synaesthetes and controls on another facial identity processing task that relies less heavily on high spatial frequency cues - the face composite task (FCT), in which joining the top halves of one face with bottom halves of another face leads to an illusion that identical top halves are different when aligned with different bottom halves but not when they are offset laterally (Young, Hellawell, and Hay, 1987). The face composite effect is absent when the two halves are misaligned and is thought to illustrate holistic face processing as aligning top and bottom parts of the face leads to a perceptual integration of these different halves into one face. Unlike the CFPT tasks used in Experiment 1, the FCT is thought to rely more prominently on low-spatial frequency information (Young et al., 1987; Rossion, 2013) and therefore permits investigation of face processing abilities in synaesthetes in which any domain general benefits for synaesthetes in using high spatial frequency visual information are less likely to aid performance.

3.3 Experiment 2: Processing of facial information using the face composite task.

Methods and Materials

Participants

16 control participants (all female, age $M = 30.56$, $SD = 3.57$) and 12 gender matched GCS (all female, age $M = 28.83$, $SD = 7.45$; none of whom took part in Experiment 1) took part in this experiment. The two groups did not differ in terms of age [$t(26) = .742$, $p = .470$]. Synaesthetes had been previously verified using the

online Eagleman Synaesthesia Test Battery (Eagleman et al., 2007) where a score below 1 indicates a presence of synaesthesia. The controls were recruited among acquaintances. Participants were given £5 gift vouchers for their participation.

Task

The face composite task was adapted from Experiment 3 in Susilo, Rezlescu and Duchaine (2013) (Figure 3.4). Composite faces were created by mixing same-sex top and bottom halves from 60 original faces (32 females), all of which were Caucasian, front-view, greyscale images with neutral expressions and similar skin tone. Lines at the edges of the faces indicated the halves. The top and bottom halves were either aligned to form a novel face, or misaligned. A black ski-cap was pasted on to cover hair cues. On each trial, a pair of composite faces was presented sequentially. The first composite face appeared for 200 ms, followed by a blank screen for 400 ms, and then the second composite face for 200 ms. The composite faces were both either aligned ("aligned" trials) or misaligned ("misaligned" trials). Example stimuli are presented in Figure 3.5. Participants were asked to indicate whether the top-halves were the same ("same" trials) or different ("different" trials) while ignoring the bottom-halves. There were 90 trials presenting upright stimuli (30 same-aligned, 30 same-misaligned, 15 different-aligned, 15 different-misaligned) and 90 trials presenting inverted stimuli. All 180 trials were randomised. Only "same" trials were included in the analysis as two different top halves are not perceived as more similar when they are aligned compared to being misaligned with identical bottom halves i.e. 'different trials' do not produce the FCE (Rossion, 2013).



Figure 3.4 Example of stimuli used in the face composite task. All four top halves are identical however they appear different when aligned with different bottom halves (first pair) and similar when the top and bottom halves are misaligned (second pair). Taken from Susilo, Rezlescu, and Duchaine (2013).

Experiment 2 Results and Discussion

First, participants' performance was analysed by examining their accuracy and reaction times data. Synaesthetes and controls showed similar performance in the four conditions (upright aligned, upright misaligned, inverted aligned, inverted misaligned) of the face composite task. Two separate 2 (group [synaesthetes, controls]) x 4 (condition [upright aligned, upright misaligned, inverted aligned, inverted misaligned]) ANOVAs conducted on accuracy and reaction times revealed no group differences or interaction on either measure (accuracy: group [$F(1, 26) = 2.529, p = .124, \eta^2 = .089$], interaction [$F(3, 78) = .207, p = .891, \eta^2 = .008$]; reaction times: group [$F(1, 26) = 1.218, p = .280, \eta^2 = .045$, interaction [$F(3, 78) = 1.141, p = .338, \eta^2 = .042$] (Figure 3.5 and 3.6). As expected a main effect of Condition was found for both reaction times [$F(3, 78) = 8.441, p < .001, \eta^2 = .245$] and accuracy [$F(3, 78) = 16.459, p < .001, \eta^2 = .388$], due to participants being overall more accurate and faster on misaligned compared to aligned trials for upright faces [accuracy: $t(27) = .637, p < .001, \text{Cohen's } d = 1.217$, reaction times: $t(27) = 3.460, p = .002, \text{Cohen's } d = -.044$] and on aligned inverted trials relative to

aligned upright condition [accuracy: $t(27) = 4.236, p < .001, \text{Cohen's } d = .804,$ reaction times: ($t(27) = 4.067, p < .001, \text{Cohen's } d = 1.212$]. Both findings are in line with existing literature on FCE (e.g. Rossion 2013).

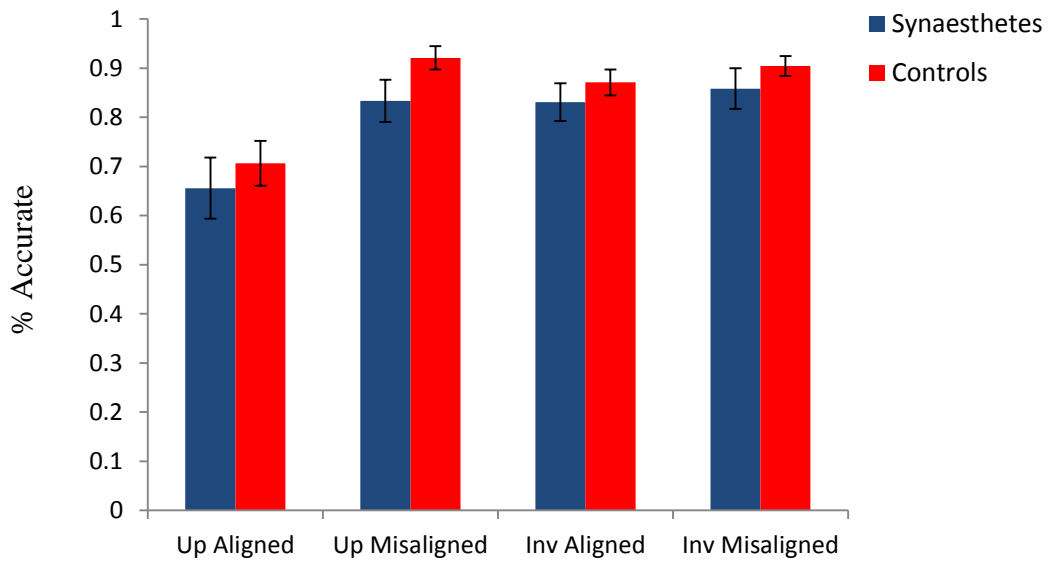


Figure 3.5 Mean accuracy scores for synaesthetes (N = 12) and controls (N = 16) on the face composite task including upright aligned, upright misaligned, inverted aligned and inverted misaligned trials.

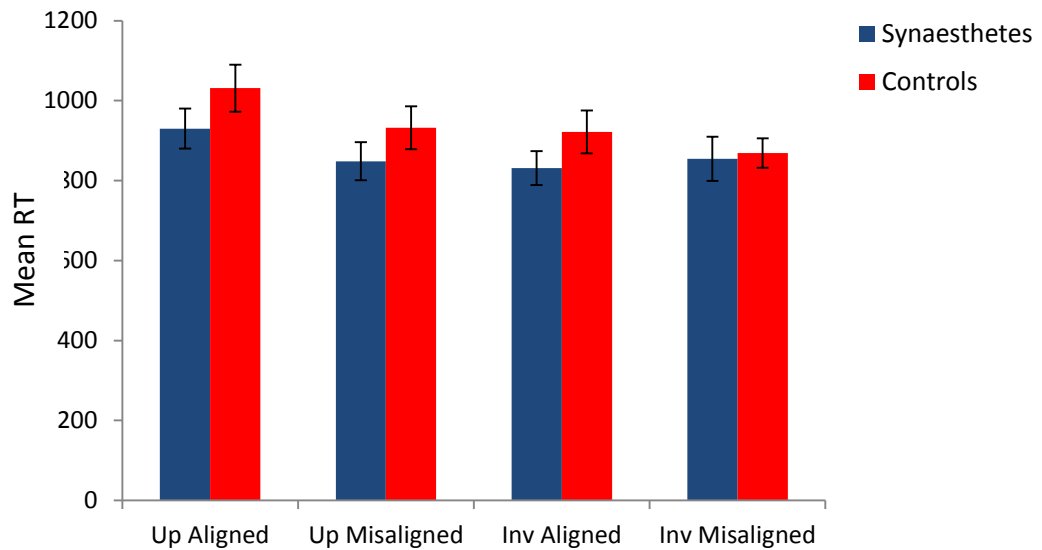
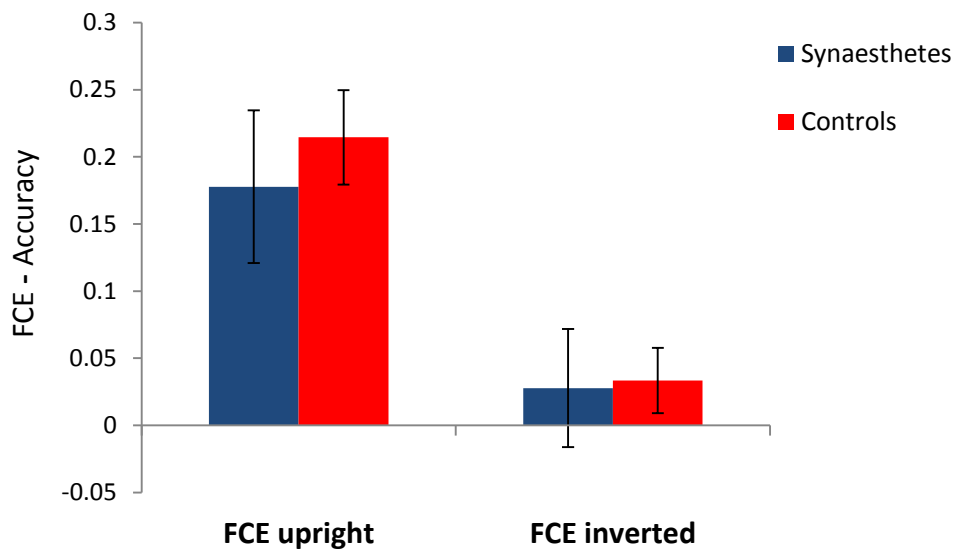


Figure 3.6 Mean reaction times for synaesthetes (N = 12) and controls (N = 16) on the face composite task including upright aligned, upright misaligned, inverted aligned and inverted misaligned trials.

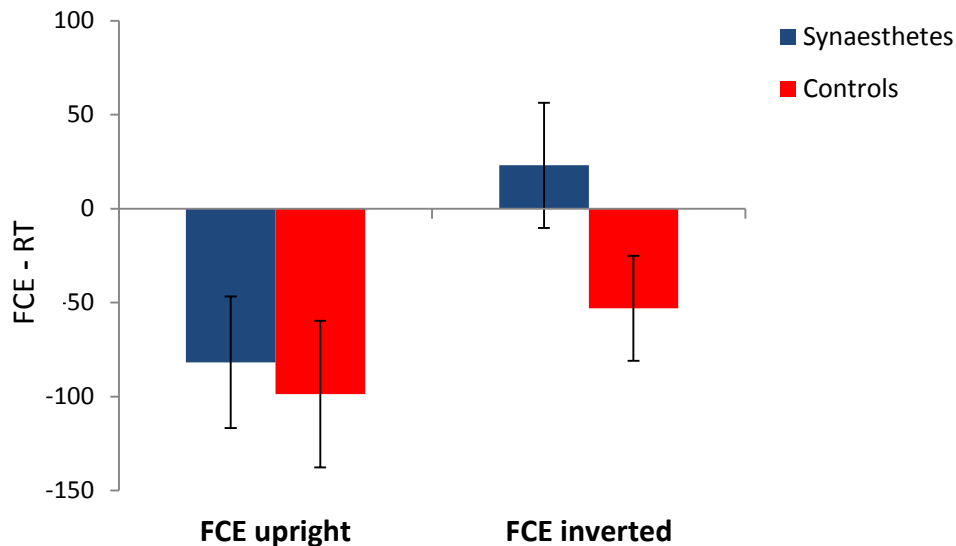
Secondly, to investigate potential group differences in the size of the FCE, two 2 (group [synaesthetes, controls]) x 2 (orientation [upright, inverted]) ANOVAs with the FCE were computed using accuracy and reaction time as dependent variables. For accuracy, FCE was calculated by subtracting average correct score for the same aligned trials from the average correct score for the same misaligned trials. For reaction time, FCE was calculated by subtracting average reaction time for the same correct aligned trials from the average reaction time for same correct misaligned trials.

The first ANOVA conducted on accuracy data revealed a significant main effect of orientation [$F(1, 26) = 13.875, p < .001, \eta^2 = .348$] indicative of a larger FCE for upright faces than for inverted faces. There was no significant main effect of group [$F(1, 26) = .383, p = .541, \eta^2 = .015$], and no interaction [$F(1, 26) = .123, p = .728, \eta^2 = .005$] (Figure 3.7). The second ANOVA on reaction time produced

similar results: a significant main effect of orientation [$F(1, 26) = 4.418, p = .045, \eta^2 = .145$] indicative of a larger FCE for upright faces than for inverted faces, no significant group difference [$F(1, 26) = 1.917, p = .178, \eta^2 = .069$] and no interaction [$F(1, 26) = .683, p = .416, \eta^2 = .026$] (Figure 3.8). In this regard, synaesthetes did not differ from controls in their face processing abilities on a task in which domain general benefits for synaesthetes in using high spatial frequency visual information were less likely to aid performance.



3.7 Face composite effect (FCE) computed on accuracy data for synaesthetes ($N = 12$) and controls ($N = 16$) on upright and inverted trials.



3.8 Face composite effect (FCE) computed on reaction times data for synaesthetes (N = 12) and controls (N = 16) on upright and inverted trials.

3.4 General Discussion

The current study sought to determine the extent to which GCS differed to controls in their social perception of faces. In Experiment 1, GCS were compared to control participants in their ability to perceive facial identity and facial emotion (happiness and anger perception) which showed an advantage in face processing (i.e. better performance for upright facial identity, but not inverted facial identity perception) for synaesthetes relative to controls. Although synaesthetes performed better on facial emotion perception compared to controls that difference was not statistically significant. There are at least three possible explanations for this pattern of data: 1) control participants were at the lower end of the spectrum in terms of their facial perception abilities relative to other typical individuals 2) the findings reflected domain-specific improvements in face perception in grapheme-colour

synaesthesia or 3) the findings were a secondary consequence of domain-general differences in perception seen between GCS and controls. Given that the tasks used in Experiment 1 promoted the use of the fine-grained visual discriminations, and prior work suggesting that synaesthetes show perceptual benefits in processing high spatial frequency visual cues (e.g. Barnett et al., 2008), it is possible that the performance benefit shown by synaesthetes in Experiment 1 reflected a domain-general advantage for synaesthetes in using high spatial frequency information. To address this, in Experiment 2 facial identity processing abilities of GCS were examined relative to control participants on a face perception task that relied less heavily on high spatial frequency cues – the face composite task (Young et al., 1987; Rossion, 2013). In that experiment no difference was found in the face composite effect between GCS and control participants, implying typical face processing in grapheme-colour synaesthesia when low-spatial frequency visual cues are more important for successful task completion.

Taken collectively, the findings from Experiment 1 and 2 are interesting in at least two ways. Firstly, at face value the findings that GCS show normal or superior social perception abilities appears to conflict with findings of enhanced schizotypy in GCS (Chapter 2; Banissy et al., 2012), and prior work showing an association between schizotypy and deficits in social perception (Abbot and Byrne, 2013; Morrison et al., 2013). It also appears to clash with recent work suggesting that the prevalence of synaesthesia may be more common in other neurodevelopmental conditions that are associated with reductions in the perception of social cues (Neufeld et al., 2013; Baron-Cohen et al., 2013). For example, recently an association between synaesthesia and autism has been suggested (Baron Cohen et al., 2013). Autism has been linked to reductions in the perception of facial identity and

facial emotions (Hedley, Brewer, and Young, 2014; Uljarevic and Hamilton, 2012). In this regard the evidence that GCS show typical or (in some cases) superior social perception abilities conflicts with putative relationships between synaesthesia and autism. It should be noted, however, that differences in the perception of facial identity and facial emotion associated with ASD are somewhat controversial. For example, recent findings suggest that it may be comorbidity between alexithymia and autism rather than autism severity that are responsible for facial emotion perception deficits previously associated with autism (Cook, Brewer, Shah, and Bird, 2013). With this in mind, it may be the case that any relationship between synaesthesia and autism is unlikely to manifest in behavioural differences in social perception.

Secondly, the findings are interesting in the context of recent work suggesting that synaesthetes who experience colour as their evoked sensations show performance advantages on tasks that privilege processing of high spatial frequency visual cues (e.g. Rothen, Meier, and Ward, 2012; Banissy et al., 2013; Barnett et al., 2008; Yaro and Ward, 2007; Banissy et al., 2009). As noted above prior work has suggested that synaesthetes who experience colour as their evoked sensation show neural differences in the processing of high spatial frequency visual cues (e.g. Barnett et al., 2008). In the context of the tasks used here, this information may be of particular utility for tasks employed in Experiment 1 given that they require participants to make fine-grained visual judgments regarding how well each image matches a target face in case of CFPT-Identity or in order to detect small featural differences between images when performing CFPT-Angry and CFPT-Happy. However, previous work has suggested that high spatial frequency visual information may be particularly facilitative in facial identity processing (Vuilleumier

et al., 2003), which is consistent with current findings of enhanced facial identity perception in GCS relative to controls, but typical processing of facial expressions of affect in this population. In contrast, the FCT does not require a similar level of fine-grained comparison. In fact, it has been suggested that FCT relies predominantly on low spatial frequencies as they play a key role in processing global and coarse visual information, especially at the early stages of visual processing (Goffaux and Rossion, 2006), which have been implicated in face composite effect (e.g. Young et al., 1987; Rossion, 2013). In this regard, differences observed on the CFPT tasks may relate to a broader sensitivity of synaesthetes who experience colour as their evoked sensation to high spatial frequency cues that aid fine-grained visual discrimination and add to prior work suggesting that GCS differ to controls in tasks in which high spatial frequency visual cues are useful (e.g. Rothen, Meier, and Ward, 2012; Banissy et al., 2013; Barnett et al., 2008; Yaro and Ward, 2007; Banissy et al., 2009).

Summary

In summary this study demonstrates that synaesthetes who experience colour as their evoked sensation outperform control participants on upright facial identity, but not inverted facial identity perception, emotion perception or the FCT. These findings suggest typical and (in some cases) superior social perception abilities in grapheme-colour synaesthesia, which are likely to reflect broader domain-general perceptual differences which have been reported in synaesthesia for colour.

CHAPTER 4: RELATIONSHIP BETWEEN SYNAESTHESIA AND ALEXITHYMIA

The purpose of this chapter was to examine the levels of alexithymia in grapheme-colour and mirror-touch synaesthesia. This subclinical trait is characterized by deficits in emotion recognition and empathy. In light of the previous findings demonstrating superior emotion recognition and enhanced empathy in MTS as well as the results from Chapter 3 showing that grapheme-colour synaesthesia is characterized by enhanced upright facial identity perception but typical emotion perception it was hypothesized that MTS would be characterized by low levels of alexithymia, while GCS were not expected to differ from controls on this trait. The findings of this study indicate that mirror-touch synaesthesia is linked to lower levels of alexithymia relative to control participants but no other significant group differences were found. Specifically the results showed that MTS scored lower on Difficulty Describing Feelings subscale of the Toronto Alexithymia Scale. The findings are discussed in relation to theories of mirror-touch synaesthesia and previous findings of enhanced social perception and cognition reported in this subtype of synaesthesia.

4.1 Introduction

Alexithymia is a personality construct characterized by compromised emotional awareness. People who score high on alexithymia have difficulties in identifying and describing their own emotional states and struggle with

differentiating between the emotional arousal and bodily sensations (Aleman, 2005). Alexithymia is a multifaceted construct as it contains affective and cognitive components (Vorst and Bermond, 2001). Its cognitive dimension relates to deficits in recognizing and labelling emotions, whereas its affective component reflects impaired ability to become emotionally aroused. Bermond and colleagues (2007) proposed that two different subtypes of alexithymia can be distinguished. One which is characterized by deficits on both affective and cognitive dimension and another one which only includes impaired cognitive component but normal or even increased emotional arousal.

This multifaceted psychological construct was first introduced based on reports from patients with psychosomatic symptoms who had problems describing their emotions (Nemiah, Freyberger, and Sifneos, 1976; Sifneos, 1972). Since then alexithymia has been associated with a number of different disorders including obsessive compulsive disorder, depression or anxiety (Robinson and Freeston, 2014; Taylor, Bagby, and Parker, 1997). It is estimated that 10% of the general population is affected by alexithymia (Linden, Wen, and Paulus, 1995; Salminen, Saarijärvi, Äärelä, Toikka, and Kauhanen, 1999), while for certain disorders e.g. autism comorbidity rate with alexithymia, is as high as 50% (Berthoz and Hill, 2005; Hill, Berthoz, and Frith, 2004; Lombardo, Barnes, Wheelwright, and Baron-Cohen, 2007).

Alexithymia has also been linked to a reduced ability to recognize facial expressions of emotions in others (e.g. Cook et al., 2013). It has been proposed that one mechanism underlying this deficit is reduced simulation indexed by diminished facial mimicry observed in individuals with increased alexithymia relative to those with low alexithymia in response to emotional faces (Sonnby-Borgström, 2009).

This interpretation builds upon the discovery of mirror neurons in the monkey brain which become activated both when a monkey performs an action and when it sees that action being performed by someone else (Gallese, Fadiga, Fogassi, and Rizzolatti, 1996; Rizzolatti and Craighero, 2004). Similar mirror neuron system for action has been reported in the human brain (Buccino et al., 2001), also for touch (Keysers, Wicker, Gazzola, Anton, Fogassi, and Gallese, 2004; Blakemore et al., 2005; Ebisch, Perucci, Ferretti, Del Gratta, Luca Romani, and Gallese, 2008) and pain (Singer et al., 2004; Aventani et al., 2005). Moreover, it has been proposed that the mirror neuron network may also play an important role in social cognition through a process of sensorimotor simulation whereby the observer re-enacts the perceived expression of emotion (Adolphs, 2002; Adolphs, 2003; Gallese, Keysers, and Rizzolatti, 2004; Goldman, and Sripada, 2005; Keysers and Gazzola, 2006). Supporting evidence for this hypothesis has been provided by electromyographic research which shows that presenting emotional expressions at a subliminal level activates corresponding facial muscles (Dimberg, Thunberg, and Elmehed, 2000) and that inhibiting such activation results in reduced emotion recognition ability (Oberman, Winkielman, and Ramachandran, 2007). Therefore, it has been suggested that diminished simulation (Sonny-Borgström, 2009) and associated reduced capacity for representing one's own feelings present in alexithymia might contribute to deficits in identifying feelings in others (e.g. Singer and Lamm, 2009; Niedenthal, 2007; Heberlein and Atkinson, 2009).

While a number of studies suggested that deficits in labelling facial expressions of emotions appear to be especially pronounced for negative valence (e.g. Parker, Prkachin, and Prkachin, 2005), results of a recent systematic review point to a rather global emotion processing deficit in alexithymia (Grynberg, Chang,

Corneille, Maurage, Vermeulen, et al., 2012). This reduced ability to identify emotions in alexithymia is manifested both in longer reaction times (Ihme et al., 2014) as well as in terms of lower accuracy when tasks are presented with temporal constraints (Parker, Prkachin, and Prkachin, 2005; Swart, Kortekaas, and Aleman, 2009). Apart from compromised emotion recognition ability, alexithymia has also been linked to reduced theory of mind (Moriguchi et al. 2006; Swart, Kortekaas, and Aleman, 2009) and deficits in empathy (e.g. Bird et al., 2010).

To date no study has investigated alexithymia in synaesthesia. Particularly interesting in this context is mirror-touch synaesthesia. As mentioned in Chapter 1, this form of synaesthesia is characterized by experiencing tactile sensations on one's own body in response to seeing someone else being touched (Banissy and Ward, 2007). It is believed that one of the mechanisms driving mirror-touch synaesthesia is hyper-activity within the mirror neuron network for touch, which is also activated in controls when observing touch to another person but without the associated overt tactile sensation (Blakemore et al., 2005; Holle et al., 2013). Interestingly prior work has demonstrated that mirror-touch synaesthesia is linked to superior emotion recognition abilities (Banissy et al., 2011) and enhanced empathy (Banissy and Ward, 2007) which is consistent with the simulation accounts of social cognition (Gallese et al., 2004; Gallese, 2006; Keysers and Gazzola, 2006) and previous findings of heightened sensorimotor simulation in mirror-touch synaesthesia (Blakemore et al., 2005; Holle et al., 2013).

In light of these findings and growing literature documenting deficits in emotion recognition (e.g. Grynberg et al., 2012) and empathy (Bird et al., 2010) associated with alexithymia as well as the fact that alexithymia has also been linked to diminished simulation (Sonnby-Borgström, 2009) it was hypothesized that MTS

would be linked with reduced levels of this subclinical construct relative to non-synaesthetic control participants (NSC). Additionally, it was the purpose of this study to establish whether there would be a difference in terms of alexithymia between MTS and GCS, who have not been linked to hyperactivity within the mirror neuron system, differences in empathy or enhanced facial emotion processing (Chapter 3).

4.2 Experiment 3: Synaesthesia and alexithymia

Method

Participants

47 control participants (age $M = 30.95$ $SD = 11.30$, 10 male, 37 female), 10 MTS (age $M = 37.60$ $SD = 8.84$, 3 male, 7 female) and 10 GCS (age $M = 35.00$ $SD = 10.18$, 1 male, 9 female) took part in this experiment. There were no significant group differences in terms of age [$F(2, 66) = 1.849$, $p = .166$] or gender [$\chi^2(2, N = 67) = 1.311$, $p = .519$]. Mirror-touch and GCS were recruited from a database of previously verified synaesthetes. GCS had been previously tested either using the online Eagleman Synaesthesia Test Battery (Eagleman et al., 2007) where a score below 1 indicates a presence of grapheme-colour synaesthesia (also see Rothen et al., 2013), or using a test-retest consistency over time method (all synaesthetes showing >85% consistency over time). MTS had been previously verified using the mirror-touch Stroop test developed by Banissy and colleagues (2007). Control participants were recruited among acquaintances and Psychology students via student participation scheme (an online platform used for advertising experiments) who were given 1 credit in return for their participation.

Materials

The Toronto Alexithymia Scale (TAS-20; Bagby, Parker, and Taylor, 1994) is a widely used twenty item self-report instrument designed to measure alexithymia. It consists of three subscales: Difficulty Identifying Feelings (DIF; consists of 7 items and reflects awareness of internal sensations and emotions), Difficulty Describing Feelings (DDF; consists of 5 items and reflects an ability to verbalise and communicate emotions to others), and Externally Oriented Thinking (EOT; consists of 8 items and reflects a tendency to attend to the outside world rather than one's own thoughts and emotions). All items are rated on a 5 point Likert scale ranging from 'strongly disagree' to 'strongly agree'. The sum of all scores produces the total alexithymia score (TAS Total), where a score of 61 and above indicates the presence of alexithymia.

Results

TAS-20 had a high internal consistency score (Cronbach's Alpha = .836). A one way ANOVA was used to analyse participants' scores on this questionnaire, which revealed a significant main effect of group [$F(2, 66) = 3.493, p = .036, \eta^2 = .098$]. Follow up paired comparisons with Bonferroni correction showed a significant group difference between MTS and controls ($p = .036$, Cohen's $d = .089$) with MTS scoring lower on alexithymia ($M = 41.40, SD = 11.65$) than controls ($M = 52.02, SD = 12.05$). No other significant group differences were found either between GCS ($M = 47.90, SD = 10.62$) and MTS ($p = .668$) or GCS and controls ($p = .960$) (Figure 4.1).

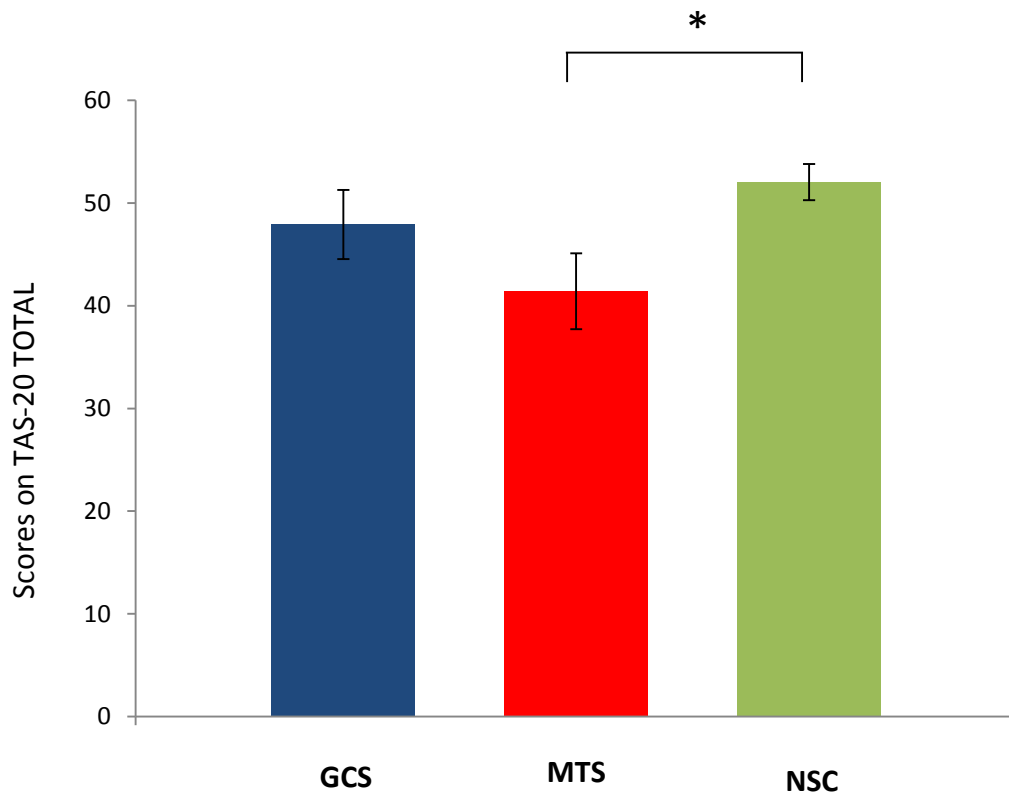


Figure 4.1 Mean total scores on Toronto Alexithymia Scale for grapheme-colour synaesthetes (GCS, N = 10), mirror-touch synaesthetes (MTS, N = 10) and control participants (NSC, N = 47). * = $p < .05$.

To further explore whether these results were due to differences on particular subscales of TAS-20 an additional 3 (group: MTS, controls, GCS) x 2 (TAS-20 subscales: DIF, DDF) ANOVA was conducted. The third subscale (EOT) was not included in this analysis due to a low consistency score (Cronbach's alpha = .518). The other two subscales had good consistency scores of .801 and .834 respectively. This analysis was conducted on z scores. The results of this analysis revealed a significant main effect of subscales [$F(1, 64) = 4.353, p = .041, \eta^2 = .064$] due to overall lower scores on DDF subscale ($M = -.244, SE = .151$) relative to DIF ($M = .050, SE = .156$). There was no effect of group [$F(2, 64) = 1.180, p = .314, \eta^2 =$

.036]. More importantly there was a significant interaction [$F(2, 64) = 6.412, p = .003, \eta^2 = .167$]. Follow up independent samples t-tests revealed a difference between MTS and controls on DDF subscale [$t(55) = 2.129, p = .038, \text{Cohen's } d = 0.76$] due to MTS scoring lower ($M = -.534, SD = .916$) than controls ($M = .198, SD = 1.00$). However this difference was not significant after applying Bonferroni correction ($p = .076$).

4.3 Discussion

Building on the previous chapters examining personality traits and social perception abilities in GCS, the purpose of this study was to examine another personality trait that is relevant to social perception, namely alexithymia. Specifically, drawing on previous findings of enhanced empathy (Banissy and Ward, 2007) and superior facial affect recognition found in MTS (Banissy et al., 2011), it was hypothesized that this form of synaesthesia would be associated with reduced levels of alexithymia which has been previously linked to difficulties in recognizing emotions in others (e.g. Grynberg et al., 2012) as well as reduced empathy (Bird et al., 2010). GCS were included in the current study as a control group as this type of synaesthesia has not been linked to the enhanced sensorimotor simulation or associated differences in facial emotion perception (Chapter 3) and as such it was not expected to differ from typical adults in terms of alexithymia levels.

The results of the statistical analysis revealed that individuals verified as MTS scored significantly lower on TAS-20 relative to controls. Although individuals with grapheme-colour synaesthesia also had lower scores than control participants, that difference was not statistically significant. Similarly there was no group difference in terms of alexithymia between MTS and GCS. It is of note that control participants in

this study had slightly elevated alexithymia scores ($M = 52.02$, $SD = 12.05$) while GCS' scores ($M = 47.9$, $SD = 10.62$) were similar to normative data (students: $M = 47.39$, $SD = 10.36$, Bagby, Parker, and Taylor, 1994; community sample: $M = 45.57$, $SD = 11.35$, Parker, Taylor, and Bagby, 2003), and MTS' scores were lower than typical adults' ($M = 41.4$, $SD = 11.65$). It thus appears that the current results are not due to a general self-report bias of different synaesthetic groups as GCS' scores resembled typical responses as demonstrated by normative data.

These results are interesting in context of the findings from Chapter 3 showing normal and in some cases enhanced social perception in GCS. Specifically, GCS showed superior facial identity processing when performing tasks which promote the use of high spatial frequency visual information (the Cambridge Face Perception Taks; Duchaine et al., 2007), to which they are particularly sensitive (Barnett et al., 2008). However, when performing tasks which rely more heavily on low spatial frequency information (the face composite task; Young et al., 1987; Rossion, 2013), synaesthetes did not show any advantage in social perception relative to controls. As such, no difference between MTS and GCS and between GCS and controls in terms of alexithymia levels appears to compliment previous findings showing superior emotion recognition abilities in MTS (Banissy et al., 2011) and enhanced social perception of faces in GCS relative to controls but only when performing tasks which utilize high spatial frequency information (Chapter 3).

Additionally, these findings are interesting in the context of neural mechanisms reported to underlie mirror-touch synaesthesia. Namely, one theory (hereafter referred to as Threshold Theory) states that hyperactivity within the so-called mirror network for touch involved both in experiencing touch and observing touch to another person (including primary and secondary somatosensory cortex,

premotor cortex, parietal cortex) is the neural correlate of mirror-touch synaesthesia (Holle, Banissy and Ward, 2013; Blakemore et al., 2005, Ward and Banissy, 2015). This theory draws on the notion of a mirror system for action previously shown to be activated both for self-generated and observed actions (Rizzolatti and Craighero, 2004). It has also been suggested that this mechanism may play a key role in empathy and mind-reading as it allows the observer to simulate another person's emotions by recruiting the same brain regions that are active when experiencing emotions (Gallese and Goldman, 1998). At the same time reduced simulation has been proposed to underlie deficits in emotion processing found in alexithymia (Sonny-Borgström, 2009). Given that prior work suggests that individuals with MTS show heightened sensorimotor simulation and previous studies showing enhanced emotion recognition and empathy in MTS relative to controls (Banissy et al., 2011; Banissy and Ward, 2007; Goller et al., 2013), the current findings of lower levels of alexithymia found in MTS relative to controls are in line with this.

The fact that MTS did differ from controls in terms of their levels of alexithymia while no statistical difference was found between GCS and controls, may reflect the different neural mechanisms thought to underlie these two forms of synaesthesia. As noted above, mirror-touch synaesthesia has been linked with atypical simulation processes that are thought to be important in a variety of socio-cognitive tasks (e.g. empathy, emotion recognition), but grapheme-colour synaesthesia has not. However, GCS also did not differ in terms of their scores on TAS-20 from MTS.

More detailed analysis of individual subscales of TAS-20 revealed that MTS scored lower on Difficulty Describing Feelings (DDF) compared to non-synaesthetic control participants, which relates to an ability to label one's own emotions, but

which also has been linked to deficits in identifying emotions in others (e.g. Parker, Prkachin, and Prkachin, 2005). However, these results need to be treated with caution as the difference is not statistically significant when controlling for multiple comparisons and thus requires further replication. Nevertheless, these results appear to compliment previous findings of enhanced ability to recognize emotions in MTS reported by Banissy and colleagues (2011). In this study MTS outperformed controls on an emotion recognition task which entailed showing participants an adjective describing an emotional state which was subsequently followed by three images showing the same person with different facial expressions. Participants' task was to choose one of the three images which best represented the emotional label. Interestingly, while there was a tendency for MTS to be more accurate on a same-different emotion matching task, which required participants to indicate whether the sample face followed by a target face showed the same or different emotional expression, paired comparisons did not show a significant group difference. Therefore, current findings suggest that MTS have an enhanced ability to label emotions indexed by lower scores on Difficulty Describing Feelings (DDF), which is consistent with prior work showing superior emotion recognition in MTS using a task which relies on the ability to label facial expressions of affect.

Summary

In summary, current findings of reduced alexithymia in MTS relative to typical adults are in line with prior work showing enhanced sensorimotor simulation, superior emotion processing and greater empathy found in this group. Lower scores on DDF subscale of TAS-20 found in mirror-touch synaesthesia relative to controls also compliment prior data showing that MTS are better at labeling the emotions of

others (Banissy et al., 2011) and work suggesting that higher trait alexithymia is associated with a deficit in this domain (Cook et al., 2013).

CHAPTER 5: INTEROCEPTIVE SENSITIVITY IN SYNAESTHESIA

Interoceptive sensitivity is an ability to monitor internal bodily changes such as e.g. one's own heartbeat. It has been previously shown that interoceptive sensitivity can modulate the malleability of body representation, self-other processing as well as emotional arousal. For instance, reduced interoceptive sensitivity has been linked to greater malleability of body representation indexed by enhanced susceptibility to the body ownership illusions such as the enfacement illusion and the rubber hand illusion. On the other hand, higher interoceptive sensitivity has been linked to lower levels of alexithymia. In light of previous work demonstrating greater flexibility of the body representation in mirror-touch synaesthesia as well as lower levels of alexithymia found in this group in Chapter 4 it was the purpose of this study to establish whether this form of synaesthesia would be associated with differences in interoceptive sensitivity relative to controls. The findings demonstrate that MTS are characterized by lower interoceptive sensitivity relative to both GCS and controls. Additionally this research sought to elucidate whether interoceptive sensitivity contributes to emotion recognition ability in typical adults. The findings suggest that the ability to process facial expressions of affect does not rely on the levels of interoceptive sensitivity.

5.1 Introduction

Building on the findings of lower levels of alexithymia in MTS relative to controls (Chapter 4) and previous work demonstrating an inverse association between alexithymia and interoceptive sensitivity (IS; Herbert et al., 2011) I aimed to elucidate whether MTS would differ in terms of this ability relative to GCS and typical controls.

Interoceptive sensitivity (IS) is the ability to detect physiological changes within one's own body (Critchley et al., 2004). It is typically measured with heartbeat detection tasks where participants are asked to count the number of heartbeats within a specific time interval. Although the literature has used IS and interoceptive awareness (IA) interchangeably they are two distinctive phenomena (Garfinkel and Critchley, 2013). While IS is an ability to detect internal bodily sensations and can be objectively measured using accuracy scores, IA entails explicit knowledge of one's ability to detect these bodily fluctuations i.e. being aware whether one has good or bad IS (Garfinkel and Critchley, 2013). Recently Garfinkel, Seth, Barrett, Suzuki and Critchley (2015) proposed that there is an additional third component of interoception called interoceptive sensibility, which entails self-reported tendency for interoception. This study will only focus on IS as defined by Garfinkel and Critchley (2013).

IS has been previously linked to a number of broader traits. For instance, Tajadura-Jiménez and Tsakiris (2014) found that IS modulates the malleability of self-representations measured with the 'enfacement illusion'. In this paradigm participants are first presented with a video where an unfamiliar person's facial features are gradually morphed into their own face. Participants are asked to stop the video when the face looks more like their own than the other person's. Subsequently

they are subjected to multi-sensory stimulation which involves synchronous stroking of their own and the unfamiliar person's face, which is then followed by the same self-recognition test performed prior to the stimulation condition. Typically observing and experiencing simultaneous touch leads to incorporating the unfamiliar person's features into participants' own body representations. This is indexed by participants indicating images which they had rated as looking less like themselves prior to the touch condition to contain more of their own features after multi-sensory stimulation. Tajadura-Jiménez and Tsakiris (2014) measured participants' IS with a heartbeat detection task which consisted in reporting the number of heartbeats after four different time intervals (25, 35, 45 and 100 sec). Their results showed that low IS was linked to a greater enfacement illusion following multisensory stimulation, thus suggesting that low IS mediates greater malleability of self-other boundaries.

Previously Tsakiris, Tajadura-Jiménez and Costantini (2011) also demonstrated the modulatory role of IS in malleability of the boundaries of body-representation using the Rubber Hand Illusion (RHI). In this classic paradigm simultaneous stroking of one's own hand hidden from view and observing a prosthetic hand being stroked results in a sense of body-ownership of the fake hand (Botvinick and Cohen, 1998). The authors of this study found that RHI was larger in those participants with lower IS, which they also measured with a heartbeat detection task.

These findings are interesting in the context of synaesthesia and in particular mirror-touch synaesthesia. As mentioned in Chapter 1 MTS is a condition where observing touch to another person induces tactile sensations on one's own body (e.g. Banissy, 2013). MTS have been previously found to be highly susceptible to the enfacement illusion as merely showing videos of another person being touched

without experiencing synchronous real touch on MTS' own body was sufficient to induce this illusion (Maiester et al., 2013). Aimola-Davies and White (2013) reported similar findings in terms of the RHI where showing touch to a prosthetic hand was sufficient to induce the illusion in MTS in the absence of multisensory stimulation, thus providing further evidence for a highly malleable body representation in this group of individuals.

Another line of research investigated the relationship between IS and the ability to control self-other representations by measuring imitation inhibition with a well-established finger lifting paradigm (Brass et al., 2005). In this task participants are asked to lift either their index or middle finger depending on a number appearing on the screen next to a video where a stimulus hand remains static, performs the same action as the participant or lifts the other finger. Performance on this task is measured with a congruency effect whereby reaction time tends to be faster and accuracy higher on congruent trials and the reverse is typically true for incongruent trials. In a recent study Ainley, Brass and Tsakiris (2014) found that high IS was linked with greater difficulty in inhibiting imitation on the finger lifting paradigm suggesting reduced control of self-other representation. These findings appear to clash with previous reports of an association between low IS and decreased self-other distinction as demonstrated by body ownership paradigms (Tajadura-Jiménez and Tsakiris, 2013; Tsakiris et al., 2011).

Interestingly, recent findings by Santiesteban, Bird, Tew, Cioffi and Banissy (2015) suggest that mirror-touch synaesthesia is linked with a greater tendency to imitate as measured with the afore-mentioned finger-lifting paradigm. Specifically, the authors report that MTS have a selective deficit in inhibiting the representation of others, as they did not differ from control participants on tasks which required

enhancing the other representations and inhibiting the representation of the self. These results are in line with previous findings of reduced grey matter volume in the right temporoparietal junction (TPJ) and the dorsal medial prefrontal cortex (mPFC) in MTS relative to controls (Holle, Banissy and Ward, 2013). These brain regions have been previously implicated to play a role in self-other representations (e.g. Brass et al., 2009; Lombardo et al., 2010; Santiesteban et al., 2012; Spengler et al., 2010; van Overwalle, 2009) and thus it has been suggested that reduced grey matter volume in these areas might contribute to atypical self-other processing and the actual experience of mirror-touch synaesthesia (Banissy and Ward, 2013; Ward and Banissy, 2015).

Prior work has also suggested a relationship between heightened IS and greater self-reported intensity of emotional experience (e.g. Barrett, Quigley, Bliss-Moreau, and Aronson, 2004; Wiens Mezzacappa, and Katkin, 2000), increased self-reported arousal in response to emotional stimuli (Pollatos, Kirsch, and Schandry, 2005) increased physiological response to affective images (Pollatos and Schandry, 2008) as well as sensitivity to the emotions of others (Terasawa, Moriguchi, Tochizawa, and Umeda, 2014). At the same time mirror-touch synaesthesia has been linked to enhanced emotional reactivity compared to synaesthetic and non-synaesthetic control participants (Banissy and Ward, 2007). This subscale of the Empathy Quotient (Baron-Cohen, and Wheelwright, 2004) reflects a propensity for an emotional reaction to the mental states of others (Lawrence, Shaw, Baker, Baron-Cohen and David, 2004). Mirror-touch synaesthesia has also been associated with heightened emotion recognition abilities relative to controls (Banissy et al., 2011). Recently it has been suggested that this advantage might be linked to deficits in inhibiting the other representation found in MTS (Santiesteban et al., 2015), which in turn may

prevent one's own emotional state from influencing the representation of emotions of others, as prior findings suggested that emotion recognition may be affected by one's current emotional state (Schmid and Mast, 2010). Although several prominent emotion theories suggest that perception of physiological changes gives rise to emotional experiences (e.g. James, 1894; Damasio, 2000; Critchley et al., 2004; Craig, 2009) the link between IS and emotion recognition has not been directly tested to date.

As mentioned earlier IS has also been reported to be inversely associated with alexithymia which is a personality construct characterized by deficits in identifying and describing emotions, suggesting that higher IS is linked to lower levels of this trait and vice versa (Herbert, Herbert and Pollatos, 2011). As reported in Chapter 4 of this thesis mirror-touch synaesthesia has also been associated with lower alexithymia levels relative to controls which in light of prior findings could suggest that mirror-touch synaesthesia might be linked to altered levels of IS relative to typical adults. However, in light of previous research which presented a conflicting image regarding the role of IS in different aspects of self-other distinction and social cognition (Fig 5.1) no directional prediction regarding the level of IS in MTS was made. Therefore the purpose of this study was to establish whether MTS differ in terms of IS relative to typical adults as well as GCS. Additionally, this study sought to elucidate the potential role of IS in social perception and more specifically in the ability to process facial expressions of emotions by examining this relationship in a group of non-synaesthetic adult participants.

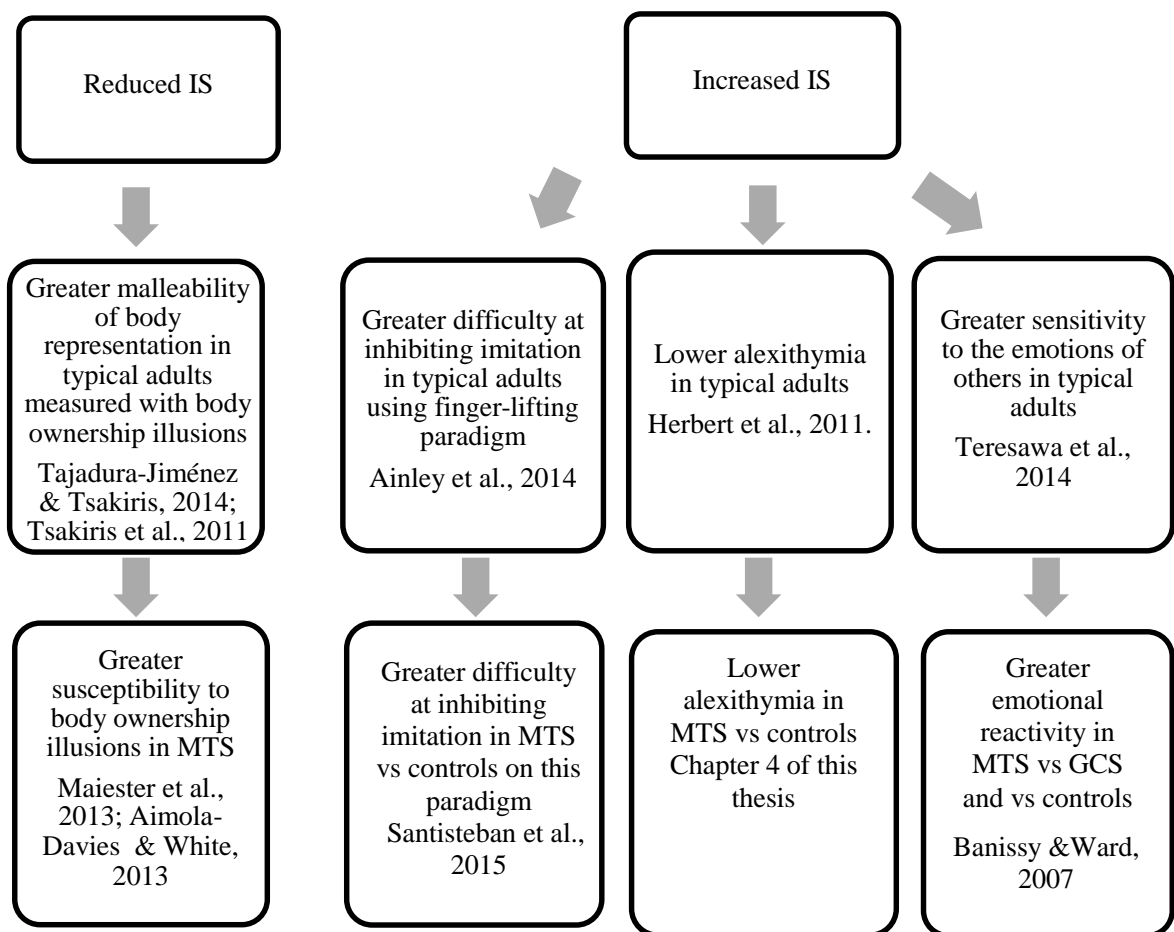


Figure 5.1 Diagram showing existing findings on the association between interoceptive sensitivity (IS), body representation, imitation inhibition, alexithymia, sensitivity to emotions of others and mirror-touch synaesthesia (MTS).

5.2 Experiment 4: Interoceptive sensitivity in MTS, GCS and controls

Prior work in typical adults presents a conflicting image regarding the role of IS in self-other distinction and social cognition. For instance, Ainley and colleagues (2014) found that high IS was linked with greater difficulty in inhibiting imitation, which was also found in MTS (Santisteban et al., 2015). At the same time body

ownership paradigms (Tajadura-Jiménez and Tsakiris, 2013; Tsakiris et al., 2011) which demonstrated greater malleability of self-other representations in MTS (Maiester et al., 2013; Aimola-Davies and White, 2013) suggested a link between low IS and deficits in self-other distinction. The aim of this experiment was to examine whether MTS differ in terms of their ability to detect internal body changes known as interoceptive sensitivity (IS; e.g. Critchley et al., 2004) compared to controls and GCS.

Method

Participants

8 MTS (5 female, 3 male, age $M = 25.87$, $SD = 6.68$), 34 non-synaesthetic control participants (NSC; 21 female, 13 male, age $M = 24.11$ $SD = 5.54$) and 12 GCS (11 female, 1 male, age $M = 26$, $SD = 6.52$) took part in this experiment. Participants did not differ significantly in terms of age [$F(2, 53) = .780$, $p = .464$] or gender [$\chi^2(2) = 4.570$, $p = .102$]. MTS and GCS were recruited from a database of previously verified synaesthetes. GCS had been previously tested using the online Eagleman Synaesthesia Test Battery (Eagleman et al., 2007) where a score below 1 indicates a presence of grapheme-colour synaesthesia (also see Rothen et al., 2013). MTS had been previously verified using the mirror-touch Stroop test developed by Banissy and colleagues (2007). Synaesthetes were paid £10 for participating in this experiment. Control participants were recruited from the student population via posters displayed at the university buildings and through student participation scheme (an online platform used for advertising experiments). They were either paid £10 or given 1 credit for their participation. Controls and GCS also took part in Experiment 1 in Chapter 3.

Procedure

IS was measured with a heartbeat detection task (Tsakiris et al., 2011). In this task participants were asked to silently count the number of their heart beats during different time intervals (20, 30 and 40 s each repeated twice). The six trials were presented in a random order. The onset and the end of each trial were signaled with a beep sound. Participants were instructed not to take their pulse or cross their legs or arms in order not to feel their pulse. Participants' actual pulse was measured with finger pulse oximeter (Xpod, model 3017LP, Nonin Medical Inc., MN, USA) which was placed on their left index finger and recorded with an in-house software. For each trial, an accuracy score was calculated between 0 and 1 with higher scores indicating better IS. IS was calculated according to the following formula (as per e.g. Tsakiris et al., 2011)

$$1/6 \sum (1 - (|\text{recorded heartbeats} - \text{Counted heartbeats}|) / \text{recorded heartbeats})$$

Additionally as it has been previously shown that BMI can influence participants' IS (e.g. Pollatos et al., 2008) participants' height and weight was taken prior to the start of the heartbeat detection task.

Results

There was no significant group difference in terms of BMI [$F(2, 53) = 2.006$, $p = .145$] or a significant correlation between BMI and IS [$r(54) = -.132$, $p = .342$], suggesting that BMI did not contribute to performance on the heartbeat detection task. To examine the extent to which group membership influenced IS a one-Way ANOVA with group entered as an independent variable and IS as a dependent variable was conducted. This did not reveal a main effect of group [$F(2, 53) =$

2.008, $p = .145$, $\eta p^2 = .073$]. Two planned pairwise comparisons were carried out in order to further elucidate whether MTS differ significantly in terms of their levels of IS relative NSC and GCS. This analysis revealed a significant group difference between MTS and NSC [$t(40) = 2.480$, $p = .022$, Cohen's $d = .781$] due to MTS scoring lower on IS relative to NSC. There was also a significant group difference between MTS and GCS [$t(18) = 2.626$, $p = .017$, Cohen's $d = 1.142$] with MTS showing lower IS than GCS.

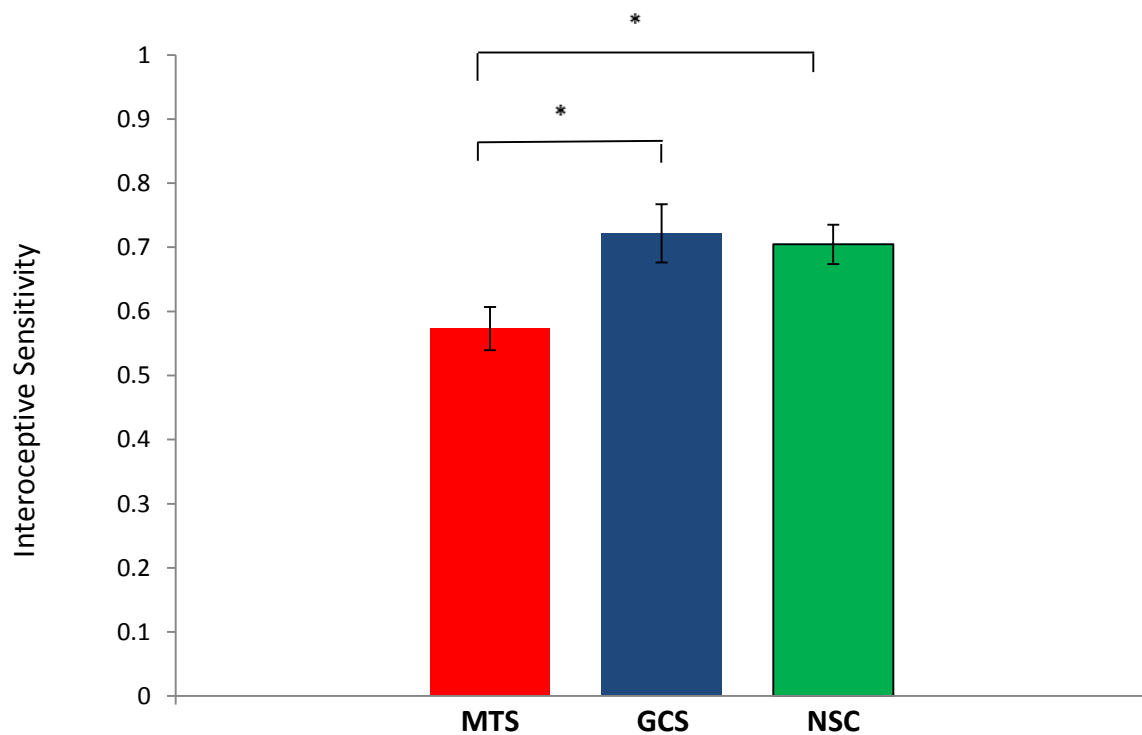


Figure 5.2 Mean scores on interoceptive sensitivity for mirror-touch synaesthetes (MTS, $N = 8$), grapheme-colour synaesthetes (GCS, $N = 12$) and controls (NSC, $N = 34$). * = $p < .05$.

5.3 Experiment 5: Interoceptive sensitivity and emotion recognition ability

Based on theories postulating an important role of sensitivity to bodily signals in emotions (e.g. James, 1894; Damasio, 2000; Critchley et al., 2004; Craig, 2009) as well as empirical findings demonstrating a link between IS and emotional experience (e.g. Barrett et al., 2004; Wiens et al., 2000; Pollatos et al., 2005; Pollatos and Schandry, 2008; Terasawa et al., 2014) this study sought to directly test whether IS contributes to an ability to recognize emotions in others.

Method

Participants

34 control participants (21 female, 13 male, age $M = 24.11$, $SD = 5.54$) took part in this experiment. They were the same participants who took part in Experiment 1 of this chapter as well as in Experiment 1 in Chapter 3. They were recruited from the student population via student participation scheme and given 1 credit in return for their participation.

Procedure

The Cambridge Face Perception Angry Expression (CFPT-Angry) and Cambridge Face Perception Happy Expression (CFPT-Happy) were used in order to assess participants' facial emotion perception abilities. Additionally, the Cambridge Face Perception Test (CFPT-Identity; Duchaine, Yovel, and Nakayama, 2007) was employed as a control task to measure facial identity perception abilities. Detailed description of these tests is included in Chapter 3. Additionally the heartbeat detection task described in Experiment 1 of this chapter was administered in order to examine participants' interoceptive sensitivity.

Results

Correlational analysis was performed to establish whether there is an association between BMI, age, gender and scores on IS as well as whether these demographic variables contribute to performance on facial emotion and identity processing tasks (CFPT-Identity, CFPT-Angry, CFPT-Happy). This analysis revealed a significant positive correlation between age and CFPT-Angry [$r(34) = .403, p = .018$], and two other positive correlations between age and CAPT-happy [$r(34) = .327, p = .059$] and between age and IS [$r(34) = .338, p = .051$] which approached significance. There were no other significant correlations.

Partial correlational analysis was performed to establish whether IS contributed to performance on CFPT-Angry, CFPT-Happy and CFPT-Identity tasks while controlling for age which turned out to be positively correlated with IS levels (although it only approached significance). This analysis revealed no association between scores on IS and performance on the afore-mentioned tasks, suggesting that IS does not contribute to facial emotion or identity processing ability.

5.4 Discussion

The purpose of this study was to investigate whether mirror-touch synaesthesia is associated with differences in terms of their levels of IS relative to typical adults as well as synaesthetic control participants. IS, which is an ability to accurately detect internal bodily changes such as e.g. being able to monitor one's own heartbeat (Critchley et al., 2004; Garfinkel and Critchley, 2013) has been previously shown to modulate body representation, self-other monitoring and alexithymia. Specifically, decreased IS has been linked to greater malleability of body representation as shown

by enhanced susceptibility to the enfacement illusion and the rubber hand illusion (Tajadura-Jiménez and Tsakiris, 2013; Tsakiris et al., 2011). On the other hand heightened IS has been associated with greater difficulty to inhibit imitation which is used as a measure of self-other monitoring (Ainley, Brass, and Tsakiris, 2014), and with lower alexithymia (e.g. Herbert et al., 2011). At the same time MTS have been found to be highly susceptible to the body-ownership illusions (Maiester et al., 2013; Aimola-Davies and White, 2013) to have deficits in terms of inhibiting their tendency to imitate (Santiesteban et al., 2015) and to be characterized by low alexithymia (Chapter 4). Thus in light of previous research which presented a conflicting image regarding the role of IS in different aspects of self-other distinction and social cognition no directional prediction regarding the level of IS in MTS was made.

Planned pairwise comparison tests revealed that MTS scored significantly lower on IS (i.e. worse) than NSC and GCS. These results are in line with the previous findings showing an association between decreased IS and malleable body representation (Tajadura-Jiménez and Tsakiris, 2013; Tsakiris et al., 2011) and findings of blurred self-other boundaries in MTS (Maiester et al., 2013; Aimola-Davies and White, 2013). They are also consistent with the theories of mirror-touch synaesthesia postulating that atypical self-other representation is one mechanism which contributes to the actual experience of mirror-touch synaesthesia (Banissy and Ward, 2013; Ward and Banissy, 2015) and prior work showing a reduction in grey matter volume in the right temporoparietal junction (TPJ) and the dorsal medial prefrontal cortex (mPFC) in MTS (Holle, Banissy and Ward, 2013), which are brain areas believed to play a key role in self-other representation (e.g. Brass et al., 2009;

Lombardo et al., 2010; Santiesteban et al., 2012; Spengler et al., 2010; van Overwalle, 2009).

At the same time current results appear to be in opposition to Ainley and colleagues' (2014) findings of an association between heightened IS and greater difficulty to inhibit imitation, since prior work suggests that individuals with mirror-touch synaesthesia show greater difficulties in this domain (Sanstesteban et al., 2015). They also seem to be at odds with the findings from Chapter 4 of this thesis suggesting that mirror-touch synaesthesia is linked with lower alexithymia relative to controls and prior research demonstrating a negative correlation between IS and alexithymia (Herbert et al., 2011). However, it has to be noted that prior work examining the relationship between IS and self-other monitoring and alexithymia was carried out in typical adults and therefore it is reasonable to suspect that a different pattern of results could be present in an atypical population such as MTS.

The second aim of this study was to examine whether differences in IS are related to facial emotion processing ability by testing a group of control participants on CFPT-Angry, CFPT-Happy and a control task which tested an ability to process facial identity i.e. CFPT-Identity (Duchaine et al., 2007). The results of the statistical analysis did not show an association between IS and facial affect or facial identity perception. Interestingly no direct link between IS and emotion perception has been reported to date despite emotion theories suggesting an important role of perception of physiological changes in emotional experience (e.g. James, 1894; Damasio, 2000; Critchley et al., 2004; Craig, 2009). It is possible that processing of facial affect and emotional arousal or sensitivity to the emotions of others are driven by separate mechanisms and as such differences in IS would only be linked to these aspects of emotional experience as has been shown by prior work (e.g. Barrett, Quigley, Bliss-

Moreau, and Aronson, 2004; Wiens Mezzacappa, and Katkin, 2000) but not the ability to process emotions.

Current results showing that MTS have lower IS relative to NSC and GCS and previous findings of superior emotion recognition ability found in this group (Banissy et al., 2011) could suggest an inverse association between these two abilities but not between IS and emotion processing as measured with CFPT tasks. It is also possible that MTS could present a different pattern of results since it is an atypical group. However, as these results are preliminary this would need to be further elucidated in future studies by directly assessing IS and facial emotion recognition in the same group of MTS as well as by examining whether differences in IS contribute to emotion recognition ability in control participants by using similar tasks to those employed by Banissy and colleagues (2011), which previously showed superior emotion recognition in MTS.

Summary

The findings of Chapter 5 suggest that mirror-touch synaesthesia is associated with lower interoceptive sensitivity relative to GCS and controls. They also indicate no relationship between interoceptive sensitivity and the ability to process facial expressions of affect and facial identity in typical adults.

CHAPTER 6: METHODOLOGICAL INTRODUCTION TO TRANSCRANIAL CURRENT STIMULATION

This chapter provides an overview of the methodological principles of transcranial current stimulation with a particular emphasis on transcranial alternating current stimulation. This review will outline the underlying physiological mechanisms, discuss different parameters which impact the effect of tACS (e.g. intensity and phase of applied stimulation), and provide a discussion of ethical considerations of using tCS. Chapter 7 of this thesis describes three studies where tACS was employed to determine the role of cortical oscillations within the gamma frequency range on the ability to recognize facial expressions of emotion in typical adults, hence an overview of this non-invasive brain stimulation method is provided below.

6.1 Introduction

Transcranial current stimulation (tCS) is a type of non-invasive brain stimulation technique which encompasses transcranial direct current stimulation (tDCS), transcranial alternating current stimulation (tACS) and transcranial random noise stimulation (tRNS). In recent years there has been a growing interest in using these methods as a tool to elucidate the neural mechanisms underlying cognition, to improve cognitive functioning and to aid neurorehabilitation (Santarnecchi et al., (2015). In this Chapter I will review these techniques with a focus on tACS as in Chapter 7 I utilize tACS as a tool to modulate facial emotion perception.

6.2 Transcranial direct current stimulation (tDCS)

The field of non-invasive current stimulation has been particularly dominated by studies employing tDCS as this technique has been in use for the longest period (for review see e.g. Costa, Lapenta, Boggio, and Ventura, 2015). tDCS uses unidirectional constant current delivered by external electrodes placed on scalp over the cortical areas of interest. The intensity of the current ranges between 1 and 2mA and the direction in which it flows is from the anode to the cathode (Zaghi, Acar, Hultgren, Boggio, and Fregni, 2009). tDCS is believed to modulate the excitability of the cortical areas leading to excitation of the target area in case of anodal stimulation or to inhibition in case of cathodal stimulation (Nitsche et al., 2008), although it has been suggested that this is not always the case (Bestmann et al., 2015). It is believed that online tDCS effects are a consequence of a modulation of the resting membrane potentials in the area of stimulation, while offline aftereffects most likely reflect mechanisms of synaptic plasticity such as long term potentiation and long term depression (Fritsch, et al. 2010). It is also believed that tDCS affects neurotransmitter concentrations with anodal tDCS being linked to an inhibitory effect on GABA concentration (e.g., Nitsche et al. 2004) while cathodal tDCS has been suggested to inhibit glutamate levels (e.g., Stagg et al., 2009). Long-term effects of repeated tDCS sessions coupled with training on cognitive performance have been reported to last up to several weeks (e.g. Vestito, Rosellini, Mantero, and Bandini, 2014).

6.3 Transcranial random noise stimulation (tRNS)

tRNS is the newest addition to the tCS techniques. It uses random level of alternating current which ranges between 0.1 and 640 Hz for every sample passed

between the two electrodes. High-frequency tRNS, which uses alternating current between 100 Hz to 640 Hz, has been shown to enhance the excitability of the cortical areas under both electrodes (Terney, Chaieb, Moliadze, Antal, and Paulus, 2008) leading to facilitation of cognitive functioning e.g. in terms of improved numerical cognition (Cappelletti et al. 2013), or better facial identity perception (Romanska, Rezlescu, Susilo, Duchaine, and Banissy, (2015). While the effects of single session of tRNS typically last about 1 hour post stimulation (Terney et al., 2008) Cappelletti and colleagues (2013) recently showed that by combining tRNS with cognitive training it was possible to boost cognitive performance up to 16 weeks after training. Although the exact mechanisms underlying tRNS remain to be elucidated it has been suggested that tRNS may cause repeated depolarization of the neuronal membrane leading to continuous depolarization and repolarization of sodium channels resulting in increased cortical excitability of the stimulated area (e.g. Chaieb, Antal, and Paulus, 2015; Chaieb et al., 2011).

6.4 Transcranial alternating current stimulation (tACS)

tACS is a relatively novel non-invasive brain stimulation method which enables modulating neural activity within physiologically relevant frequencies and which can be divided into delta (0–3Hz), theta (4–7 Hz), alpha (8–12 Hz), beta (13–30Hz), and gamma (30–200 Hz) (Antal and Paulus, 2013). Synchronized rhythmic activity within these frequencies has been implicated as an important mechanism underlying various cognitive functions. For example, brain oscillations in the theta range have been consistently linked to various memory processes. For instance, it has been found that frontal midline theta power increases with greater working memory demands (Gevins et al., 1997; Onton et al., 2005) and task difficulty

(Kahana et al., 1999). It has also been demonstrated that abnormal oscillatory activity within particular frequency bands is often associated with various cognitive impairments characteristic of disorders such as schizophrenia, Alzheimer's disease or bipolar disorder (Uhlhaas et al., 2008; Başar and Güntekin 2008). For example, schizophrenic patients with disorganized symptoms have deficits in gestalt processing measured with visual closure tasks, such as Mooney faces, or contour integration tasks. This impairment has been found to be accompanied by disorganized, asynchronous pattern of long-range oscillations within the beta band (Uhlhaas et al., 2006).

Although the exact mechanisms of tACS remain to be elucidated it is believed that tACS can interact and change ongoing brain oscillatory activity as documented by studies employing electroencephalography (e.g. Vosskuhl, Huster, and Herrmann, 2015; Zaehle et al., 2010). For instance, Zaehle and colleagues (2010) demonstrated that delivering tACS within participants' individual alpha frequency determined prior to stimulation leads to increased alpha amplitude. These results suggest that tACS can interact with and alter existing neural oscillations during the time of stimulation.

The ability of tACS to modulate ongoing rhythmic activity within particular frequencies also manifests itself in changes in perception and cognition as well as in altered behavioural responses. For example, in the visual domain tACS stimulation in the beta band over primary visual cortex has been found to evoke phosphenes (percepts of flickering light used as a measure of the visual cortex' excitability) in illuminated settings (Kanai et al., 2008, Kanai et al., 2010), while tACS stimulation in the alpha band elicited phosphenes in the dark. Similarly, tACS delivered to the primary somatosensory cortex in alpha and gamma band has been shown to induce

tactile sensation in the contralateral hand (Feurra et al., 2011). It is also possible to use tACS to modulate higher order human cognition. For instance, Polanía and colleagues (2012) recently demonstrated that tACS induced synchronization in the theta range over fronto-parietal region results in enhanced performance on a visual memory task, whereas desynchronization leads to the opposite effect. Santarnecchi and colleagues (2013) also found that stimulating the left middle frontal gyrus in gamma frequency band enhances participants' performance on Raven's matrices, which is a standard measure of fluid intelligence. tACS is therefore a powerful tool which can be used to address questions about oscillations in perceptual and cognitive tasks.

Mechanisms of tACS

tACS is delivered via two surface electrodes which are placed on scalp over a target area. Electrodes are enclosed in saline-soaked sponges or covered in conductive gel and are fixed to the head using elastic rubber bands (Figure 6.2). A low intensity sinusoidal electrical current of up to 2 mA alternating between the two electrodes is then sent through the skull.

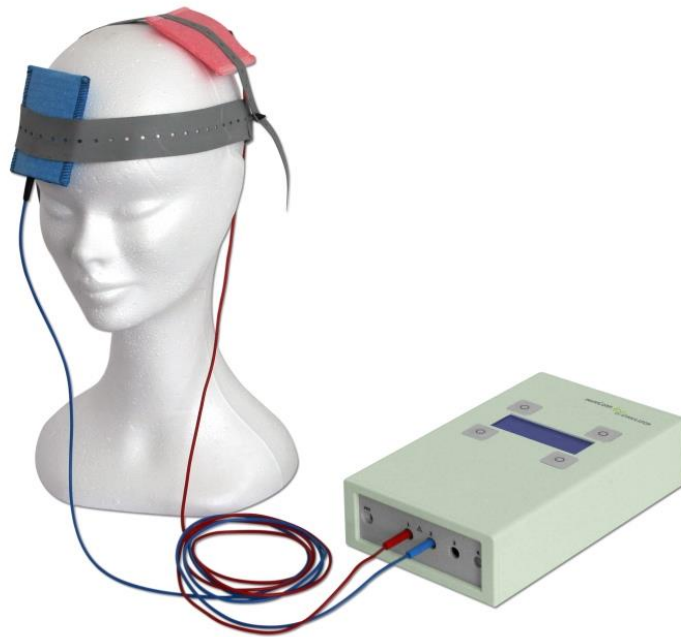


Figure 6.1 tACS device manufactured by Neuroconn. Image taken from <http://www.neuroconn.de>.

It is believed that tACS is able to interact with the ongoing neural oscillatory activity and align it to the frequency of stimulation (e.g. Helfrich et al., 2014). As noted earlier Zaehle and colleagues (2010) showed that it is possible to enhance the amplitude of the oscillations within the alpha range by delivering tACS in participants' individual alpha frequency. More recently Helfrich and colleagues (2014) delivered 10 Hz tACS to the parieto-occipital region which enhanced oscillatory activity within the alpha frequency range as shown by a simultaneous EEG recording, suggesting that tACS was able to entrain the endogenous brain activity. These results have also been corroborated by animal experiments. For instance, Fröhlich and McCormick (2010) made intracranial recordings in ferrets while stimulating cortical slices in vitro. They found that delivering sinusoidal current elicits neuronal spikes which are synchronized with the frequency of stimulation. In a different study Ozen and colleagues (2010) extended these findings

by showing that stimulating rats with electrodes placed externally on the skull leads to a similar effect suggesting that sinusoidal current applied externally can penetrate the skull and entrain neural oscillations.

Temporal resolution

While the above studies demonstrate that tACS is able to interact with the ongoing neural oscillations online it is also important to establish whether the effect of tACS persists offline. Such offline effects would have clinical relevance as inducing long-term changes to the brain activity may be therapeutic, for instance, in the treatment of disorders with disturbed neural oscillatory activity such as schizophrenia (Uhlhaas and Singer, 2006). In the context of this thesis, the findings of Chapter 7 showing that it was possible to improve facial anger processing with tACS, suggest a potential use of this technique in conditions linked to reduced facial emotion perception (e.g. ASD; Gross et al., 2012).

Currently this aspect of tACS is not well understood, however, it is thought that spike-timing dependent plasticity might underlie tACS-induced aftereffects which last beyond stimulation. A number of studies have tried to tackle this question. For instance, Groppa and colleagues (2010) found that the aftereffects of delivering tACS last for 20 min post stimulation, which was indexed by greater excitability of motor cortex shown by lower motor potentials induced by transcranial magnetic stimulation (TMS). Similarly, Helfrich and colleagues (2014) found that delivering tACS at 40 Hz enhanced inter-hemispheric phase synchronization which also lasted for 20 min after stimulation finished. Further, Neuling and colleagues (2013) replicated and extended the findings of Zaehle and colleagues (2010) by demonstrating that delivering tACS at participants' individual frequency led to

increased alpha amplitude which lasted for about 30 min after stimulation has been stopped. Some reports suggest even longer lasting aftereffects. For example, Moliadze and colleagues (2010) found that delivering tACS at 140 Hz resulted in enhanced excitability of the motor cortex for up to 60 min post stimulation. It has been shown that it is also possible to modulate cortical excitability with much higher frequencies. For instance Chaieb and colleagues (2011) found that delivering tACS at 5000 Hz results in increased excitability for up to 90 min after stimulation.

Spatial resolution

A number of studies have demonstrate that tACS is capable to target a specific cortical area and modulate its excitability. For instance Kanai and colleagues (2010) showed that tACS can selectively modulate the excitability of the visual cortex. Specifically, the authors found that delivering tACS at 20 Hz to the occipital region reduces single pulse transcranial magnetic stimulation (TMS) phosphene threshold (also delivered to the occipital lobe), and thus increases the excitability of the visual cortex. This effect was specific to beta frequency band, and was not observed when stimulating with theta, alpha, or gamma frequencies

Modelling studies have also offered some insight regarding the amount of tACS – induced intracranial electrical current. For instance Neuling and colleagues (2012b) demonstrated that 1mA of tACS delivered over the visual cortex leads to an intracranial current density of 0.1 A/m² and a cortical electric field of 0.417 V/m. However, due to individual differences in skull thickness and shape it is difficult to accurately establish the exact amount of current which reaches the brain (Di Bernardi Luft, Pereda, Banissy, and Bhattachayra, 2014).

Spatial resolution of tACS can be improved with different electrode montages e.g. when the stimulation electrode is smaller than the reference or by using multiple small electrodes instead of the larger ones typically employed in tCS research (Faria et al., 2009; Dmochowski et al., 2011). Additionally, it has been recently advocated that combining tACS with neuroimaging techniques and connectivity analysis would offer a more thorough examination of the effects of tACS on neural networks supporting different cognitive functions (Di Bernardi Luft et al., 2014). This remains to be elucidated with future work.

Intensity of stimulation

It has been recently shown that the effect of tACS depends on the intensity of stimulation, but that this relationship is non-linear (Moliadze, Atalay, Antal, and Paulus, 2012). The authors of this study recorded motor evoked potentials (MEPs) in response to single TMS pulses, while at the same time delivering tACS at 140 Hz to the primary motor cortex. Delivering tACS at 0.2 mA intensity led to enhanced motor thresholds, indicating greater cortical inhibition. On the other hand, tACS at 1mA resulted in increased excitation indexed by lower thresholds, while 0.6 mA and 0.8 mA intensities had no effect on motor thresholds whatsoever. This was interpreted by Moliadze and colleagues (2012) as evidence for greater susceptibility of inhibitory neurons relative to excitatory neurons to tACS as it was possible to stimulate them at lower intensities. At the same time, the intermediate intensities appeared to cancel inhibitory and excitatory effects altogether.

Phase of stimulation

Recently it has been proposed that the effect of tACS might also depend on the phase of the neural oscillations. Delivering tACS in phase or out of phase may result either in synchronization or desynchronization of the activity of the target area. For instance it has been shown that delivering tACS at 6Hz to the left frontal and parietal cortex in phase leads to better performance on a delayed letter discrimination task whereas delivering stimulation out of phase leads to decreased performance (Polania et al., 2012).

Duration of stimulation

Whether the effect of tACS depends on the duration of stimulation has not been tested yet. However studies which administered tDCS found that increasing the duration of stimulation leads to aftereffects prolonged by 13 min (Nitsche and Paulus, 2000), while increasing the stimulation to 26 min results in inhibition of aftereffect (Batsikadze et al., 2013). Whether a similar effect could be expected when using tACS is not clear.

Ethical considerations

Due to the fact that tACS is a relatively new technique there is a lack of specific safety guidelines relating to this form of non-invasive brain stimulation. However, tACS follows the general protocol regarding non-invasive transcranial current stimulation. To date there have not been any reports of long or medium term side effects associated with this method. Unlike transcranial magnetic stimulation (TMS), there are also no reports of seizures following tACS. TMS-induced seizures are most likely to occur in individuals who already have a degree of susceptibility to

them i.e. with a history of epilepsy or those on neuroleptic medication (Bae et al., 2007; Tharayil, Gangadhar, and Thirthalli, 2005). It is therefore essential to screen participants for any contraindications to tACS in order to eliminate any potential adverse effects of stimulation. In order to take part in a study which uses tACS participants cannot have a heart pacemaker, cochlear implant, aneurysm clip or any other electronic device or metallic object within their bodies. They also cannot have a personal or family history of epilepsy or any other medical, psychiatric or neurological disorders. Additionally 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 are not allowed to participate.

A minor concern relates to the minimal possibility of short-term effects. More specifically, tACS has sometimes been associated with minor skin irritation at the point of stimulation. Any discomfort related to this can usually be alleviated by repositioning the electrodes or applying more saline solution/gel to the sponges. Although tACS is considered safe and is used by many institutions around the world, some researchers urge caution when using non-invasive brain stimulation. This applies especially in the context of developmental studies, research using repeated sessions of stimulation as well as commercial devices designed for self-stimulation (Davis, 2014; Davis and van Koningsbruggen, 2013). As the neurophysiological underpinnings of tACS are not fully understood it is essential that tACS is delivered by a trained experimenter who follows the safety protocol. The three experiments reported in Chapter 7 of this thesis used only healthy adult participants with no contraindications to tCS. The safety protocol regarding the use of tACS was followed and all the experiments reported in the thesis were approved by the local ethics committee at Goldsmiths College.

CHAPTER 7: MECHANISMS OF FACIAL EXPRESSIONS OF AFFECT

In recent years a variety of neuroimaging studies have highlighted a role of neural oscillations in perception and cognition. However, surprisingly little is known about oscillatory activity underlying facial emotion perception. The limited number of studies that have addressed this question indicate that gamma oscillations are one mechanism underlying this process. The present study aimed to further elucidate the role of neural oscillations within the gamma range in facial emotion perception in healthy adults by using tACS. To that effect three experiments were conducted with separate groups of participants using tACS to modulate occipital oscillations while participants completed facial anger and facial identity tasks. The results of these experiments indicated that modulating occipital gamma with 40 Hz tACS enhances facial anger perception. This finding implicates an important role of occipital gamma oscillations in facial emotion perception.

7.1 Introduction

Based on the findings from Chapter 3 suggesting better facial identity perception in GCS as well as prior work demonstrating superior emotion recognition in MTS (Banissy et al., 2011) I aimed to elucidate neural oscillatory activity underpinning facial perception advantage in general population in order to provide a new window to investigate the mechanisms underlying enhanced social perception in synaesthesia.

Recently there has been a great interest in documenting the role of neural oscillations and synchrony in perception and cognition (Ward, 2003; Marshall, and Binder, 2013). For example, neural activity in the gamma band has been linked to temporal binding and gestalt perception (e.g. Brock et al., 2002; Singer, 2001). Moreover, various frequencies within the gamma range have been found to have different functional roles in low-level visual processing (e.g. in contrast perception; Laczó, Antal, Niebergall, Treue, and Paulus, 2012). Further, disrupted oscillatory activity is often associated with various cognitive and perceptual impairments in a variety of disorders (e.g. Uhlhaas, Haenschel, Nikolić, and Singer, 2008; Başar and Güntekin 2008).

Despite this, surprisingly little is known about neural oscillatory activity underlying facial emotion perception. Studies exploring this question have indicated that gamma oscillations are one mechanism underlying this process (Sato et al., 2011; Balconi and Pozzoli, 2007, Tai-Ying Liu et al., 2012). For example, in groups with deficits in emotion perception, such as Autism Spectrum Disorders (ASD; Uljarevic and Hamilton, 2013), gamma oscillations have been reported to be reduced when perceiving emotion from faces (Wright et al., 2012; Gross et al., 2012). Understanding the role that neural oscillatory activity plays in facial emotion perception may offer an interesting window to explore reasons behind differences in social perception that have been reported in synaesthetes (e.g. mirror-touch synaesthesia – Banissy et al., 2011; grapheme-colour synaesthesia – Chapter 3, this thesis).

While many of our insights into the role of neural oscillations in perception and cognition are drawn from neuroimaging, recently a number of studies have utilised tACS as a tool to probe the functional role of specific oscillations on

performance. As mentioned in Chapter 6 tACS is a relatively novel non-invasive brain stimulation technique that can be used to modulate cortical activity in a frequency dependent manner (Antal and Paulus, 2013). For example, in the visual domain tACS stimulation in the beta band evokes phosphenes in illuminated settings while tACS stimulation in the alpha band evokes phosphenes in the dark (Kanai, Chaieb, Antal, Walsh and Paulus, 2008). It is also possible to use tACS to modulate cognitive and perceptual performance. For instance, Polanía, Nitsche, Korman, Batsikadze and Paulus (2012) demonstrated that tACS induced synchronization in the theta range over fronto-parietal region results in enhanced performance on a visual memory task, and Laczó and colleagues (2012) have shown that modulating occipital gamma with tACS can improve contrast perception.

While previous studies have used other forms of transcranial current stimulation (tCS) to study social perception abilities (e.g. Lafontaine et al., 2013; Tseng et al., 2014; Romanska et al., In Press), to date no study has used tACS to examine the role of cortical oscillations in social perception. The advantage of tACS over other types of tCS (e.g. transcranial direct current stimulation or transcranial random noise stimulation) is that it cannot only provide information about brain areas involved in social perception, but also about the role individual frequency bands play in this process (Antal and Paulus, 2013). Based on prior findings linking occipital gamma with facial emotion perception, two studies were conducted using tACS as a tool to examine the extent to which modulating occipital gamma would influence emotion perception abilities of healthy adults. In the light of previous findings it was hypothesised that using tACS to modulate occipital gamma would enhance facial emotion recognition.

7.2 Experiment 6: The role of occipital gamma and occipital alpha in anger perception

Experiment 1 used a within participants design in order to examine the degree to which modulating occipital gamma or occipital alpha with tACS would influence facial expression perception. Based on prior work linking occipital gamma to emotion perception abilities (e.g. Wright et al., 2012; Gross et al., 2012) it was predicted that modulating occipital gamma with tACS would enhance performance relative to occipital alpha stimulation. Since there was no a priori reason to assume that occipital alpha stimulation would differ from sham stimulation, this form of stimulation was chosen as an active control condition in order to examine the extent to which occipital gamma stimulation may influence performance in a frequency specific manner.

Method

Participants

30 healthy adult participants (21 female, 9 male, mean age 25.33 ± 7.04) took part in this experiment. All participants were healthy volunteers, without any known developmental or neurological disorders and no contraindications to tACS. They were naive with respect to the experimental hypothesis. Participants provided written informed consent to take part in the experiment. They were either paid £5 for participating in the experiment or were awarded course credits.

Task

To examine facial expression abilities, the Cambridge Face Perception Angry Expression (CFPT-Angry) was used. No other emotions were included at this stage in order to avoid a complex design. Detailed description of this task is included in Chapter 3. Performance on this task was measured using an error score representing total deviations calculated by summing the deviations of each image from its correct location. For instance if the picture was three spaces from its correct position the error score for that trial would be three. Error scores on each trial were summed to determine the total number of errors, which was used to calculate the percentage of correct responses. Chance performance for CFPT-Angry is 36%.

Stimulation Parameters

A battery-driven DC-Plus stimulator (neuroConn) was used. Stimulation was delivered using 5 cm x 7cm conductive-rubber electrodes enclosed in saline-soaked sponges. The reference electrode was placed over Cz and the stimulating electrode over Oz, according to the international 10-20 system. Two types of stimulation were delivered: gamma (40 Hz) and alpha (10 Hz). The current intensity was set at peak-to-peak amplitude of 1 mA and the experiment was carried out in an illuminated room. The stimulation waveform was sinusoidal throughout the whole session with no DC offset. Participants completed CFPT-Angry twice, while tACS within the gamma band and alpha band was delivered. The order of stimulation was counterbalanced across participants to control for a potential practice effect

Results and Discussion

A paired samples t-test was conducted to compare participants' emotion perception performances following gamma or alpha tACS. This revealed that participants performed better on CFPT-Angry when stimulated within the gamma frequency band ($M = 83.59$, $SD = 7.75$) compared to stimulation within the alpha range ($M = 80.92$, $SD = 7.66$) [$t(29) = 2.593$, $p = 0.015$ Cohen's $d = 0.346$] (Figure 7.1). Therefore modulating occipital gamma with tACS resulted in an improvement in anger perception abilities. These findings compliment prior brain imaging work linking occipital gamma with facial emotion perception (e.g. Wright et al., 2012; Gross et al., 2012) and suggest that occipital gamma plays a key role in facial emotion processing

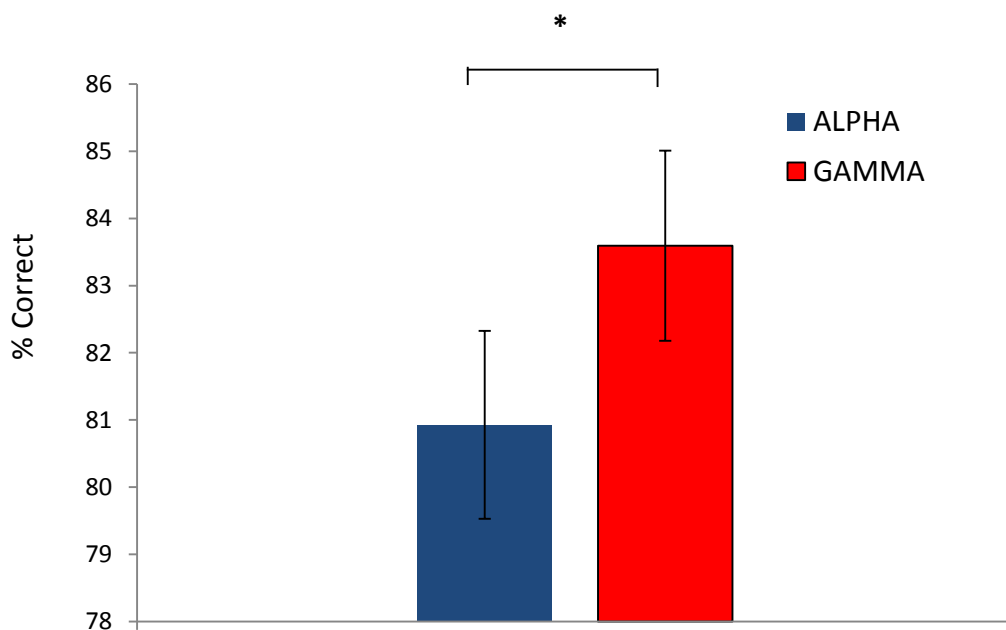


Figure 7.1 Mean percentage of correct responses on the Cambridge Face Perception Task-Angry when delivering transcranial alternating current stimulation to the primary visual cortex in the gamma and alpha band. * = $p < .05$.

7.3 Experiment 7: The role of occipital gamma in anger and facial identity perception

Experiment 1 showed that modulating occipital gamma with tACS resulted in an improvement in anger perception relative to tACS in the alpha band. While these findings point to an important role of occipital gamma in anger perception, the extent to which the pattern of data from Experiment 1 holds when comparing performances relative to a condition in which no neurophysiological change due to active tACS took place remains unclear. The second study was conducted in a new group of participants in attempt to determine whether modulating occipital gamma with tACS would result in similar improvements in anger perception when compared to sham tACS. Additionally, this study sought to examine the extent to which the improvement seen in Experiment 1 is specific to anger perception by testing participants' abilities to perceive facial identity. Based on the findings from Experiment 1 and prior neuroimaging studies (e.g. Wright et al., 2012; Gross et al., 2012) it was predicted that modulating occipital gamma would improve anger perception.

Method

Participants

22 naive adult participants took part in this experiment (13 female, 9 male, mean age 25.68 ± 5.78). All participants were healthy volunteers, without any known developmental or neurological disorders and no contraindications to tACS. They were naive with respect to the experimental hypothesis. Participants provided written informed consent to take part in the experiment. They were paid £10 for their participation. None of the participants had taken part in Experiment 1.

Tasks

As with Experiment 1, facial emotion perception was measured using the CFPT-Angry. To examine facial identity, the Cambridge Face Perception Identity Test (CFPT-Identity) was employed (Duchaine et al., 2007). Detailed description of this task is included in Chapter 3. Performance was measured using an error score as per the facial emotion version of the task, which was subsequently transformed into a percentage of correct responses. Each task was performed in a counterbalanced order while tACS in the gamma frequency or sham stimulation was delivered.

Stimulation parameters

The brain stimulation parameters were identical to Experiment 1. The only difference was that in this study gamma (40Hz) or sham tACS was applied. In the gamma condition stimulation began at the start of each task and ceased at the end of each task. In the sham condition, participants received 10 seconds of stimulation in the gamma frequency range at the start of the task in order to evoke the somatosensory sensation of being stimulated. It has been shown that naive subjects cannot distinguish between sham and active transcranial current stimulation (Gandiga, Hummel and Cohen, 2006). The stimulation conditions were counterbalanced across participants.

Results and Discussion

One participant was identified as an outlier on CFPT- Identity inverted trials due to a poor performance close to chance level (2.63 SDs away from the group mean). They were therefore removed from all analyses.

Based on the findings from Experiment 1, planned paired comparisons were conducted comparing performances on the CFPT-Angry. This revealed that participants were more accurate on the CFPT-Angry when stimulated within the gamma band ($M = 82.59$, $SD = 6.07$) compared to sham stimulation ($M = 79.25$, $SD = 5.75$) [$t(20) = 2.230$, $p = 0.037$, Cohen's $d = 0.564$] (Figure 7.2), thus demonstrating that improvements in anger perception observed in Experiment 1 replicate when modulating occipital gamma relative to a stimulation condition in which no neurophysiological change takes place.

In addition, a 2 (Stimulation Condition) x 3 (Trial Type) ANOVA was conducted to compare participants' performances following tACS across CFPT-Angry, CFPT-Identity upright trials, and CFPT-Identity inverted trials (Figure 7.2). This revealed a main effect of task [$F(2,40) = 181.009$, $p < .001$, $\eta_p^2 = .901$], with participants performing better overall on CFPT-Angry and CFPT-Identity upright trials relative to CFPT-Identity inverted trials ($p < .001$ Bonferonni Corrected). There was no main effect of stimulation [$F(1, 20) = 1.165$, $p = .293$, $\eta_p^2 = .055$]. Despite descriptively similar performances on CFPT-Identity upright (sham: $M = 78.76$, $SD = 5.12$; gamma: $M = 79.45$, $SD = 6.86$) and CFPT-Identity inverted trials (sham: $M = 57.67$, $SD = 5.66$; gamma: $M = 57.34$, $SD = 8.74$) across stimulation conditions (Figure 7.2), no significant interaction was found [$F(2, 40) = 1.166$, $p = .322$, $\eta_p^2 = .055$]. In this regard, while participants showed a significant improvement on CFPT-Angry following occipital gamma stimulation relative to sham (and relative to alpha stimulation in Experiment 1) that was not observed for facial identity perception, the task specific nature of this improvement remains unclear.

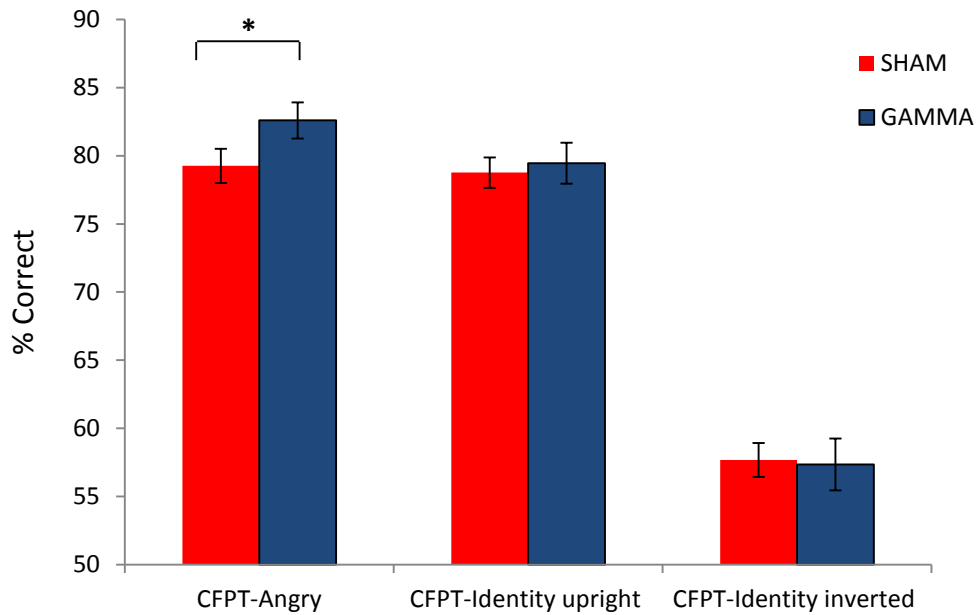


Figure 7.2. Mean percentage of correct responses following occipital gamma or sham transcranial alternating current stimulation on the Cambridge Face Perception Task-Angry, Cambridge Face Perception Task -Identity upright trials, and Cambridge Face Perception Task -Identity inverted trials. * = $p < .05$.

7.4 Experiment 8: The role of occipital gamma at 40 Hz and 100 Hz in anger perception

The first two studies demonstrated an improvement in facial affect perception measured with CFPT-Anger following tACS at 40 Hz relative to 10Hz stimulation and sham stimulation. While this provides some evidence for frequency-specific modulation of emotion perception following 40Hz stimulation, it could be argued that stimulating at any higher frequency might influence emotion perception. To address this, a third study was conducted with a new group of participants, where effects of tACS at 40 Hz were compared with stimulation at 100 Hz.

Method

Participants

15 healthy adult participants (8 female, 7 male, mean age 23.86 ± 3.48) took part in this experiment. None of the participants took part in Experiments 1 or 2. All participants reported to have no known developmental or neurological disorders and no contraindications to tACS. They were naive regarding the experimental hypothesis. Participants provided written informed consent and were paid £20 in return for taking part in this experiment.

Task

To examine facial affect perception, the same Cambridge Face Perception Angry Test (CFPT-Angry) was used, as in Experiment 1 and 2. Performance on this task was measured using percentage of correct responses.

Stimulation Parameters

The equipment and all stimulation parameters were identical to Experiment 1 and 2. The only difference was that in this study gamma at 40Hz or 100 Hz tACS was applied. Stimulation began at the start of CFPT-Angry task and ceased at the end of it with 5second fade-in and fade-out time. Participants performed the task twice, three days apart. The stimulation conditions were counterbalanced across participants.

Results and Discussion

A paired samples t-test was conducted to compare participants' anger perception following tACS in the gamma frequency band at 40 Hz and 100 Hz. The

results indicated that participants' performance on CFPT-Angry was better when stimulated with 40 Hz ($M = 83.18$, $SD = 7.68$) compared to stimulation with 100 Hz ($M = 77.85$, $SD = 6.89$) [$t(14) = 3.644$, $p = 0.003$ Cohen's $d = 0.730$] (Fig. 4). Therefore the improved performance on CFPT-Angry appears specific to 40Hz stimulation and is not simply a result of delivering tACS at a higher frequency.

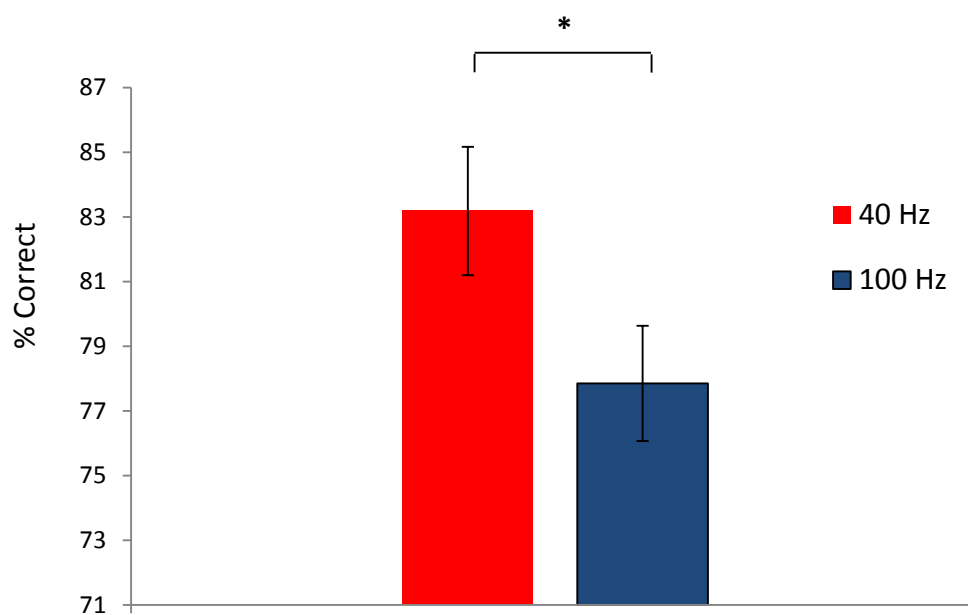


Figure 7.3 Mean percentage of correct responses following occipital gamma transcranial alternating current stimulation at 40 Hz and 100 Hz on the Cambridge Face Perception Task-Angry. * * = $p < .005$.

7.5 General Discussion

The aim of this study was to explore the role of neural oscillatory activity within the gamma frequency range in emotion perception using tACS. Across the three studies, it has been shown that tACS in the gamma band at 40 Hz significantly

facilitates facial anger perception abilities relative to tACS in the alpha band (Experiment 1), sham tACS (Experiment 2), and tACS delivered at 100 HZ (Experiment 3). These findings compliment prior neuroimaging work demonstrating the role of occipital gamma in facial emotion processing (e.g. Wright et al., 2012; Gross et al., 2012) by showing that directly modulating occipital gamma activity at 40 Hz with tACS results in improved facial anger perception.

The findings provide further evidence for the idea that tACS is a powerful brain stimulation technique capable of interacting with the ongoing brain activity and producing tangible outcomes, in this case enhanced processing of emotions. Although the exact mechanisms of tACS are not entirely understood (Antal and Paulus, 2013) these results suggest that tACS is indeed able to target a particular brain area of interest and entrain neural oscillatory activity in the frequency of stimulation. Current findings showing that it was possible to enhance facial anger perception using tACS highlights the potential utility of this technique as a tool for modulating facial emotion processing and add to the growing literature showing that tACS can be used to successfully modulate human perception and cognition (e.g. Laczó et al., 2012; Polanía et al., 2012; Santarnecchi et al., 2013). The findings also raise the interesting possibility about the potential to use tACS to modulate occipital gamma in conditions where reduced levels of occipital gamma have been associated with declines in facial emotion perception (e.g. Gross et al., 2012). It is of note, however, that given the likely variability in terms of levels of cortical excitation between typical and atypical groups (e.g. Coghlan et al., 2012; Krause and Cohen Kadosh, 2014) extensions to atypical groups should be approached with caution.

Additionally, as various frequencies and brain structures have been implicated in emotional processing (e.g. Güntekin and Başar, 2014; Güntekin and Başar, 2009)

it is also feasible to suspect that not just occipital gamma, but also other frequencies distributed across a number of different cortical regions are involved in facial emotion recognition. For example, it has been found that greater theta synchronization is associated with explicit recognition of facial expressions of emotions as opposed to neutral faces, especially in individuals who report to be more emotionally involved (Knyazev, Slobodskoj-Plusnin, and Bocharov, 2009). While a frequency specific improvement in performance was found following gamma stimulation at 40 Hz relative to 10Hz and 100 Hz tACS, it will also be interesting to examine the role of other cortical oscillations in emotion processing with future work.

It is also important to consider that these studies focused on the perception of anger, thus the extent to which our findings hold for all or some emotions remains unclear. Prior work has suggested that enhanced gamma power in this region also facilitates processing of other types of emotions (e.g. Wright et al., 2012; Gross et al., 2012). Based on current data it can be said with confidence that this result holds for anger perception, but caution should be taken with regards to inferences about other emotional expressions.

Finally, some discussion is warranted in relation to the task specific nature of these effects. While it was possible to establish a significant improvement in anger perception (Experiment 1 and 2), no significant modulation of facial identity perception was observed (Experiment 2). While this may hint at task-specificity, a difference between significance and non-significance is not necessarily by itself significantly different (Gelman and Stern, 2006; Nieuwenhuis, Forstmann, and Wagenmakers, 2011). Given that no significant interaction between task type (anger perception, facial identity perception of upright faces, facial identity perception of

inverted faces) and stimulation was observed in Experiment 2, inferences about task-specific role of occipital gamma in facial emotion versus facial identity processing need to be made with caution. At least two reasons may account for the lack of interaction found in Experiment 2: 1) the interaction in Experiment 2 may suffer from reduced statistical power and / or 2) given that occipital gamma has been linked to holistic processing (Singer, 2001; Rodriguez et al., 1999) which is important for facial identity perception, delivering tACS in this frequency is likely to affect both anger and identity perception. To date relatively few studies have examined the role of cortical oscillations in facial identity perception. This is an important avenue to explore in future studies.

Taking into account enhanced social perception abilities reported in synaesthesia (grapheme-colour synaesthesia: Chapter 3, this thesis; mirror-touch synaesthesia: Banissy et al., 2011) current findings also offer an interesting window to further explore the mechanisms underlying this advantage by examining whether it is associated with an altered rhythmic brain activity in this group, particularly within the occipital gamma oscillations.

Summary

In summary, this study shows that modulating occipital gamma at 40 Hz enhances the perception of facial emotion across three studies. These findings highlight that gamma oscillations play a key role in facial anger perception, and show that it is possible to enhance this ability in healthy adults by modulating occipital gamma with tACS.

CHAPTER 8: CONCLUSIONS

This chapter provides a summary of the empirical findings reported in this thesis. It discusses broader differences associated with two different forms of synaesthesia: grapheme-colour and mirror-touch synaesthesia and provides an overview of the findings related to the role of neural oscillations in facial affect and identity perception in typical adults.

As mentioned in Chapter 1, there has been growing interest in using synaesthesia to investigate wider aspects of perception and cognition which extend beyond the synaesthetic experience itself. For instance, recent work has demonstrated an association between synaesthesia and enhanced memory (Rothen, Meier, and Ward, 2012), sensory perception (Banissy, Walsh, and Ward, 2009; Banissy et al., 2013; Yaro and Ward, 2007), and creativity (Ward, Thompson-Lake, Ely, and Kaminski, 2008).

The aim of this thesis was to further elucidate broader differences in personality and social perception associated with synaesthesia. Additionally this thesis sought to examine neural mechanisms underlying social perception in typical adults to open new avenues for examining the differences in this domain in synaesthesia. This thesis sought to address the following questions:

1. Is grapheme-colour synaesthesia linked to differences in imagery and personality relative to typical adults? (Chapter 2)
2. Does the presence of grapheme-colour synaesthesia have consequences for social perception? (Chapter 3)

3. Does mirror-touch synaesthesia differ in terms of alexithymia relative to grapheme-colour synaesthesia and general population? (Chapter 4)
4. Is mirror-touch synaesthesia linked to altered levels of interoceptive sensitivity relative to grapheme-colour synaesthesia and general population? (Chapter 5)
5. What are the neural mechanisms underlying social perception in typical adults? (Chapter 7)

The first aim of this thesis was to replicate previous findings linking synaesthesia for colour with enhanced self-reported positive and disorganised schizotypy (Banissy et al., 2012), and mental imagery vividness (Barnett & Newell, 2008; Spiller et al., 2015). The findings of Study 1 (Chapter 2) indicated that GCS score higher on positive schizotypy, but not other aspects of schizotypy thus only partially replicating previous findings of Banissy and colleagues (2012). Consistent with previous findings, current results also indicated that GCS report greater vividness of visual imagery compared to controls (Barnett & Newell, 2008; Spiller et al., 2015).

Secondly, I also sought to establish whether greater self-reported imagery vividness present in synaesthesia for colour mediates elevated levels of schizotypy in this population by examining these traits in the same group of synaesthetes. Results of a mediation analysis showed no relationship between positive schizotypy and self-reported mental imagery vividness in GCS. These findings are consistent with prior work demonstrating that while non-synaesthetic individuals with increased schizotypal traits score higher on vividness of mental imagery these two constructs appear to be independent of each other (Oertel et al. 2009). It therefore remains to be

established with future work what contributes to elevated positive schizotypy and self-reported vividness of mental imagery in synaesthesia for colour as well as in general population. Additionally, as this study tested GCS (some of whom also reported other forms of synaesthesia) on vividness of visual imagery it is possible to make inferences only relating to visual forms of synaesthesia and imagery within the visual domain. Future work should address the question of whether current findings would extend to other forms of synaesthesia and imagery in different modalities.

Building on prior work showing lower agreeableness and increased openness to experience in synaesthetes (Banissy et al., 2013), it was the aim of the second study (Chapter 2) to investigate whether synaesthesia would be associated with altered levels of two other conceptually similar personality characteristics, namely self-monitoring (Snyder and Gangestad, 1986) and sensation seeking (Garcia et al., 2005). The results of this study did not show any differences relating to these personality dimensions between GCS and typical controls suggesting that grapheme-colour synaesthesia is linked to a specific personality profile and that it is not a result of a general self-report bias.

In light of the findings from Chapter 2 and prior work showing an association between grapheme-colour synaesthesia and increased schizotypal traits (Banissy et al., 2012), which in non-synaesthetic individuals have been linked to reduced emotion recognition (Abott and Byrne, 2013; Morrison, Brown and Cohen, 2013), another purpose of this thesis was to explore whether synaesthesia would also be linked to deficits in social perception. Moreover, recent findings also point to an association between synaesthesia and Autism Spectrum Disorder (ASD; Neufeld et al., 2013; Asher et al., 2009; Bouvet et al., 2014; Baron-Cohen et al., 2013), which has also been linked to deficits in facial emotion and identity processing (Hedley et

al., 2014; Uljarevic and Hamilton, 2012; Weigelt et al., 2012), further suggesting that GCS may show reduced social processing ability relative to controls. Contrary to the experimental hypothesis the findings of Experiment 1 reported in Chapter 3 revealed that GCS outperformed control participants on tasks involving upright facial identity, while there was no group difference in terms of facial identity processing using inverted faces or facial emotion processing (Cambridge Face Perception tasks, Duchaine et al., 2007). While these results appear to show domain-specific processing advantage in grapheme-colour synaesthesia, it is possible that they reflect wider perceptual differences previously associated with this form of synaesthesia. Specifically, grapheme-colour synaesthesia has been linked to increased sensitivity to high spatial frequency visual information (e.g. Barnett et al., 2008) which may be especially relevant when performing the Cambridge Face Perception Tasks employed in Experiment 1 (Chapter 3) as they rely on making fine-grained visual judgments. It is therefore possible that the perceptual advantage observed in Experiment 1 reflects a domain general advantage for synaesthetes in processing high spatial frequency cues which in turn aid fine-grained visual discrimination. The fact that no group difference was found for inverted identity processing most likely reflects greater task difficulty in this orientation (Rossion, 2008), while a lack of statistically significant difference between GCS and controls on emotion processing tasks is likely to be due to the fact that high spatial frequency visual cues are thought to be of particular relevance to identity perception and to a lesser extent to emotion processing (Vuilleumier et al., 2003).

In order to further elucidate the nature of the perceptual advantage found in grapheme-colour synaesthesia in the first experiment reported in Chapter 3, another experiment was run using the face composite task (FCT), which relies more heavily

on low-spatial frequency information (Young et al., 1987; Rossion, 2013). This task entails judging whether two identical top halves are the same or different when they are aligned or misaligned with different bottom halves. The face composite effect reflects an illusion that the top halves appear different when aligned with different bottom halves due to holistic face processing mechanisms. The findings of Experiment 2 reported in Chapter 3 showed no difference between GCS and control participants in terms of performance on the FCT, suggesting typical face processing in this form of synaesthesia when employing tasks which rely more on low-spatial frequency visual information. In this regard, perceptual advantage indexed by synaesthetes' performance on CFPT tasks in Experiment 1 is most likely related to a broader sensitivity of synaesthetes to high spatial frequency information (e.g. Barnett et al., 2008).

Building on the findings from Chapter 3 suggesting that GCS show superior and in some cases typical facial identity and emotion perception as well as prior work showing superior emotion recognition (Banissy et al., 2011) and enhanced empathy (Banissy and Ward, 2007) in MTS it was the purpose of Experiment 3 (Chapter 4) to establish whether these two types of synaesthesia would be associated with different levels of alexithymia. This personality construct is characterized by compromised emotional awareness (Aleman, 2005) and it has been linked to substantial difficulties in emotion recognition (e.g. Cook et al., 2013; Grynberg et al., 2012) and empathy (Bird et al., 2010), accompanied by reduced simulation (Sonnby-Borgström, 2009). At the same time one mechanism thought to underpin mirror-touch synaesthesia is hyper-activity within the mirror network for touch (Blakemore et al., 2005; Holle et al., 2013), and mirror system has been implicated as a mechanism involved in social cognition through a process of sensorimotor

simulation of the emotional states observed in others (Adolphs, 2002; Adolphs, 2003; Gallese et al., 2004; Goldman and Sripada, 2005; Keysers and Gazzola, 2006). Therefore it was hypothesized that MTS would be characterized by low levels of alexithymia, whereas GCS were not expected to differ from controls on this trait, as this type of synaesthesia has not been linked to hyperactivity within the mirror system, differences in empathy or enhanced emotion recognition.

The findings reported in Chapter 4 demonstrated that MTS scored significantly lower on the Toronto Alexithymia Scale (TAS-20; Bagby et al., 1994) relative to controls but that there was no difference between MTS and GCS, or between GCS and controls. Additionally, the results suggested that the difference relates to MTS scoring lower on Difficulty Describing Feelings (DDF) subscale of TAS-20 which reflects an ability to label emotional states. These findings compliment prior work showing enhanced emotion recognition ability in mirror-touch synaesthesia on tasks which rely on labeling facial expressions of emotions (Banissy et al., 2011).

Based on the findings from Chapter 4 showing reduced levels of alexithymia in MTS relative to controls and prior work showing an inverse association between alexithymia and interoceptive sensitivity (IS; Herbert et al., 2011) it was the aim of this thesis to establish whether MTS would differ in terms of this ability compared to GCS and controls. IS is the ability to detect internal bodily fluctuations which is most commonly assessed with heartbeat detection tasks (e.g. Critchley et al., 2004). Apart from alexithymia this ability has also been shown to mediate body representation and self-other monitoring. For instance, reduced IS has been linked to greater malleability of body representation indexed by susceptibility to the body ownership illusions (Tajadura-Jiménez and Tsakiris, 2013; Tsakiris et al., 2011), while greater IS has been associated with enhanced imitation which is used as a

measure of self-other monitoring (Ainley, Brass, and Tsakiris, 2014). Interestingly, mirror-touch synaesthesia has been linked to increased malleability of self-other representations (Maiester et al., 2013; Aimola-Davies and White, 2013), enhanced tendency to imitate (Santiesteban et al., 2015) and, as shown in Chapter 4, to low levels of alexithymia. Based on these conflicting reports no directional prediction regarding the levels of IS in MTS was made.

The findings of Experiment 4 showed that MTS had lower IS relative to both GSC and controls, which is consistent with some of the previous research e.g. prior work showing a link between reduced IS and greater malleability of body representation (Tajadura-Jiménez and Tsakiris, 2013; Tsakiris et al., 2011) and findings of enhanced susceptibility to body-ownership paradigms previously found in mirror-touch synaesthesia (Maiester et al., 2013; Aimola-Davies and White, 2013). They are also in line with the atypical self-other representation mechanism thought to underlie this form of synaesthesia (Banissy and Ward, 2013; Ward and Banissy, 2015).

Additionally, this thesis sought to determine whether differences in IS are linked to facial emotion processing abilities. To this end, the same Cambridge Face Perception tasks used in Chapter 3 were given to a group of typical adults, having previously measured their IS with heartbeat detection task. The findings of Experiment 5 did not show any relationship between processing of facial expressions of emotions and IS. Although differences in IS have been previously linked to the intensity of emotional experience and sensitivity to the emotions of others (e.g. Barrett et al., 2004; Wiens et al., 2000) it is possible that IS is not related to emotion processing. Future work should address this question as evidence in this area is currently lacking.

Chapter 7 investigated the role of neural oscillatory activity in social perception in general population in order to provide a new avenue to explore the mechanisms underpinning enhanced social perception abilities in GCS (Chapter 3, this thesis) and MTS (Banissy et al., 2011). Specifically, building on prior work suggesting a key role of occipital gamma oscillations in emotion processing (e.g. Wright et al., 2012; Gross et al., 2012) the three studies reported in Chapter 7 aimed to further examine the modulatory effect of occipital gamma on emotion perception in typical adults using tACS. This non-invasive brain stimulation technique enables stimulating target brain areas in physiologically relevant frequencies, making it an ideal tool to investigate the role of neural oscillations in cognitive functions (e.g. Antal and Paulus, 2013). In the light of previous findings it was predicted that delivering tACS to the primary visual cortex in the gamma frequency band would enhance facial emotion processing.

Current results suggest that tACS in the gamma band at 40 Hz facilitates facial anger processing compared to tACS in the alpha band (Experiment 6), sham stimulation (Experiment 7), and tACS at 100 HZ (Experiment 8). These findings are consistent with prior work indicating occipital gamma as a crucial mechanism underpinning facial emotion processing (e.g. Wright et al., 2012; Gross et al., 2012) by demonstrating that modulating occipital gamma oscillations at 40 Hz with tACS leads to enhanced facial anger perception. They also demonstrate that tACS is able to interact with ongoing rhythmic activity resulting in measurable changes in perception.

Although previous findings suggested that enhanced occipital gamma power improves processing of other types of emotions (e.g. Wright et al., 2012; Gross et al., 2012), the studies reported in Chapter 7 only focused on facial anger processing and

therefore future work should further explore whether delivering tACS at 40 Hz would also result in facilitated processing of other emotions. Additionally, as various frequencies and brain structures have been implicated in emotional processing (e.g. Güntekin and Başar, 2014; Güntekin and Başar, 2009) the role of cortical oscillations in other frequencies should also be examined. Moreover, while the results of Experiment 7 showed that tACS at 40 Hz did not significantly modulate facial identity perception, no significant interaction between task type and stimulation was observed either and thus any inferences about task-specific role of tACS-induced occipital gamma oscillations need to be made with caution. Future work should further investigate the role of cortical oscillations in facial identity perception.

Finally current findings of a key role of occipital gamma oscillations in social perception in typical adults offer an interesting window to explore the mechanisms underpinning this advantage in GCS (Chapter 3, this thesis) and MTS (Banissy et al., 2011). Specifically, future work should further examine whether these differences are linked to an altered neural oscillatory activity in this population, especially within the occipital gamma.

General Summary

In summary, this thesis explored personality traits and social perception in two forms of synaesthesia: grapheme-colour synaesthesia and mirror-touch synaesthesia. Current findings show that grapheme-colour synaesthesia is linked to an altered personality profile relative to typical adults and that it is characterized by typical and (in some cases) superior social perception abilities, which are most likely a consequence of perceptual differences related to sensitivity to high spatial frequency information found in this group. At the same time, MTS were found to possess low

alexithymia and low IS, which is consistent with the theories of this form of synaesthesia. Additionally, this thesis explored the neural mechanisms underlying social perception in typical adults using non-invasive brain stimulation. This stream of research demonstrated that enhancing occipital gamma oscillations facilitates facial anger perception offering a new avenue to further explore the neural mechanisms underpinning enhanced social perception found in grapheme-colour and mirror-touch synaesthesia.

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