The Plastic Self: Investigating the Processes of Self-Face Recognition

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Declaration of Authorship

I, Sophie Payne, hereby declare that this thesis and the work presented in it is entirely my own. Where I have consulted the work of others, this is always clearly stated.

Signed:

Date:

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Abstract

This thesis investigates self-face recognition and the plasticity of self-representations through several different behavioural and brain stimulation manipulations. The experiments in Chapters 3 and 4 explore the involvement of the temporoparietal area in self-other discrimination processes. Using transcranial direct current stimulation (tDCS) to modulate neural excitability in this region, the experiments in these chapters explore self-other face discrimination and mental body rotation. Enhancing neural excitability in this area appears to enhance familiar other-recognition and the ability to take another's spatial perspective. Chapters 5 and 6 target brain areas associated with multisensory bodily illusions with tDCS, and investigate their involvement in self-updating. Chapter 5 explores the contribution of the intraparietal sulcus to multisensory integration during the Enfacement illusion. Chapter 6 investigates the effect of tDCS on somatosensory cortex during a modified enfacement illusion paradigm to investigate self-updating. Chapters 7 and 8 explore the novel use of a self-association paradigm to update bodily and conceptual aspects of self. The experiments in these chapters demonstrate that a previously unfamiliar face can be incorporated into the conceptual self-representation. Chapter 7 investigates the existence of a bidirectional modulatory link between conceptual and bodily aspects of self, and found that changes to the conceptual self did not have an effect on the bodily self-representation. The experiment in Chapter 8 investigates the nature of the association created between the self-representation and the novel face in Chapter 7 by testing whether the newly associated face affects recognition of well-established perceptual and conceptual aspects of self.

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1 Introduction

This thesis will investigate the cognitive and neural mechanisms supporting self-face recognition. The current chapter will start with a review of face perception literature, followed by a review of the literature on self-face processing in an attempt to answer the question of whether the self-face is special. The next sections will outline the key processes involved in self-face recognition, and review developmental, behavioural, neurostimulation and neuroimaging research to give an overview of the cognitive and neural mechanisms underpinning the ability to acquire, maintain and update a mental representation of one's own face.

1.1 The Self in Psychology

The self has often been regarded as 'special', with processing of self-relevant information being thought of as distinct from the processing of non-self-related information (Kircher et al., 2000). With the use of modern research techniques such as neuroimaging and brain stimulation, the study of the self has now started to be grounded in the brain, and research can investigate whether the self is distinct at a neural level. The study of the self is often divided into two complementary streams of research. These are the study of the conceptual-self, reflecting memory-based knowledge constituting varied semantic and episodic information about the self, and the bodily-, or physical-self, reflecting the study of visual, sensory, and proprioceptive representations of one's face and body. Body-ownership: the sense of one's body as belonging to the self and existing as an entity distinct from the bodies of others, and the sense of agency: as being the agent of one's actions, combine to form a minimal, bodily, sense of self (Tsakiris, 2010). This bodily sense of the self, along with the ability for kinaesthetic-visual matching, has been argued to form the basis for explicit mirror self-face recognition (Mitchell, 1997). Self-face recognition is the ability to represent the visual properties of one's own face as distinct from the faces of others, and consequently to recognise that the face you see in the mirror belongs to you. Self-face recognition, and the awareness of the physical self as distinct from others around us, appears to be critically important for the development of self-awareness and an abstract, conceptual sense of self (Rochat, 1995), preceding an awareness of the self as a social being among others, and the identification with one's public appearance (Zahavi & Roepstorff, 2011). In this light, self-face recognition can be seen as critical for the development of social cognitive abilities, providing the basis for social interaction. This thesis will investigate the cognitive and neural mechanisms that underpin some of the key processes involved in self-face recognition, and by extension, the representation of the physical self.

1.2 Face Perception in General: How are faces unique?

The human face-recognition system represents one of the most highly advanced skill sets in human perception. Faces are the most unique aspect of an individual, facilitating recognition above and beyond other distinctive features such as voice, hair style, and body shape. Prosopagnosia, the loss of the ability to recognise individuals from their faces, has a severe impact on the lives of those living with the disorder, demonstrating how vital this skill is (Yardley, McDermott, Pisarski, Duchaine, & Nakayama, 2008). Faces also provide important cues for the recognition of other types of social information, such as emotion and speech comprehension. Not only can the human face-recognition system draw on invariant information in order to identify individuals from their facial features alone, changeable aspects of faces such as expression and gaze direction also provide vital information for social communication between individuals (Haxby, Hoffman, & Gobbini, 2000). It is unsurprising, therefore, that from a very early age infants show a preference for faces over any other object (Farroni et al., 2005; Morton & Johnson, 1991; Sanefuji et al., 2011), and that this preference remains present throughout the lifespan (Haxby et al., 2000). Arguably no other visually perceived aspect of a person provides such a rich and varied source of information.

Because of the social importance of faces, it has been suggested that faces may be ‘special’ stimuli, and that areas of the brain may have become specialised for the function of facial recognition. In favour of the *domain-specificity hypothesis*, several researchers have argued that what sets face perception apart from object recognition is the importance of configural information in the visual representation of faces (Carey & Diamond, 1977; Diamond & Carey, 1986; Rhodes, 2013). These authors argue that second-order features - the spatial relationships between the individual, first-order, features of the face (e.g. nose, eyes, mouth) - are especially important in face recognition, and that this reliance on configural processing is unique to faces, making them special relative to non-face objects.

If this is the case, then the recognition of faces should be particularly disrupted by manipulations that change the configuration of features, or affect configural processing. One such manipulation tested participants’ recognition of individual facial features (e.g. nose, eyes) when they were presented in novel configurations (Tanaka & Sengco, 1997). At the beginning of the experiment participants were presented with novel faces to learn. Following the learning phase, participants were shown individual facial features of the learned faces in one of three different configurations: 1) in isolation, 2) in a new face configuration, 3) in the original face configuration. Recognition of features was best in the original configuration, followed by the new configuration, and was poorest in isolation. The findings suggested that participants were not representing the first-order features of each face in isolation, but rather holistically: relative to other features within the face. Critically, recognition of the features of non-face stimuli such as houses was not affected by configuration alterations, suggesting that participants represented the first-order features of these stimuli in isolation.

The stimuli inversion paradigm has also been used to highlight the importance of configural processing for face-recognition. Inversion of a stimulus impairs configural processing, and so recognition of faces should be disproportionally affected by inversion relative to other classes of visual stimuli. In (1969), Yin showed that identity-recognition of faces is heavily impaired when faces are inverted, as opposed to presented upright. Critically, no effect of the manipulation was found for non-face objects, in which recognition performance was comparable regardless of orientation (Yin, 1969). The finding that faces are disproportionally affected by rotation has been replicated by a number of studies (Scapinello & Yarmey, 1970; Yarmey, 1971).

The findings that face-recognition is disproportionally affected by manipulations of configuration and configural processing have been used to support the idea that face-processing is qualitatively different to the processing of other classes of visual stimuli. As well as qualitative differences, face-processing can also be thought of as special in terms of having specialised networks within the brain developed specifically to process human faces. The most compelling evidence for a dissociation between face and object processing in the brain comes from research into prosopagnosia.

Prosopagnosics suffer from an selective inability to recognise faces, while showing no impairment in object-recognition (Duchaine & Nakayama, 2005; Riddoch, Johnston, Bracewell, Boutsen, & Humphreys, 2008). The opposite deficit has also been researched: following traumatic brain injury patient CK presented with a specific deficit in object-recognition, but his ability to recognise faces remained intact (Moscovitch, Winocur, & Behrmann, 1997). This double dissociation suggests that different neural mechanisms underlie the recognition of faces and non-face objects. In line with this, neuroimaging research has identified face-selective regions in the human brain. Separate areas within the ventral visual cortex, right extrastriate cortex and fusiform gyrus appear to be involved in the process of face versus object recognition (Gauthier et al., 2000; Gauthier, Anderson, Tarr, Skudlarski, & Gore, 1997; Grill-Spector, Knouf, & Kanwisher, 2004; Haxby et al., 1991, 1994; Ishai, Ungerleider, Martin, Schouten, & Haxby, 1999; Kanwisher, McDermott, & Chun, 1997; McCarthy, Puce, Gore, & Allison, 1997; Puce, Allison, Asgari, Gore, & McCarthy, 1996; Sergent, Ohta, & Macdonald, 1992). Put together, these findings suggest that different cognitive processes, supported by distinct neural regions, underpin the recognition of faces and non-face objects.

On the other hand, it has also been speculated that what may seem to make faces special is not something unique about faces, but rather reflects expertise and familiarity with human faces – the expertise hypothesis. In support of this, Diamond and Carey (1986) showed that, for participants with expertise in a particular dog breed, recognition of individual dogs of that breed was just as sensitive to inversion as was recognition of human faces. Diamond and Carey (1986) suggest that faces are not special in terms of their reliance on configural processing. They argue that, for other classes of object that: 1) share the same basic configuration, and 2) individuals of that class can be recognised on the basis of their second order relational features, one can become an expert and exploit those features to distinguish between individuals of that class in the same way as one distinguishes between faces. In support of this, Gauthier and Tarr (1997) trained participants to become experts in a novel class of objects ('greebles'), and showed that recognition of individual 'greeble' features was sensitive to configural manipulations, just as the recognition of human faces is. This suggests that faces are not special in terms of having distinguishing features that are particularly sensitive to inversion, and a review of research on the face-inversion effect concluded that the effect of inversion on face-recognition does not provide evidence for the existence of a specialised process for face-recognition (Valentine, 1988). Rather, this evidence would suggest that what may make faces 'special' is the fact that they represent a class of visual stimuli in which the majority of humans are experts (above and beyond any other class of objects).

In support of this, Bornstein, Sroka, and Munitz (1969) showed that prosopagnosics who formally had expertise with particular animals lost the ability to distinguish between individuals of that species at the same time that they lost the ability to recognise faces. Prosopagnosics have also been shown to have difficulty recognising unique members of a class of visual stimuli that share similarity in shape and configuration (e.g. cars, certain animals) (Damasio, Damasio, & Van Hoesen, 1982). Furthermore, expertise with a particular class of visual object is associated with recruitment of brain areas involved in face recognition, specifically the fusiform face area (FFA) and right occipital face area (Gauthier, Skudlarski, Gore, & Anderson, 2000; Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999), suggesting that it is the level of expertise with an object class that determines the recruitment of FFA, rather than a specialisation of the FFA for faces.

However, evidence in favour of the expertise hypothesis remains inconclusive. Three neuroimaging studies of expertise in the recruitment of FFA for non-face objects reported no effects for objects of expertise (Grill-Spector et al., 2004; Op de Beeck, Baker, DiCarlo, & Kanwisher, 2006; Yue, Tjan, & Biederman, 2006), and an attempt to replicate previous behavioural findings supporting the expertise hypothesis in dog experts failed to show configural 'face-like' processing for the dog stimuli (Robbins & McKone, 2007). Furthermore, a review of the face-processing literature covering behavioural and neurological research concluded that evidence strongly supported the domain specificity hypothesis of face- and object-recognition, rather than expertise (McKone, Kanwisher, & Duchaine, 2007).

1.3 Is the Self-Face Special?

Beyond the question of whether faces represent special stimuli in the visual processing system, is the idea that recognition of the self-face may be a unique process distinct from the recognition of other faces. Certainly the experiential nature of looking at one's own face is intuitively different than that of recognising the face of any other person, but does this reflect distinct cognitive and neural mechanisms involved in processing of the self-face relative to other faces? Behavioural research suggests that this may be the case.

There is a large body of research indicating that the self-face is processed differently to other faces. Firstly, there appears to be a distinct behavioural advantage for the processing of the self-face over the faces of others. Tong and Nakayama (1999) found that the self-face was identified faster among an array of distractor faces than a stranger's face, and this temporal advantage for the self-face persisted even when the faces were presented at different viewing angles (front, three-quarters and profile views), or inverted. However, Tong and Nakayama (1999) did not think that this pointed to the self-face as 'special', but rather that the self-bias in face processing reflected the robust representation of the self-face as an overlearned stimulus, and that a similar processing advantage would be evident for other highly familiar faces due to extensive visual exposure leading to more efficient processing. However, evidence from Keenan et al. (1999) disputes this viewpoint. Keenan et al. (1999) compared explicit identity discrimination responses to the self, highly familiar (friend or co-worker), and unfamiliar (stranger) faces. Faces were presented in both upright and inverted orientations, and across both orientations, responses to the self-face were significantly faster relative to all non-self faces. Despite the friend or co-worker faces being highly familiar to the participant, a self-face advantage was still observed, suggesting that the advantage for self-faces cannot be explained purely by familiarity.

The self-face advantage is not only evident in explicit tests of identity discrimination, but also in implicit face-recognition tasks where participants make judgements about the orientation of a face. Sui and Han (2007) found that participants responded faster when judging the orientation of their own face, relative to a familiar other's face. This highlights a self-face bias in not only identity discrimination, but also perceptual processing of facial features. These findings suggest that there is something special about the way the self-face is processed compared to other faces - both highly familiar and unfamiliar - that leads to behavioural advantages in the identification and recognition process.

There is evidence to suggest that individuals rely on different types of information when processing their own face relative to familiar others. Brédart

(2003) showed participants pairs of images of their own face, or a colleague's. One photo in each pair was mirror reversed, while the other was an original. For the self-face, participants indicated which image showed their face as they see it in the mirror, and, for their colleague's, which one was a better likeness. The majority of participants were able to correctly identify both the true images, but their decision making process was different depending on the identity of the face. Participants reported relying more on asymmetric facial features to identify their own mirror image than their colleague's face, and the use of this strategy also predicted higher accuracy during self-recognition. The results suggest that individuals do not rely on the same type of information when identifying images of the self and images of familiar faces, suggesting that different cognitive processes may be engaged in both types of face-recognition.

Research into categorical perception effects can shed light on the potential processing differences between the self-face and other faces. Categorical perception refers to the way in which particular stimuli are discriminated by the brain, simplifying what would be a large number of stimuli into fewer, distinct categories. Categorical perception in faces can be observed by the abrupt transition in face identity that is perceived along a morphing continuum between a pair of familiar faces. Photos along the continuum will be clearly perceived as either one of the known identities. What makes the self-face special, however, is that categorical perception of the self-face is possible under conditions in which categorical perception of other familiar-faces is eliminated. Keyes (2012) showed that categorical perception of highly familiar face morphs was impaired when the faces were presented upside-down. For the self-face, however, catergorical perception effects persisted even when the stimuli were inverted. This suggests that categorical perception of familiar faces is linked with configural processing, which was impaired when the faces were inverted. The lack of an impairment for the inverted self-face suggests that categorical perception of the self-face is supported by both configural and featural processing. This suggests that self-face representations contain strong configural *and* featural elements.

In summary, converging evidence suggests that self-face recognition is underpinned by distinct cognitive processes, setting it apart from the recognition of other faces. The next sections of this Chapter will focus on understanding the cognitive and neural mechanisms that support self-face recognition.

1.4 Understanding the Mechanisms of Self-Face Recognition

Understanding self-face recognition is not as simple as understanding the differences in perceptual processing between the self-face and other faces. In the investigation of self-face recognition, it is critical to address the question of the mechanisms involved in the initial acquisition of a mental representation of the self-face, assuming that infants are not born with an innate knowledge of their physical appearance. Along similar lines, it is also important to understand the mechanism involved in updating the mental self-face representation as an individual's physical appearance changes over time. Accordingly, Tajadura-Jiménez, Longo, Coleman, and Tsakiris (2012) suggested that the study of self-recognition should distinguish between three key processes:

1. Self-identification: The process by which an infant comes to acquire a representation of their own face through matching their own sensorimotor signals with those they observe in the mirror and identifying with their reflection.
2. Self-recognition: The process by which a stored mental representation of the self-face is maintained, allowing for diachronic recognition of one's own face.
3. Self-updating: The process by which the stored mental representation of the self-face is updated to reflect changes in an individual's physical appearance.

The following three sections of this Chapter will explore the three processes of self-face recognition (i.e. self-identification, self-recognition and self-updating). Starting with the question of self-identification, the next section will review the developmental trajectory of self-face recognition. Following this, the use of multisensory body illusions for studying self-identification and self-updating will be discussed. Finally, the process of self-recognition will be explored in a review of the neural correlates of self-face recognition.

1.5 The Development of a Self-Face Representation: An Implicit Self-Other Distinction from Birth?

Recognising an image of one's face requires a comparison between an external stimulus and an internal, mental representation of the self-face, but how is this mental representation initially acquired? Converging evidence suggests that the process of *self-identification* may rely on an innate sensitivity to multisensory contingency. From a very young age, infants show a sensitivity to the contingency between their own actions and the sensory outcomes of those actions. From 24 hours of age, infants more often turn towards touch received on their cheek when the touch is administered by an experimenter, compared with self-stimulation (spontaneously touching their own cheek) (Rochat & Hespos, 1997), suggesting that from birth infants are able to distinguish between self-produced and external tactile stimulation. Ten-week-old infants also display a sensitivity to contingency between their leg movements and the movements of a mobile hanging above them, showing significantly more leg kicking when the mobile moves as a result of their leg movements than when the mobile is manipulated by an experimenter (Rovee & Rovee, 1969). By five-months, infants are able to discriminate between a live-feed of their own legs and pre-recorded video of their own (or another infant's) legs (Bahrick et al., 1985), while infants of nine-months are able to discriminate between a live-feed and a delayed video of their own face (Lewis & Brooks-Gunn, 1979), showing a sensitivity to contingency between their own proprioceptive signals and visual feedback. This research shows that very young infants are sensitive to the contingency between their own actions and the sensory consequences of those actions across multiple modalities (i.e. visual and tactile).

Even in the absence of self-generated movement, two studies suggest that infants can still discriminate between self and other through the perception of visuo-tactile contingency. Filippetti, Johnson, and Lloyd-Fox (2013) showed that, from 12 hours after birth, newborns will preferentially look at a video showing an infant's face being stroked in synchrony with touch that they are receiving to their own face, rather than a face stroked in asynchrony. Importantly, the newborns had no preference for contingency when the videos showed an inverted infant's face being touched, suggesting that their sensitivity for multisensory synchrony is specifically related to bodily stimuli. Furthermore, Zmyj, Jank, Schütz-Bosbach, and Daum (2011) showed that 7 and 10 month old infants were able to discriminate between two videos of life-like doll baby legs being stroked in synchrony or asynchrony with touch on their own legs. Again, the sensitivity to the visuo-tactile contingency was only apparent when the stimuli was body related; infants displayed no preference when the videos showed wooden blocks being stroked. Bahrick et al. (1985) suggested that an infant's ability to detect multisensory contingency between proprioceptive and visual information underlies the development of visual self-recognition. The ability to detect synchrony across sensory modalities may provide vital information allowing newborns to distinguish the self from others, and subsequently to develop a coherent mental representation of their physical body.

It is not until five months that infants start to display some discrimination between self and other on the basis of featural elements rather than sensorimotor contingency. Bahrick and Moss (1996) presented two, three, five and eight month old infants with pre-recorded videos and still images of themselves and a peer. By five months, infants were able to discriminate between themselves and another infant in a video, and by eight months, infants could also discriminate between themselves and the peer in still images. This ability to discriminate was reflected by a preference to look at the peer rather than the self across both ages and mediums, a finding that has been replicated by other groups (Legerstee, Anderson, & Schaffer, 1998; Rochat & Striano, 2002). Bahrick and Moss (1996) suggested that this ability to discriminate showed that infants were familiar with their physical appearance by five months of age, however, it is important to note that this familiarity does not provide evidence that infants of five or eight months possess an abstract concept of themselves, or recognise that the image represents them. It is likely that the infants' preference for looking at the image of the peer over themselves is based upon a preference for novelty; as the majority of infants were exposed to mirrors during their daily life, their visual appearance would have been highly familiar to them. It is not until later, around 18 months, that infants start to explicitly recognise their own reflection.

By around 18 to 24 months of age, human infants start to recognise themselves in a mirror (Amsterdam, 1972; Brooks-Gunn & Lewis, 1984). The classic 'rogue mark test', first developed by Gallup (1970) for use in primates, and later by Amsterdam (1972) for use in human infants, tests whether an organism is able to recognise its own face in a mirror. Passing the mark test is widely considered to reflect the developmental milestone of explicit mirror self-recognition (MSR). Since Amsterdam (1972) first developed the original mark test for use in human infants, the basic paradigm has changed very little. For the test, children are covertly marked typically on or around the nose, usually by the mother pretending to wipe the infant's face. The covert application ensures that the mark can only be discovered by noticing its presence on the mirror image of the self. The infants are then placed in front of a mirror and observed for signs of mirror-guided mark-directed behaviours. Within the literature, the use of the term 'mark-directed behaviour' has varied widely. For example, the term has been used to refer to mark touching, nose touching and looking at the mark in the mirror (Amsterdam, 1972); touching in the region of the mark, verbalisations about the mark or of a referential and self-labelling nature (i.e. speaking about the nose, or the infant's name) (Asendorpf & Baudonnière, 1993; Lewis & Brooks-Gunn, 1979); and looking at the mark or the nose (Bertenthal &

Fischer, 1978; Schulman & Kaplowitz, 1977). Despite these differences in the definition of mark-directed behaviour, most research converges on the idea that MSR starts to emerge around 18 and 24 months of age (Bard, Todd, Bernier, Love, & Leavens, 2006).

Researchers also disagree on what passing the mark test means. While there is a general consensus that success at the mark test reflects ‘mirror-self recognition’, there are arguments as to what self-recognition means in terms of self-awareness. Gallup, for instance, argued that the ability to recognise one’s own face in the mirror represents a marker for self-awareness (Gallup, 1979, 1998). Gallup’s classic cognitivist interpretation of success at the mirror mark test states that any animal capable of passing the test must be in possession of a conceptual self-awareness (Gallup, 1977). It should be emphasised that in Gallup’s opinion, mirror self-recognition does not lead to a self-concept, but rather is a way of testing whether an animal already possesses a sense of self-identity (Gallup, 1977). However, others disagree that passing the mark test reflects self-awareness in the infant. Reports of children who previously passed the mirror mark test that, when seeing a red mark on their mother’s nose, touched their own nose, suggest that passing the test does not necessarily infer that an infant understands that the person they see in the mirror is ‘me’ (Mitchell, 1993).

The ability for MSR could reflect a more basic process of mapping the body onto the mirror surface, allowing an infant to look at parts of their body that they are not normally able to see (Rochat & Zahavi, 2011), and compare this image with a mental representation of the self-face (Asendorpf, 2002). This explanation implies that an infant passing the mark test does possess a stored representation of their own body (one in which the red mark does not exist), but also that they require the contingency between their own movements and the movements they observe in the mirror to recognise that the reflection represents themselves. This is supported by research showing that three year old infants will remove a covertly applied sticker when looking at their face in a mirror (or live video), but are unable to use the same information provided in a photograph (or delayed video) of themselves to complete the same task (Povinelli, Landau, & Perilloux, 1996; Povinelli & Simon, 1998). By four to five years of age the majority of children are able to use information about themselves in a delayed video to remove a covertly applied sticker, suggesting that it is not until later in development that children have an abstract sense of the self as existing through time. For younger children, the contingency between visual and proprioceptive cues, afforded by the mirror surface, seem to be critical to allow themselves to recognise their reflection.

In summary, prior to the existence of a stored mental representation of their physical appearance, infants are able to discriminate between self and other on the basis of contingency between multisensory signals. It has been suggested that this form of intermodal matching underlies the development of explicit self-recognition, allowing for the formation of a visual representation of one's face through the matching of proprioceptive, sensorimotor and visual information during mirror exposure (Bahrick et al., 1985). The formation of a visual representation of self subsequently paves the way for explicit self-recognition and conceptual self-awareness in later development (Rochat, 1995). In this sense, multisensory integration can be seen as vital for the development of self-face recognition.

1.6 Self-Identification and Self-Updating

1.6.1 Multisensory Theories of Body-Representation

The evidence reviewed in the previous section converges on the idea that multisensory matching plays an important role in the formation of a representation of the self-face. Multisensory models of body-ownership form a useful basis for understanding and investigating the specific processes of self-identification and self-updating. Body-ownership refers to the feeling that sensations relating to the body are experienced uniquely by the individual, and that the body belongs to the self (Gallagher, 2000). The current section outlines multisensory theories of body ownership and multisensory integration paradigms used to experimentally investigate the conditions required for multisensory matching to lead to a sense of body-ownership.

Botvinick and Cohen (1998) proposed that the only requirement for the attribution of a body part to the self was intermodal matching. The rubber hand illusion (RHI) provides evidence that a sense of ownership can be induced over a fake rubber hand through the use of a simply multisensory integration paradigm (Botvinick & Cohen, 1998; Ehrsson, Spence, & Passingham, 2004; Tsakiris & Haggard, 2005). During the illusion, participants observe touch to a fake rubber hand, while feeling synchronous touch on their own hidden hand. This induces the feeling that the observed touch is in fact the touch that is felt, and can lead to an illusory sense of ownership over the fake hand. The RHI paradigm provides a way in which body-ownership can be manipulated in a controlled, experimental setting. When the observed and felt touch are out of synchrony, the illusion is abolished. Interestingly, physical similarity to the rubber hand does not influence body-ownership, but the experience of ownership over the rubber hand influences the perceived similarity between the rubber hand and the real hand, suggesting that multisensory integration may play a part in updating mental representations of the physical body (Longo, Schüür, Kammers, Tsakiris, & Haggard, 2009). In line with this, experience of ownership appears to affect the way that one's own body is experienced, such that the rubber hand, rather than being represented as an additional limb, replaces the existing, real hand. Reports of subjective experiences of ownership (Longo, Schüür, Kammers, Tsakiris, & Haggard, 2008), and physiological changes experienced during RHI (Moseley et al., 2008) suggest that the rubber hand is incorporated into the existing body schema and replaces the real hand.

Armel and Ramachandran (2003) went one step further by suggesting that any object could be incorporated into one's body representation so long as synchronous intermodal matching was present. To investigate this, Armel and Ramachandran (2003) performed the RHI with participants, before 'injuring' the rubber hand. Skin Conductance Responses (SCR) measured from the participant's real hand at the point the rubber had was injured were significantly higher in the synchronous condition than the asynchronous condition, reflecting a sense of induced bodily ownership over the rubber hand in the synchronous condition. Critically, the same pattern of SCRs was also identified when a table was stroked in synchrony with the participant's hidden hand, and then injured. Armel and Ramachandran (2003) argued that this showed that any object, provided the appropriate intermodal matching is present, can be incorporated into the body-representation. However, other research disputes this, suggesting that intermodal matching between one's occluded hand and an external object, while necessary, is not sufficient for the object to be experienced as part of one's body.

A number of studies have provided evidence to suggest that induction of body-ownership is not successful when the object attempting to be incorporated does not resemble a hand (Graziano, Cooke, & Taylor, 2000; Haans, Ijsselsteijn, & de Kort, 2008; Holmes, Snijders, & Spence, 2006; Tsakiris, Costantini, & Haggard, 2008; Tsakiris & Haggard, 2005). The RHI is also abolished when the rubber hand is placed in an implausible location anatomically or posturally (Costantini & Haggard, 2007; Graziano et al., 2000; Lloyd, 2007; Tsakiris & Haggard, 2005). These findings suggest that synchronous multisensory stimulation, while necessary, is not sufficient for induction of body-ownership over a fake limb, as suggested by Botvinick and Cohen (1998) and Armel and Ramachandran (2003). The object to be incorporated needs to resemble the limb it is replacing, as well as be in an anatomically and posturally congruent location with regards to the individual. In line with this, Tsakiris (2010) proposed a top-down account of body-ownership, in which multisensory stimulation is integrated alongside a reference model that codes for anatomical and structural information about the body (e.g. Graziano & Botvinick, 2002). The integration of multisensory signals such as those presented in the RHI creates a conflict between the current online representation of the body (proprioceptive signals), and the felt and observed touch. In order for a resolution of this conflict, the current body-representation must be updated to reflect a coherent representation of the body within the environment, such that the observed touch to the rubber hand, integrated with the felt touch on the real hand, result in a change in perceived location of the hand towards the rubber hand. Interestingly, the findings of Filippetti et al. (2013) and Zmyj et al. (2011), showing that infants were sensitive to contingency only when the stimuli were body related, is in line with this model of body ownership.

1.6.2 From Body-Ownership to Self-Identification

While the RHI can inform researchers about the processes of body-ownership, the experiential nature of identifying with a face is somewhat different. A facial-analogue of the RHI, the Enfacement Illusion, can be used to explore the processes underpinning self-face recognition (Tsakiris, 2008). The Enfacement paradigm has been considered as a model of self-identification, reflecting the same processes by which initial representations of the self-face are acquired and subsequently updated (Tajadura-Jiménez, Longo, et al., 2012). Therefore, its use in studying the plasticity of self-face representations is invaluable.

In the Enfacement Illusion, synchronous tactile stimulation applied to the participant's cheek and an observed other's cheek causes a blurring between the self and the other, namely, that the participant incorporates a part of the other's face into their own self-face representation. This incorporation of the other causes a change in self-identification, and critically, only occurs following synchronous interpersonal multisensory stimulation (IMS). Tajadura-Jiménez, Longo, et al. (2012) identified three factors contributing to the experience of Enfacement. Firstly: self-identification, which refers to feelings of causal relationship between felt and observed touch, resemblance between the other's face and the self, a sense that the other's face was indeed the self-face or belonged to the self, that one was being imitated by or imitating the Enfacement face, and that one was looking into a mirror. Secondly: self-similarity, which relates to the feeling that the other's face and the self-face resembled each other, and that the experience of the self-face became less vivid during the illusion.

And lastly, ‘affect’, which refers to feelings about the other person, such that they seem attractive or trustworthy. The authors argue that the first two factors match two key processes in self-face recognition: *self-identification* and *self-recognition.* The authors identify that the biggest differences in experience between synchronous and asynchronous stimulation lie in the first two factors of self-identification and similarity. Although there is a difference in affect between the two conditions, it is smaller than the change in the other two factors across conditions.

Tajadura-Jiménez, Longo, et al. (2012) investigated the qualitative experience of both synchronous and asynchronous IMS. While illusions inducing changes in self-identification and body-ownership may rely on similar mechanisms of multisensory integration, the qualitative experience of the two differs dramatically. Firstly, the conscious experience during RHI, in either synchronicity condition, remains very qualitatively similar, differing mainly quantitatively, with higher ratings given in the synchronous condition. However, the conscious experience of Enfacement differs qualitatively depending on whether the stroking is synchronous or asynchronous. When stroking is synchronous, participants generally focus on physical similarity between the two faces, whereas during asynchronous stimulation, the focus is mainly on the multisensory stimulation, feelings of control and imitation of the other’s face, and a ‘mirror-like’ experience, rather than any physical similarities. The effect of Enfacement appears then to be the creation of resemblance and similarity between the self and the other, with multisensory integration being the cause. Asynchrony disrupts this process of increasing similarity, and the focus is put on the felt touch rather than any similarity between the self and other.

This revealed that there are two separate components to the illusion. The sense of similarity, and the sensorimotor experience during the IMS. Multisensory stimulation appears to be the cause of self-identification with the other person’s face, but is not regarded by an individual as part of the experience of identification. Sensorimotor experience only becomes relevant during asynchronous stimulation when the focus is drawn to that and no feelings of similarity are induced. This highlights important differences between self-identification and body-ownership. While the mechanisms behind both processes may be similar - both rely on the integration of multisensory signals – the dimensionality of the two experiences differs. The experience during RHI is centred largely on a shift in body representation from an embodied first-person perspective. Self-identification is driven by not only integration of information from a first-person perspective, but also a third person perspective, as an individual identifies with the face in front of them. The findings from research with the Enfacement Illusion provide evidence in an experimental setting that the integration of synchronous multisensory signals can lead to a change in the self-face representation. The Enfacement Illusion therefore provides a useful tool for studying the neural underpinnings of self-identification and self-updating.

1.6.3 Neural Correlates of Self-Identification and Self-Updating

Apps, Tajadura-Jiménez, Sereno, Blanke, and Tsakiris (2013) investigated the neural correlates of the Enfacement Illusion, highlighting neural regions which may be involved in the processes of self-identification and self-updating. They found activity in the right temporoparietal junction (rTPJ), intraparietal sulcus (IPS) and inferior occipital gyrus (IOG) that was modulated by the interaction of congruency and synchronicity during the Enfacement Illusion, and varied parametrically with the subjectively reported strength of the illusory experience. This suggests that the experience of identification with a face relies on the involvement of multisensory (rTPJ, IPS) and unimodal (IOG) brain areas.

Activity in the IOG was thought to reflect the plasticity of this area, allowing for representations of low-level facial features to be updated. Activity in the OFA (part of IOG) reflects processing of individual facial features rather than configural processing of facial identity (Barton, 2008; Kanwisher & Barton, 2011), suggesting that intermodal matching may cause updating of the self-face features in this area to resemble more closely the features of the face seen during the Enfacement Illusion, reflecting the assimilation of the other's features into the self-face representation that has been documented behaviourally (Tajadura-Jiménez, Grehl, & Tsakiris, 2012; Tajadura-Jiménez, Longo, et al., 2012; Tsakiris, 2008). Activity in IPS was speculated to reflect the integration of multisensory signals. IPS receives input from superior temporal sulci and the IOG – both implicated in face processing (Allison, Puce, & McCarthy, 2000; Haxby et al., 2000; Barraclough & Perrett, 2011; Kanwisher & Barton, 2011), as well as vestibular and somatosensory input (Seltzer & Pandya, 1980, 1986; Lopez & Blanke, 2011), suggesting that it is involved in integrating multisensory information during the Enfacement Illusion, playing a critical role in producing the experience of identifying with the observed face. Interestingly, there was a reduction in activity in TPJ during sycnrhonous stimulation. The TPJ is suggested to be involved in representing the self as distinct from others, leading to the suggestion that the reduction in activity observed during sycnrhonous IMS reflects that the other's face started to be represented as the self-face.

In summary, the Enfacement Illusion provides a useful tool for investigating the cognitive and neural mechanisms underpinning self-identification and self-updating. To date, however, there is little research utilising the Enfacement Illusion paradigm to directly investigate the roles of specific brain areas in these processes. Initially, fMRI research suggests that self-identification and self-updating rely on an interplay between multimodal and unimodal areas of the brain, but further investigation is required to elucidate the roles of individual areas to the experience of Enfacement.

1.7 Self-Recognition

1.7.1 The Neural Correlates of Self-Recognition

This section will explore the neural correlates of self-face recognition in an attempt to understand the specific brain areas underpinning the process of *self-recognition.* This section is split into four areas of research:

1. Hemispheric dominance in self-face recognition
2. Functional neuroimaging research
3. Electroencephalogram research
4. Non-invasive brain stimulation research

1.7.2 Hemispheric Specialisation in Self-Face Recognition

Evidence for hemispheric specialisation in self-face processing is often drawn from research comparing RTs in left and right hands as a measure of hemispheric dominance. Evidence suggests that if task processing is strongly lateralised to a particular hemisphere, responses made by the contralateral hand will show a temporal advantage (Hodges, Lyons, Cockell, Reed, & Elliott, 1997). A number of studies have shown a left hand advantage for recognising the self-face, suggesting a right hemisphere specialisation (Keenan et al., 1999; Ma & Han, 2010; Keenan, Freund, & Hamilton, 2000; Keenan, Ganis, Freund, & Pascual-Leone, 2000; Platek, Keenan, Gallup, & Mohamed, 2004). Keenan, Nelson, O'Connor, and Pascual-Leone (2001) have also investigated self-recognition in patients undergoing hemispheric anaesthesia in preparation for epilepsy surgery. During anaesthesia of each hemisphere, Keenan et al. (2001) presented patients with a morphed photo of theirs and a famous person's face. Following anaesthesia, patients were given a forced choice task in which they chose which of two photographs (100% self or 100% other) was shown to them previously. Following right hemisphere anaesthesia, four of the five patients chose the famous face, while following left hemisphere anaesthesia, all five patients selected the 'self' face, further supporting a right hemisphere dominance in self-recognition. Keenan et al. (2001) elicited motor-evoked potentials (MEPs) using transcranial magnetic stimulation as a proxy measure of hemisphere activation while healthy participants viewed images containing the self-face or a familiar face. MEPs elicited from stimulation to the right hemisphere were significantly larger when viewing an image containing the self-face than any other face/hemisphere combination. Larger MEPs while viewing the self-face suggest higher levels of activation, again supporting a right hemisphere dominance in self-face processing.

Despite this evidence for right hemisphere dominance in self-face recognition, research also exists to support a left-hemisphere bias in this process. Brady, Campbell, and Flaherty (2004) created mirror-symmetric chimeric faces (composed of the left or right side of a photograph of a face) of the participant's own face and a friend's face, and asked participants to choose which of two composite faces best resembled the original. When participants chose which of two chimeric faces best resembled themselves, they chose the face made up of the mirror-right side of their face, corresponding to the side of their face that lies in their right visual field (and left hemisphere) when they look at themselves in the mirror. When asked to choose which chimeric face best resembled their friend, they chose the composite made from the right side of the friend's face, representing the side that would fall within their left visual field. This provides evidence to suggest a bias in left hemisphere processing for self-recognition. Furthermore, hemisphere bias in self-recognition has also been investigated in split-brain patient JW. Turk et al. (2002) highlights that JW was capable of self-recognition when images of the self-face were presented to either visual field, suggesting that both hemispheres are independently capable of self-face recognition. However, it was evident that JW's right hemisphere showed an advantage for recognition of familiar faces, while the left hemisphere was biased towards self-recognition. This double dissociation suggests that the processes of self- and other-face recognition rely on distinct mechanisms in the brain.

The evidence presented above demonstrates that hemisphere dominance in self-recognition is a controversial issue. Across the literature there is no consensus as to whether either hemisphere plays a dominant role in identification of the self-face, however, critically, the study of a split-brain patient indicates that both hemispheres are independently capable of self-recognition. The next section of this review will focus on neuroimaging research to highlight which brain regions are preferentially involved in self-face recognition relative to the processing of familiar-faces.

1.7.3 Neuroimaging Research

Behavioural data suggests that processing of the self-face is special, above and beyond familiarity and experience. Explicit identity discrimination and perceptual processing tasks demonstrate a temporal advantage for self-face processing over other highly familiar faces. Self-face processing also appears to rely on different types of information, with evidence from categorical perception paradigms suggesting that featural processing is more heavily involved in the perception of the self-face than other familiar faces. The combined evidence suggests that distinct neural mechanisms may underlie the perception of the self-face and other familiar faces.

Research into the neural correlates of self-face recognition has expanded rapidly over the past 10 years. One main assumption in the neuroimaging literature is that presenting participants with images of their own face while in an MRI scanner is an easy way of investigating the neural correlates of self-recognition (Devue & Brédart, 2011), however, beyond this common assumption, the paradigms employed within the literature vary extensively. There are differences in the tasks used, the control stimuli chosen, and the aims of the studies themselves. Therefore, Table 1.1 summarises the tasks, stimuli, aims and contrasts used by the studies in this review. Following this is a summary of the areas most commonly implicated in the process of self-recognition.

1.7.4 Brain Areas Involved in Self-Recognition

Evidence from neuroimaging studies suggests a wide neural network underlying visual self-recognition, spanning across both hemispheres and encompassing multiple cortices. This section will cover the most consistently activated brain areas in the study of self-recognition. Table 1.2 provides a comprehensive list of brain areas implicated in self-face processing.

Table 1.1: Neuroimaging studies of self-recognition.

Study	fMRI/ PET	Contrast used for analysis	Stimuli	Task	Secondary Task	Aim
Apps et al. (2012)	fMRI	Self>Familiar (friend)	Morphed face photos	Explicit identification (right index 'self', right middle 'other')		Self-recognition – past & current face
Devue et al. (2007)	fMRI	Self>Familiar (colleague)	Altered photos of faces and bodies	Identify unaltered images of the self and familiar other		Self-face recognition
Kaplan et al. (2008)	fMRI	Self>Familiar (friend)	Photos of faces, sounds of voices	Explicit identification (right index 'self', right middle 'other')		Self-recognition (faces & voices)
Kircher et al. (2000)	fMRI	Self > Unfamiliar	Morphed face photos & personality trait words	Explicit identification task (two buttons with right thumb)	Discrimination of trait adjectives	Self-judgements
Kircher et al. (2001)	fMRI	Self>Unfamiliar	Morphed face photos	Explicit identification		Self-face recognition
Ma and Han (2012)	fMRI	Self>Familiar (friend)	Morphed face photos	Explicit identification		Self-face recognition – properties vs. identity
Morita et al. (2008)	fMRI	Self>Unfamiliar	Photos of faces (ranging from good to bad)	Photogenic judgements		Self-evaluation
Morita et al. (2014)	fMRI	Self>Unfamiliar	Photos of faces (ranging from good to bad)	Embarrassment ratings		Self-face recognition & embarrassment
Oikawa et al. (2012)	fMRI	a) Self>Familiar b) Self>Unfamiliar	Photos of faces	Familiarity judgement		Self-face evaluation & self-esteem
Platek et al. (2004)	fMRI	Self>Familiar (famous)	Photos of faces	Mental identification	Mental state attribution – Mind in the Eyes	Self-awareness/ mental state attribution
Platek et al. (2006)	fMRI	Self>familiar	Photos of faces	Explicit identification		Self-face recognition
Platek and Kemp (2009)	fMRI	Self>Familiar (sibling, friend)	Photos of faces, morphed face photos	Familiarity judgements		Kin-face recognition
Ramasubbu et al. (2011)	fMRI	Self>Familiar (mother, friend)	Photos of faces	Passive viewing	Valence & salience judgements	Self-face recognition & evaluation
Scheepers et al. (2013)	fMRI	Self>Familiar (student, friend)	Photos of faces	Think about person in photo	Identify group affiliation	Self-face recognition & in-group vs. out-group face perception
Sugiura et al. (2005)	fMRI	Self>Unfamiliar	Photos of faces	Familiarity judgements (right index 'familiar', right middle 'unfamiliar')		Self-face recognition
Sugiura et al. (2006)	fMRI	Self>Familiar (friend) masked by Familiar>Unfamiliar	Photos and videos of faces and bodies	Familiarity judgements (right index 'familiar', right middle 'unfamiliar')		Self-recognition (face & body)
Sugiura et al. (2008)	fMRI	Self>Familiar (friend)	Photos of faces and names	Familiarity judgements (right index 'familiar', right middle 'unfamiliar')		Self-recognition (face & name)
Sugiura et al. (2012)	fMRI	Self>Familiar (friend)	Photos of faces	Familiarity judgement		Self-face recognition in social context
Sui and Han (2007)	fMRI	Self>familiar	Photos of faces	Head orientation judgements		Self-construal priming on self-recognition
Taylor et al. (2009)	fMRI	Self>Unfamiliar	Photos of faces	Passive observation		Self-face recognition
Uddin et al. (2005)	fMRI	Self>Familiar (friend/colleague – gender matched)	Morphed face photos	Explicit discrimination (right index 'self', right middle 'other')		Self-face recognition
Sugiura et al. (2000)	PET	Self-face > Unfamiliar	Photos of faces	Passive (observation) and active (explicit discrimination) recognition		Sustained attention on self-recognition

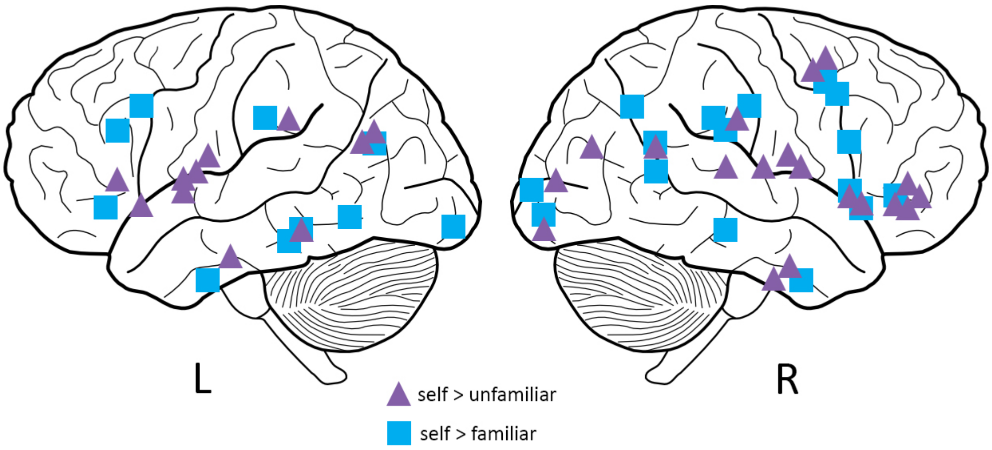

Figure 1.1: A visual representation of the brain areas identified in self-face recognition in the studies included in this review. Triangles represent studies that used a self > unfamiliar contrast, and squares represent studies that used a self > familiar contrast.

1.7.4.1 Superior Frontal Gyrus

Three studies contrasting the self-face with a familiar face found selective activation in the right superior frontal gyrus (Platek et al., 2006, 2004; Platek & Kemp, 2009). Platek et al. (2006) specifically found activation in this area in the self versus familiar contrast, and not in a self versus unfamiliar contrast, suggesting the activation reflects the self-specificity aspect of the self-face and not familiarity. Platek et al. (2004) found that both images of the self-face and performance of a mental state attribution task elicited activation in this area. These patterns of activation are consistent with a model of self-awareness, that involves the modelling of both the self and others, in the right hemisphere spanning frontal and parietal regions (Decety & Chaminade, 2003).

1.7.4.2 Inferior Frontal Gyrus

Activation in the right inferior frontal gyrus has been reported in six studies comparing self-face activation with activation to a familiar face (Devue et al., 2007; Kaplan et al., 2008; Platek et al., 2004; Sugiura et al., 2008; Uddin et al., 2005), and in one comparing self-face to an unknown face (Sugiura et al., 2000). Activation in the left IFG has been reported in two studies contrasting the self-face with an unknown face (Kircher et al., 2000, 2001). This area has been hypothesised to underlie the process of discrimination between the self and another individual (Devue et al., 2007; Uddin et al., 2005). This is supported by evidence from research using tasks that require participants to discriminate between the self and another face (Kircher et al., 2000, 2001; Devue et al., 2007; Uddin et al., 2005). Uddin et al. (2005) specifically found that as the amount of self in an image increased, so did activation in this area.

Evidence also suggests that this area is involved in processing self-relevant information, and is not specific to self-face recognition. Kircher et al. (2000) found the left IFG was selectively activated during the processing of self-relevant words compared to words that were not related to the self, and activation in this area has also been reported in response to listening to the self-voice (Kaplan et al., 2008). Sugiura et al. (2000) also suggests that activity in the right IFG may reflect sustained attention to the stored representation of the self-face.

1.7.4.3 Insular Cortex

A number of studies have found selective activation in the insula cortex elicited by the self-face. In the left hemisphere: once during comparison with a familiar face (Platek et al., 2006), and twice with unknown faces (Morita et al., 2008; Sugiura et al., 2000). And twice in the right insula when contrasting the self-face with an unfamiliar face (Kircher et al., 2000, 2001). Devue et al. (2007) also identified right anterior insula activation during the processing of the self-face as well as self-body, suggesting that this area is implied in the integration of different aspects of the physical self into one self-concept. Further evidence suggests that this area is involved in not only physical aspects of the self, but also abstract self-processing. Kircher et al. (2000) demonstrated that activation in this area was shared by both the self-face as well self-relevant adjectives, suggesting that this area integrates self-relevant information regardless of modality. It has also been suggested that this area processes self-relevant information for evaluation, supported by Morita et al. (2008), who found that activation in the right insular cortex was positively correlated with scores on a public self-consciousness scale, and bilateral insular cortex activation was observed during attractiveness ratings of the self-face versus that of unfamiliar others.

1.7.4.4 Cingulate Cortex

The cingulate cortex has been implicated in the self-recognition process in two studies comparing self-face activation to familiar faces (Devue et al., 2007; Platek & Kemp, 2009), and four studies using unknown faces as controls (Kircher et al., 2000, 2001; Morita et al., 2008; Sugiura et al., 2000). In a similar fashion to the insula, the cingulate cortex has been implicated in abstract self-relevant processing. It is involved when individuals attend to self-relevant information (over non-self-relevant information) regardless of modality (Northoff & Bermpohl, 2004). Devue et al. (2007) also found this area to be activated to not only the self-face but also photographs of the self-body.

1.7.4.5 Occipital Lobes

Activation in the occipital lobes, extending to both the fusiform and inferior temporal gyri (Morita et al., 2008), may reflect the early stages of face processing before identification, on the basis of familiarity (Devue et al., 2007). Devue et al. (2007) found specific activation for faces contrasted with bodies bilaterally in the middle occipital gyrus, which also extended to the right fusiform gyrus, suggesting this area plays a specific role in face processing.

1.7.4.6 Fusiform Gyrus and Inferior Temporal Gyrus

Evidence suggests that the fusiform gyrus and inferior temporal gyrus are involved in familiarity judgements, rather than differentiation processes between the self and others. Sugiura et al. (2006) found familiarity dependent activation in these areas when participants performed a familiarity judgement task while viewing images of their own body. They also found that these areas were not activated for the self-name, suggesting this region is specialised for self-body and face processing in contrast with more general self-processing areas. If these areas are not involved in identification, then the difference in activation to faces of different types may reflect a difference in processing style for own face versus other faces, rather than purely familiarity.

1.7.4.7 Inferior Parietal Lobule

Three studies have found self-specific activation in the inferior parietal lobule when comparing the self-face to familiar faces (Kaplan et al., 2008; Platek et al., 2006; Uddin et al., 2005), and two during comparison with an unfamiliar face (Kircher et al., 2000, 2001). This region has been suggested to be involved in self-other differentiation, but at a general level and across sensorial modalities, rather than the specific differentiation of faces (Platek et al., 2006; Uddin et al., 2005).

1.7.4.8 Supramarginal Gyrus

This region is implicated bilaterally in self-recognition (Sugiura et al., 2006, 2008; Platek & Kemp, 2009). When the supramarginal gyrus is damaged it can lead to asomatognosia, which has lead to the suggestion that this region may play a role in representing the self-face as part of one's body (Sugiura et al., 2000). This area may also form, together with the occipito-parital junction, part of a neural network involved in the representation of the self in physical space (Platek et al., 2006; Sugiura et al., 2000; Uddin et al., 2005).

1.7.4.9 Precuneus

Activity in this area is suggested to reflect integrative processes involved in the integration of self-referential stimuli of different modalities into the self-concept (Northoff & Bermpohl, 2004).

Table 1.2: Brain areas implicated in self-recognition

Area	**References**
Fusiform gyrus (L)	(Sugiura et al., 2000, 2005, 2006; Kircher et al., 2001)
Fusiform gyrus (R)	(Sugiura et al., 2006)
Supramarginal Gyrus (R) / inferior parietal lobe	(Sugiura et al., 2000, 2006, 2008, 2012; Uddin et al., 2005)
Supramarginal Gyrus (L) / inferior parietal lobe	(Kircher et al., 2001; Platek & Kemp, 2009)
Putamen (L)	(Sugiura et al., 2000)
Midbrain (R)	(Sugiura et al., 2005; Morita et al., 2014)
Hypothalamus (R)	(Sugiura et al., 2000)
Thalamus (R)	(Morita et al., 2014)
Lenticular/subthalamic nucleus (R)	(Kircher et al., 2001)
Precentral sulcus (R)	(Sugiura et al., 2008, 2006)
Precentral gyrus (R)	(Morita et al., 2008)
Precentral (L)	(Ramasubbu et al., 2011)
Anterior cingulate (L)	(Platek & Kemp, 2009; Taylor et al., 2009)
Anterior cingulate (R)	(Sugiura et al., 2000; Kircher et al., 2000, 2001; Morita et al., 2008; Platek & Kemp, 2009; Taylor et al., 2009)
Cingulate gyrus (L)	(Taylor et al., 2009)
Cingulate gyrus (R)	(Taylor et al., 2009)
Middle cingulate cortex	(Morita et al., 2014)
Presupplementary motor area (R)	(Sugiura et al., 2000)
Supplementary motor area	(Morita et al., 2014)

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Table 1.2 – *Continued from previous page*

Area	**References**
insular (L)	(Sugiura et al., 2000; Morita et al., 2008, 2014)
Insular (R)	(Kircher et al., 2000, 2001; Devue et al., 2007; Morita et al., 2008; Ramasubbu et al., 2011; Morita et al., 2014)
Pulvinar (R)	(Sugiura et al., 2000)
Anterior insula (L)	(Sugiura et al., 2000)
Hippocampal formation (R)	(Kircher et al., 2000, 2001)
Precruneus (R)	(Kircher et al., 2000, 2001; Scheepers et al., 2013)
Precuneus (L)	(Platek & Kemp, 2009; Scheepers et al., 2013)
Subthalamic nucleus (R)	(Kircher et al., 2000)
Cerebellum (L)	(Kircher et al., 2000)
Cerebellum (R)	(Kircher et al., 2001)
Parahippocampal gyrus (R)	(Platek & Kemp, 2009; Sugiura et al., 2005)
Parahippocampal gyrus (L)	(Sugiura et al., 2005)
Middle temporal lobe (R)	(Kircher et al., 2000)
Middle temporal gyrus (L)	(Platek et al., 2006; Sugiura et al., 2006)
Inferior temporal gyrus (R)	(Sugiura et al., 2008, 2006; Morita et al., 2014; Sugiura et al., 2012; Oikawa et al., 2012; Apps et al., 2012)
Inferior temporal gyrus (L)	(Morita et al., 2014)
Superior temporal (L)	(Kircher et al., 2001)
Superior temporal gyrus (R)	(Platek & Kemp, 2009)
Temporal cortex (R)	(Scheepers et al., 2013)
Temporal cortex (L)	(Scheepers et al., 2013)
Inferior parietal lobule (L)	(Kircher et al., 2000; Ramasubbu et al., 2011; Scheepers et al., 2013)

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Table 1.2 – *Continued from previous page*

Area	**References**
Inferior parietal lobule (R)	(Platek et al., 2006; Kaplan et al., 2008; Scheepers et al., 2013)
Superior parietal lobule (R)	(Uddin et al., 2005; Scheepers et al., 2013; Oikawa et al., 2012; Apps et al., 2012)
Superior parietal lobule (L)	(Ramasubbu et al., 2011)
Posterior superior parietal lobule (R)	(Sugiura et al., 2006)
Intraparietal sulcus (R)	(Sugiura et al., 2012)
Postcentral sulcus (R)	(Sugiura et al., 2012)
Postcentral gyrus (R)	(Scheepers et al., 2013)
Ventral premotor cortex (R)	(Morita et al., 2014)
Frontal operculum (R)	(Sugiura et al., 2005)
Prefrontal Regions (L)	(Kircher et al., 2000, 2001; Sugiura et al., 2000)
Inferior frontal gyrus (L)	(Kircher et al., 2001; Scheepers et al., 2013)
Inferior frontal gyrus (R)	(Uddin et al., 2005; Sugiura et al., 2008, 2000; Morita et al., 2014; Sugiura et al., 2012; Oikawa et al., 2012; Platek et al., 2004; Devue et al., 2007; Kaplan et al., 2008; Ramasubbu et al., 2011; Scheepers et al., 2013)
Mid-inferior frontal gyrus (R)	(Morita et al., 2014; Sugiura et al., 2006; Scheepers et al., 2013; Oikawa et al., 2012)
Mid-inferior frontal gyrus (L)	(Morita et al., 2014; Scheepers et al., 2013)
Middle frontal gyrus (L)	(Kircher et al., 2001; Taylor et al., 2009)
Middle frontal gyrus (R)	(Platek et al., 2004, 2006)
Medial frontal gyrus (R)	(Platek et al., 2006; Sugiura et al., 2000; Taylor et al., 2009)

Continued on next page

Table 1.2 – *Continued from previous page*

Area	**References**
Medial frontal gyrus (L)	(Platek & Kemp, 2009; Taylor et al., 2009)
Superior frontal gyrus (R)	(Platek et al., 2004, 2006; Platek & Kemp, 2009; Ramasubbu et al., 2011)
Inferior occipital gyrus (R)	(Uddin et al., 2005; Kaplan et al., 2008; Apps et al., 2012)
Inferior occipital gyrus (L)	(Morita et al., 2014)
Anterior occipital cortex (R)	(Morita et al., 2008)
Posterior occipital cortex (R)	(Morita et al., 2008)
Occipital cortex (R)	(Scheepers et al., 2013)
Occipital cortex (L)	(Scheepers et al., 2013)
Occipito-temporo-parietal junction (R)	(Morita et al., 2014, 2008; Sugiura et al., 2005)
Occipito-temporo-parietal junction (L)	(Morita et al., 2014)
Occipito-parietal junction (R)	(Sugiura et al., 2006)
Occipital cortex (L)	(Morita et al., 2008)
Inferior occipital cortex (R)	(Morita et al., 2014)
Superior occipital (L)	(Ramasubbu et al., 2011)
Occipital face area	(Apps et al., 2012)

1.7.4.10 Summary

Results from neuroimaging studies suggest a wide and bilateral neural network involved in the processing of the self-face, spanning frontal, occipital, parietal and temporal brain regions. It is currently difficult using current popular paradigms to separate activation purely driven by the recognition of the self-face from automatic evaluative and emotional processes elicited by the perception of one's own face. Identification of the self may lead to evaluative processes, as well as eliciting emotional responses, which may be reflected in the activations identified. Brain activation driven purely by recognition of the self-face, un-confounded by these types of processes which are often driven by perception of the self-face, needs further investigation.

1.7.5 Electroencephalogram Research

Evidence from EEG studies can also highlight self-specific processing in the human brain. Ninomiya, Onitsuka, Chen, Sato, and Tashiro (1998) demonstrated that the P300, a component reflecting the evaluation of stimulus significance, was enhanced in response to the self-face relative to unfamiliar-faces, suggesting a heightened relevance of the self-face. Keyes, Brady, Reilly, and Foxe (2010) identified an increased vertex positive ERP at frontocentral sites and enhanced N170 over occipito-temporal recording sites for self-faces relative to both familiar (friend) and unfamiliar faces, as well as reduced P2 and N2 components over posterior and frontocentral sites respectively. A distinction between personally familiar and unfamiliar faces was not identified until 250ms after stimulus onset, suggesting that the self-face elicits special processes of recognition. The early discrimination of the self-face from both familiar and unfamiliar faces is thought to reflect early categorisation processes based on the identity of the face (Jacques & Rossion, 2006). Sui, Zhu, and Han (2006) demonstrated that, following encoding of facial structure, an automatic process of self-face recognition occurs. During 500-700ms after stimulus onset, an increased positivity for self-face stimuli relative to familiar-faces can be observed in a passive observation task. This difference between self-face and familiar-face processing is reduced under an attended condition. While the ERP to self-faces was unaffected by level of attention, the neural response to familiar faces became more similar to that of the self-face when the familiar face stimuli was attended to. This demonstrates that the self-face elicits an automatic process of recognition regardless of the level of attention provided to it.

1.7.6 Transcranial Magnetic Stimulation Research

Research using transcranial magnetic stimulation (TMS) is able to provide evidence for the causal role of particular brain areas in self-face recognition. Uddin, Molnar-Szakacs, Zaidel, and Iacoboni (2006) applied 20 minutes of repetitive transcranial magnetic stimulation (rTMS) to the right inferior parietal lobule (IPL) to create a virtual lesion. Participants performed a self-face recognition task before and after receiving stimulation, in which they had to indicate the identity of a series of morphed faces, created by morphing a photo of the participant's face with a personally familiar face. Following stimulation, the amount of faces identified as 'self' by participants, while actually containing over 50% of the other's face, increased relative to before stimulation. This indicates that impaired functioning within the IPL resulted in a disruption of the ability to correctly identify images of the self, leading to more liberal self-recognition behaviour in which participants accepted faces containing a minority of their own face as resembling themselves. Heinisch, Dinse, Tegenthoff, Juckel, and Brüne (2011) expanded upon this finding to investigate whether the effect was specific to self-face recognition, or affected the recognition of faces in general. Using a morphing videos paradigm, participants viewed videos that morphed either from a familiar face into their own, or their own to the other face. Participants indicated the point in the videos at which the face started to resemble more themselves, or the other person, depending on the direction of morphing. In line with the findings of Uddin et al. (2006), Heinisch et al. (2011) found that rTMS disrupted self-face recognition in the direction of the other face. Participants responded to videos morphing from a familiar face into their own earlier following stimulation, accepting as their own a face that contained more of the other's face than before stimulation. The authors found no effect of stimulation on videos in the other direction, suggesting that the effect is specific to self-face recognition, and not the recognition of faces in general.

1.8 Bodily Representations of Self Beyond the Body

Embodied accounts of social cognition propose that body representations play an important role in social cognitive processes (Gallese, Keysers, & Rizzolatti, 2004). Research has shown that the observation of others' bodies can elicit corresponding patterns of activation in parts of our own brains, thought to be part of the human mirror neuron system (Iacoboni et al., 1999), suggesting that representations of our own and others' bodies can overlap. Such accounts suggest that the perception of others' bodies in relation to our own plays an important role in social cognitive processes such as empathy and action understanding. Recently, research using paradigms of body illusions has demonstrated how changes in the perception of similarity between one's own and the bodies of an outgroup can affect perception and behaviour towards that group. Farmer, Maister, and Tsakiris (2014) recruited white participants and created the illusion of ownership over a dark-skinned rubber hand using the RHI. Following embodiment with the dark-skinned hand, Farmer et al. (2014) found a reduction in implicit racial bias. Peck, Seinfeld, Aglioti, and Slater (2013) found the same result when virtual reality was used to create the illusion of ownership over an entire dark-skinned body in white participants. Along similar lines, Banakou, Groten, and Slater (2013) used virtual reality to create a sense of ownership over a child-like body in adult participants. Ownership over the body caused participants to overestimate the size of objects (compared to a baseline condition in which embodiment did not occur), as well as cause participants to classify child-like attributes with themselves faster than adult-like attributes. These studies provide evidence that changes in the way the bodily self is perceived in relation to other groups can change perception and behaviour towards those groups.

Maister, Slater, Sanchez-Vives, and Tsakiris (2014) suggest that changes in the self-body representation are able to lead to changes in perception and behaviour of other groups through processes of self-association. Firstly, the illusory sense of ownership over the body part belonging to the out-group member creates an increase in perceived perceptual similarity between the self and the out-group. Secondly, the new perceived similarity between the self and the out-group leads to the conceptual representation of the self becoming associated with the conceptual representations of the out-group. Through this association, positive attitudes relating to the self are extended to members of the out-group, leading to a positive change in perception and behaviour towards members of that outgroup. This suggests that changes in the physical representation can have a modulatory effect on other aspects of self – i.e. changes to the bodily self-representation can change the conceptual representation of the self. The idea that changes to one aspect of the self can lead to corresponding changes in another aspect of self raises the question of whether the representation of the physical self can be altered in ways other than multisensory integration, for example, through changes to the way the self is conceptualised.

One study suggests that the physical representation of the self can be altered through means other than the integration of multisensory signals. Farmer, McKay, and Tsakiris (2013) ran an experiment in which participants played a trust-game with another individual, whose behaviour was either trustworthy or untrustworthy towards the participant. Before and after the trust game, participants completed a self-face recognition task in which they rated images created by morphing the other's face with their own face. Following trustworthy behaviour by the other, participants judged images containing a higher percentage of the other's face as looking more similar to themselves. This study highlights that it is possible to change the perception of one's physical features, and the degree of perceived physical similarity between the self and another person, without multisensory driven updating. However, the mechanisms by which this type of updating can occur are unclear.

1.9 Gaps in Research of Self-Face Recognition

Because of the critical importance of self-face recognition in self-awareness and social cognition, the neural correlates and cognitive mechanisms of self-identification, self-recognition and self-updating constitute an important topic requiring further empirical investigation. The wealth of neuroimaging literature has highlighted a large number of areas within the brain that show activation associated with self-recognition (e.g. Devue et al., 2007), and to a lesser extent, self-updating and self-identification (Apps et al., 2013; Bufalari, Porciello, Sperduti, & Minio-Paluello, 2014). While these neuroimaging studies are able to highlight correlations between self-face recognition processes and indirect measures of brain activity, providing insight into which areas of the brain are involved in self-face recognition, they cannot provide causal evidence for the role of these brain areas in self-face recognition. Presently, three studies have used TMS to investigate the causal role of the rTPJ in self-recognition (Heinisch et al., 2011; Heinisch, Krüger, & Brüne, 2012; Uddin et al., 2006). These studies found that the application of low-frequency TMS to this area altered discrimination of the self-face from a familiar other's face, suggesting that rTPJ is causally involved in maintaining a representation of the self-face (i.e. the process of *self-recognition*). To date, however, no studies have used non-invasive brain stimulation to investigate the role of any area of the brain in the processes of self-identification and self-updating. There is, therefore, a lack of causal evidence to implicate specific areas of the brain in the processes that underpin self-face recognition.

Apps et al.'s (2013) fMRI study of the Enfacement Illusion shed some light on which areas of the brain may be involved in the processing of self-identification and self-updating during multisensory integration. The authors found activity that varied parametrically with the reported strength of the Enfacement Illusion in IPS, as well as rTPJ and IOG. As IPS receives input from superior temporal sulci and the IOG – both implicated in face processing (Allison et al., 2000; Haxby et al., 2000; Barraclough & Perrett, 2011; Kanwisher & Barton, 2011), as well as vestibular and somatosensory input (Seltzer & Pandya, 1980, 1986; Lopez & Blanke, 2011), it may be involved in integrating multisensory information during the Enfacement Illusion, playing a critical role in producing the experience of identifying with the observed face. As such, IPS is a candidate for study with brain stimulation, as this could elucidate its involvement in self-identification and self-updating during multisensory integration.

Furthermore, before tactile stimulation can be integrated with visual information, touch on the skin is first mapped onto the body in the primary somatosensory area (S1). Activation of the body map in this area is critical for the accurate perception of touch on the body, and therefore plays an important role in the experience of multisensory stimulation during the Enfacement Illusion, in which tactile stimulation is experienced in synchrony with observed touch on another's face. Accurate mapping of touch on the body in S1 is therefore critically important in the processes of self-identification and self-updating, and the causal contribution of this area to these processes during the Enfacement Illusion warrants investigation.

Lastly, there is little research investigating whether the self-face representation can be updated by means other than multisensory integration. The specific mechanisms will be elucidated in later Chapters, but in summary, as discussed in the above section of this review, there is evidence to suggest that changes to the mental representation of one's body are able to modulate aspects of the conceptual self-representation (Maister et al., 2014). It is unclear, however, whether bidirectional modulatory links exist between conceptual and perceptual representations of self. In other words, can the mental representation of one's body be affected by changes to the conceptual self-representation?

1.10 Present Thesis

The present thesis aims to investigate the cognitive and neural mechanisms involved in the processes of self-face recognition. The way in which we perceive our own face and body is highly important for social-cognition, influencing the way in which we perceive and behave towards others (Maister et al., 2014). With this in mind, understanding the mechanisms that support the maintenance and updating of our mental self-face representation could provide important insight not only within the domain of self-recognition, but also for wider social-cognition. Considering this aim, the experiments in the following chapters can be split in to two sections:

Chapters 3, 4, 5, and 6 employ transcranial direct current stimulation (tDCS) to directly investigate the causal role of neural regions in the processes of *self-recognition*, *self-identification* and *self-updating.* A comprehensive discussion of the methodology of tDCS will follow in the next Chapter, but, in summary, tDCS is a form of non-invasive brain stimulation which can be used to modulate the excitability of neuronal populations, and is therefore a useful tool to investigate the involvement of specific areas of the brain in cognitive processes. While there is a vast amount of neuroimaging research providing insight into the neural correlates of these processes, there is little causal evidence to implicate specific brain areas in the individual processes of self-face recognition (i.e., self-identification, self-recognition and self-updating). In light of this, chapters 3 and 4 target the right temporoparietal area to further investigate its role in self-other discrimination and self-recognition. Specifically, Chapter 3 aims to follow closely the work of Heinisch et al. (2011, 2012) and Uddin et al. (2006), further expanding upon the understanding of the right temporoparietal area in self-recognition by investigating the effect of tDCS on this process. Chapter 4 investigates the hypothesis that the right temporoparietal area is important for the discrimination of self and other not only at the low-level of physical appearance (in *self-recognition*), but also for higher-level social cognition processes such as mental perspective taking. Chapters 5 and 6 use tDCS to explore the processes of *self-identification* and *self-updating.* Specifically, Chapter 5 explores the involvement of IPS in integrating multisensory signals during Enfacement, while Chapter 6 investigates the role of S1 in processing somatosensory input during the Enfacement Illusion.

The next section, comprising Chapters 7 and 8, explores the novel use of a self-association paradigm to update bodily and conceptual aspects of self, to investigate whether the self-face representation can be updated by means other than multisensory integration. Chapter 7 investigates whether associating a novel face with the self can update the self-face representation. Chapter 8 investigates the nature of the association created between the self-representation and the novel face in the self-association paradigm, by testing whether the newly associated face affects recognition of well-established perceptual and conceptual aspects of self.

2 Transcranial Direct Current Stimulation: Methodological Considerations

This Chapter will discuss the methodological considerations of using transcranial direct current stimulation (tDCS) to investigate human cognitive functions. TDCS is a noninvasive form of brain stimulation that delivers a low-intensity direct current to cortical areas of the brain between two electrodes placed on the scalp (in some cases, the second, 'reference' electrode is placed elsewhere, such as the neck or arm) (Paulus, 2003). Depending on the placement of the electrodes, the stimulation is considered to be 'anodal' or 'cathodal'. This simply refers to which electrode (i.e. the anode or the cathode) has been placed over the brain region of interest. TDCS has the potential to positively, or negatively modulate cortical excitability depending on the polarity of the stimulation delivered (Nitsche & Paulus, 2000a). Anodal tDCS generally increases excitability, while cathodal tDCS typically decreases excitability (Iyer et al., 2005; Nitsche & Paulus, 2000a). This type of stimulation can lead to sustained modulations in cortical excitability, with the duration of the after-effect being dependent on the intensity and duration of the stimulation period (Nitsche & Paulus, 2001). TDCS is considered to be a relatively safe method of modulating neuronal excitability of the cortex, and is associated with infrequently reported minor adverse effects such as a mild itching sensation, headache, and nausea (Poreisz, Boros, Antal, & Paulus, 2007).

2.1 Temporal Effects of tDCS

The duration of the modulation in cortical excitability induced by tDCS appears to be dependent upon the intensity and duration of the stimulation period (Nitsche & Paulus, 2000a; Shekhawat, Stinear, & Searchfield, 2013). Studies of the effect of tDCS over the primary motor cortex can elucidate the duration of the effect the stimulation has. Paradigms typically use TMS to elicit motor evoked potentials (MEPs) and record these from peripheral muscles as an indirect measure of motor cortex excitability. The MEPs elicited during (or following) tDCS can be compared with MEPs elicited before stimulation to explore the duration of the change in excitability due to tDCS. Very short periods of stimulation elicit changes in cortical excitability that are short-lived: 'intra-tDCS' effects that do not extend beyond the end of the stimulation (Nitsche & Paulus, 2000a). Four seconds of tDCS has been shown to elicit intra-tDCS changes in excitability of up to 30% relative to non-tDCS levels, a change that is generally smaller compared with the longer-lasting effects.

In animals, direct current applied directly to the cortex for as little as 5 minutes has been shown to modulate cortical excitability for hours following the end of the stimulation period (Bindman, Lippold, & Redfearn, 1964). In humans, changes in cortical excitability elicited by tDCS can also persist beyond the end of the stimulation period, with the duration of the after-effect being dependent on the intensity and duration of the stimulation period. TDCS of at least 0.3mA lasting at least three minutes appears to be necessary for changes in cortical excitability to persist beyond the end of the stimulation (Nitsche & Paulus, 2000a). Nitsche and Paulus (2000a) applied stimulation over the motor cortex for 5 minutes with either anodal or cathodal tDCS, and observed changes in excitability lasting up to 5 minutes following the end of the stimulation. Longer lasting effects have also been shown: nine minutes of cathodal tDCS at 1mA reduced MEPs for up to 60 minutes (Nitsche et al., 2003), and changes in cortical excitability following 13 minutes of tDCS at 1mA lasted up to 90 minutes following the end of the stimulation (Nitsche & Paulus, 2001).

2.2 Mechanisms of Action

In contrast with TMS, which induces action potentials during stimulation (Bolognini & Ro, 2010), the effects of tDCS are thought to be in part due to a modulation in the rate of spontaneous neuronal firing (Priori, Hallett, & Rothwell, 2009). The current densities produced by tDCS in the brain fall below the required amount for producing action potentials in cortical neurons (Wagner et al., 2007; Tehovnik, 1996), however, studies in animals show that even small changes in polarization (of the magnitude of those induced by tDCS) are able to change the rate of neuronal discharge (Bindman et al., 1964; Purpura & McMurtry, 1965). Anodal stimulation is thought to lead to a depolarization of the resting membrane potential, while cathodal stimulation causes hyperpolarization, supported by intracellular recordings in animals (Purpura & McMurtry, 1965). Studies on the effect of tDCS on the human motor system provide further evidence that tDCS affects resting membrane potentials. (Nitsche & Paulus, 2000a) targeted the human motor cortex with anodal and cathodal tDCS. They used TMS to elicit motor evoked potentials (MEPs), recording these from peripheral muscles as an indirect measure of motor cortex excitability. Nitsche and Paulus (2000a) found that anodal tDCS increased MEP size, while cathodal tDCS led to a decrease in the size of MEPs.

There is also evidence that the effects of tDCS act at a synaptic level. For example, research in rats which interrupted electrical activity by inducing hypothermia (stopping spontaneous neuronal firing), found that the after-effects of polarization were not eradicated (Gartside, 1968). This finding suggests that tDCS does not only affect spontaneous firing rates of neurons, but also has a lasting effect on synaptic strength. Nitsche et al. (2003) suggest that tDCS may affect synaptic strength through long-term potentiation (LTP) and long-term depression (LTD). LTP is a long term facilitation of neuronal excitability (Cooke & Bliss, 2006), which anodal tDCS may induce through increased pre-synaptic activity coupled with postsynaptic depolarization. LTD is a long lasting reduction in neuronal activity (Malenka & Bear, 2004), which cathodal tDCS may induce through a reduction in presynaptic discharge, and a hyperpolarization of the postsynaptic neuron (Nitsche et al., 2003).

In summary, the mechanisms of action of tDCS on cortical excitability changes are not completely clear, however, it appears to involve a combination of both modulations at the synaptic level, as well as hyperpolarization and depolarization of the resting membrane potential. It has been suggested that intra-tDCS effects reflect changes in the polarization of the resting membrane potential, which changes in excitability that persist beyond the end of the stimulation period rely on changes at the synaptic level (Arul-Anandam & Loo, 2009).

2.3 Safety Considerations

tDCS is considered to be a relatively safe method of modulating cortical excitability in humans when the safety guidelines are followed concerning current intensity, electrode size and duration of stimulation (Iyer et al., 2005; Nitsche & Paulus, 2000a, 2001; Nitsche et al., 2003). Nitsche et al. (2004) conducted an MRI study in which they scanned participants immediately, 30, and 60 minutes after they received 13 minutes of anodal or 7 minutes of cathodal (known to induce long lasting changes in cortical excitability) tDCS. The authors reported that the tDCS did not induce brain edema, structural alternations of brain tissue, or alterations of the blood brain barrier. Iyer et al. (2005) conducted a Phase 1 study investigating the safety of frontal tDCS. 103 participants received stimulation between 1 and 2 mA, and the study found no adverse effects of the stimulation on cognitive or psychomotor measures. A further study reviewing 567 cases of tDCS in healthy participants and patients. TDCS was associated with a number of different mild adverse effects including: a tingling sensation during stimulation (70.6%), feelings of fatigue (35.3%) and itching sensations underneath the electrode (30.4%), but no significant adverse effects of the stimulation were observed (Poreisz et al., 2007). Overall, tDCS appears to present a relative safe method of manipulating cortical excitability in humans when applied according to current tDCS safety guidelines.

2.4 Directionality of the Effects in the Motor and Cognitive Domains

As mentioned previously, the effects of tDCS on motor cortex excitability show a dichotomy between anodal and cathodal stimulation. Anodal tDCS causes an increase in excitability as measured by increased MEP size (thought to reflect neuronal depolarization), which cathodal tDCS results in a decrease in excitability and MEP size (thought to reflect hyperpolarization). This directional effect in the motor domain has been robustly reported, with a meta-analysis of human tDCS studies reporting that the majority of those investigating the effects of tDCS on MEPs reported the same anodal cathodal dichotomy (Jacobson, Koslowsky, & Lavidor, 2012). On the other hand, studies investigating the effect of tDCS on cognitive processes paint a different picture. While some studies in the cognitive domain have found clear effects of anodal and cathodal tDCS reflecting that of the motor domain (Fecteau et al. 2007; Sparing et al. 2009; Stone and Tesche 2009), more often than not, a significant effect of anodal tDCS is reported, without a significant effect of cathodal tDCS (Jacobson et al., 2012).

There are a number of interpretations of the lack of a clear anodal-facilitation / cathodal-inhibition effect in the cognitive domain. One explanation considers the noise that the measures generally used to assess cognitive processes introduce. Whereas measuring MEPs (as is typically done in studies of tDCS in the motor domain) involves the stimulated area only, cognitive processes are measured in a large range of ways. For example, one cognitive process may be measured with a variety of behavioral tasks including measures of RTs and accuracy. These different measures introduce noise into testing process. Another explanation for the lack of a clear cathodal effect on cognitive processes focuses on the fact that cognitive processes are more likely to be underpinned by a large network of brain areas. While increasing excitability in one of the regions involved in a cognitive process with anodal tDCS may facilitate processing throughout the whole network, cathodal stimulation over only one area may not have an inhibitory effect as other parts of the network are able to compensate for the decreased excitability in one area. The issues of directionality of the tDCS effect in the cognitive domain will be revisited in the following chapters when discussing the results of the experiments.

Despite the lack of a clear cathodal tDCS effect in the cognitive domain, evidence does suggest that targeting the regions that are thought to underpin cognitive processes can result in changes in performance, demonstrating that tDCS can be used as an effective tool for studying the neural basis of cognitive processing. In the next 4 Chapters of this thesis, tDCS will be used to investigate the neural mechanisms thought to support the processes of self-face recognition.

2.5 tDCS in Social Cognition

tDCS is becoming an ever more popular methodological tool to study social cognition, and can be used to highlight the causal involvement of cortical regions in specific cognitive functions. This section will provide a short discussion on how tDCS has been used previously to investigate social cognitive processes. Relevant to this thesis are studies on self-other processing and body representation. See Table 2.1 for a list of the most relevant tDCS studies. One area of particular interest both in the literature and this thesis is the temporoparietal area. A number of studies have used tDCS to investigate the role of the temporoparietal region in self-other processing. For example, Santiesteban, Banissy, Catmur, and Bird (2012) compared the effects of Anodal and Cathodal tDCS (relative to sham stimulation) over the rTPJ on two tasks requiring discrimination between self and other representations. Anodal tDCS over rTPJ enhanced performance on an imitation inhibition task – requiring the representation of the other to be inhibited, and a perspective taking task – requiring the representation of the other to be enhanced, relative to cathodal tDCS and sham stimulation. Conversely, there was no effect of tDCS on a control self-other attribution task that did not involve discrimination between the self and another. The results suggest that the rTPJ is involved in controlling co-activated representations of self and other. This finding is especially interesting when considering Apps et al.'s (2013) finding that the magnitude of TPJ activation during the Enfacement Illusion was negatively correlated with the subjective strength of the illusion, suggesting that as participants identify with the IMS face they begin to represent it as their own.

While Santiesteban et al. (2012) found a selective effect of anodal tDCS over rTPJ on imitation inhibition and perspective taking, others have also found an effect of cathodal tDCS on similar tasks. Mai et al. (2016) applied anodal, cathodal or sham stimulation over rTPJ, and investigated the effect on theory of mind (TOM) and cognitive empathy. Cathodal tDCS decreased the accuracy of TOM judgements about another's intention, and judgements about another's emotion (cognitive empathy). The authors found no effect of anodal stimulation on either task, which they suggest may be due to ceiling effects on the tasks limiting room for improvement following anodal tDCS. The findings suggest that inhibiting cortical excitability in may impair the ability to accurately represent another's mental state – in line with the suggestion that this area is involved in representing and self and others, and highlights that cathodal stimulation can also provide insight into cognitive functioning.

tDCS is also a valuable tool for investigating the lateralization of function. Santiesteban et al. (2015) again investigated the role of TPJ in visual perspective taking and imitation inhibition, with the addition of a theory of mind task. This time, the authors compared anodal tDCS of the right and left TPJ, as well as using an active control site (occipital cortex) not previously implicated in social cognitive processing. The addition of an active control site in which stimulation is applied to a region not thought to be involved in the tested process allows for stronger conclusions to be drawn about the localization of function, as it can be used to rule out a general effect of stimulation on the brain. Previously, neuroimaging research had provided inconsistent support for the lateralization the TPJ in these processes, showing activation of the rTPJ in imitation inhibition (Spengler, von Cramon, & Brass, 2009) and lTPJ in perspective taking (Schurz, Aichhorn, Martin, & Perner, 2013) exclusively,

Table 2.1: tDCS Studies of self-other processing and body-representation

Study	Areas Stimulated	Tasks	Results
Santiesteban et al. (2012)	Anodal rTPJ, Cathodal rTPJ, Sham	Visual Perspective Taking, Imitation Inhibition, Self-Referential (control task).	Anodal tDCS over rTPJ increased performance on the imitation inhibition task and the perspective taking task, relative to cathodal tDCS and sham stimulation. Conversely, there was no effect of either type of tDCS on a self-referential task that did not involve discrimination between the self and another.
Spitoni et al. (2013)	Anodal right angular gyrus, Cathodal right angular gyrus, Sham	Body Representation - Tactile Distance Detection	Anodal tDCS over the right angular gyrus (but not the left, or sham tDCS) improved the detection of tactile stimuli of different sizes on the contralateral limbs. Provides evidence that the right parietal lobe is selectively involved in body representation, and specifically a metric component of body processing that is used to process distances between tactile stimulation.
Hogeveen et al. (2014)	Anodal rTPJ, Anodal right inferior frontal cortex (IFC)	Social Interaction Task (requiring imitation), Imitation Inhibition, Non-imitative (control task).	Anodal tDCS over IFC improved performance on both imitative tasks, both increasing imitation during the social interaction task and decreasing imitation during the inhibition task. tDCS over rTPJ improved performance on the imitation inhibition task but did not change the amount of imitation during the social interaction task. The findings support the idea that the TPJ is involved indirectly in the control of imitation by controlling representations of self and other, while the IFC appears to modulate imitation directly based on task demands.
Santiesteban et al. (2015)	Anodal rTPJ, Anodal lTPJ, Anodal Occipital Cortex (active control)	Visual Perspective Taking, Imitation Inhibition, Theory of Mind.	Anodal stimulation of both left and right TPJ resulted in better performance in the perspective taking and imitation inhibition tasks compared with anodal tDCS of occipital cortex. Conversely, there was no effect of the stimulation on either site on performance in the theory of mind task.
Sellaro et al. (2015)	Anodal rTPJ, Cathodal rTPJ, Sham	Moral Judgement	Participants receiving anodal tDCS over rTPJ assigned less blame to individuals who caused harm accidentally harm, than participants who received cathodal tDCS to rTPJ or sham stimulation. rTPJ involved in belief attribution for performing moral judgements.
Sowden et al. (2015)	Anodal rTPJ, Anodal mid-occipital (MO; active control)	Lie-detection.	In an initial experiment, the author's found that participants were significantly better at judging whether the another individual was telling the truth (i.e. expressing their true opinion on a topic), when the opinion expressed by the individual was consistent with the participant's own opinion, rather than inconsistent. In the tDCS experiment, both groups (rTPJ and MO) were equally accurate when the expressed opinion was consistent with the participant's own opinion, however, when the expressed opinion was inconsistent with the participant's, those who received anodal tDCS over rTPJ were significantly more accurate than those who received anodal tDCS over MO.
Mai et al. (2016)	Anodal rTPJ, Cathodal rTPJ, Sham	Theory of Mind, Cognitive Empathy.	Cathodal tDCS over rTPJ reduced the accuracy of theory of mind judgments and attribution of emotional states relative to anodal and sham stimulation. There was no effect of anodal tDCS.

and bilateral activation of TPJ in theory of mind (e.g. Jenkins & Mitchell, 2010). The results showed that anodal stimulation of both the left and right TPJ enhanced performance on the imitation inhibition and perspective taking tasks, suggesting bilateral involvement of the TPJ in these processes. Neither left or right tDCS affected performance on the theory of mind task. These findings highlight the use of tDCS not only in investigating lateralization of function, but also as a complimentary tool for expanding upon the findings of neuroimaging research. As discussed in Chapter 1, this thesis aims to expand upon neuroimaging research by Apps et al. (2013) to investigate the neural underpinnings of self-face recognition, which highlighted the involvement of not only TPJ but also IPS in the processes of self-identification and self-updating.

Much of the tDCS research that is most relevant to the current thesis has focused on self-other discrimination processes and the TPJ. This thesis aims to expand upon this with a focus on the bodily self and recognition of the self-face. The following two experimental chapters use tDCS to explore the role of TPJ in self-other face discrimination and mental body representation. Furthermore, this thesis will use tDCS to investigate the processes of self-identification and self-updating, which have not yet benefitted from tDCS research. Neuroimaging research as highlighted the involvement of IPS in multisensory integration during the Enfacement Illusion, and the somatosensory cortex (S1) during the perception of touch to the self and others. Chapters 5 and 6 will use tDCS to explore the involvement of these two areas in self-identification and self-updating.

3 The role of the right temporoparietal area in self-recognition

3.1 Introduction

[1]The ability to discriminate self from others is crucial for both self-awareness and social cognition. The process of self-recognition, as described in Chapter 1 as the ability to maintain an updated mental representation of the self-face, relies on the ability to distinguish between what is self, and what is not self. Chapter 1 of this thesis reviewed the literature on the neural underpinnings of self-other discrimination and described a widely distributed set of neural regions able to discriminate between images of the self-face and other faces (e.g. Devue et al., 2007). Despite the wealth of neuroimaging studies exploring the correlates of self-recognition, there has been little research providing causal evidence for the involvement of specific brain areas in self-recognition.

Three studies to date have investigated self-recognition with noninvasive brain stimulation. One study investigated the role of the inferior parietal lobule (IPL; Uddin et al., 2006), while the other two specifically targeted the temporoparietal junction (encompassed in the IPL) (Heinisch et al., 2011, 2012). Uddin et al. (2006) used low-frequency repetitive transcranial magnetic stimulation (rTMS) to investigate the involvement of right and left IPL in self-other face discrimination. rTMS is often used to impair typical functioning in a cortical area to provide causal evidence of its involvement in a cognitive function. If

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[1] This experiment has been published as Payne, S., & Tsakiris, M. (2016). Anodal transcranial direct current stimulation of right temporoparietal area inhibits self-recognition. *Cognitive, Affective, & Behavioral Neuroscience,* 1-8.

performance in a task is disrupted following stimulation, it supports an active role of the targeted area in the tested process. Uddin et al. (2006) presented participants with a face-recognition task before and after 20 minutes of rTMS. During the task, participants were presented with static images of faces (created by morphing the participant's own face with that of a highly familiar individual – resulting in six images along the morphing spectrum, with varying degrees of self-face visible: 0%, 20%, 40%, 60%, 80%) and were required to indicate whether the face looked more like their own face, or the familiar person's face. Following the application of rTMS to rIPL (but not lIPL), Uddin et al. (2006) reported a disruption in the participants' ability to discriminate their own and the other's face. Following stimulation, participants were more likely to identify morphed face images containing 60% of the other's face, and only 40% of their own face, as their own face, than preceding stimulation. In other words, more of the self-other morphed images were recognised as 'self' following stimulation. In line with this, Heinisch et al. (2011, 2012) found concurrent results after applying low-frequency rTMS over rTPJ between two morphing-video self-recognition tasks. Participants watched videos that morphed from their own face to a familiar face (self-to-other), or a familiar face into their own face (other-to-self), and pressed a button to indicate when they noticed a change in identity of the face. Over two experiments, Heinisch et al. (2011, 2012) showed that following stimulation of rTPJ participants again identified more of the self-other morph as resembling themselves than before stimulation. This was apparent in both self-to-other and other-to-self directions of morphing video. In other words, when the video morphed from self to other, participants indicated that the face started to look more like the other at a later point, when more of the other's features had become visible. In the other-to-self direction, participants indicated that the face started to look more like themselves at an earlier point, when more of the other's features were still visible. Taken together, these findings indicate that disruption of normal brain activity in the right temporoparietal area alters self-other discrimination by facilitating self-face recognition, as participants recognise more of a self-other morphing spectrum (be it static morphed images, or morphing videos) as representing their own face (See Figure 3.1).

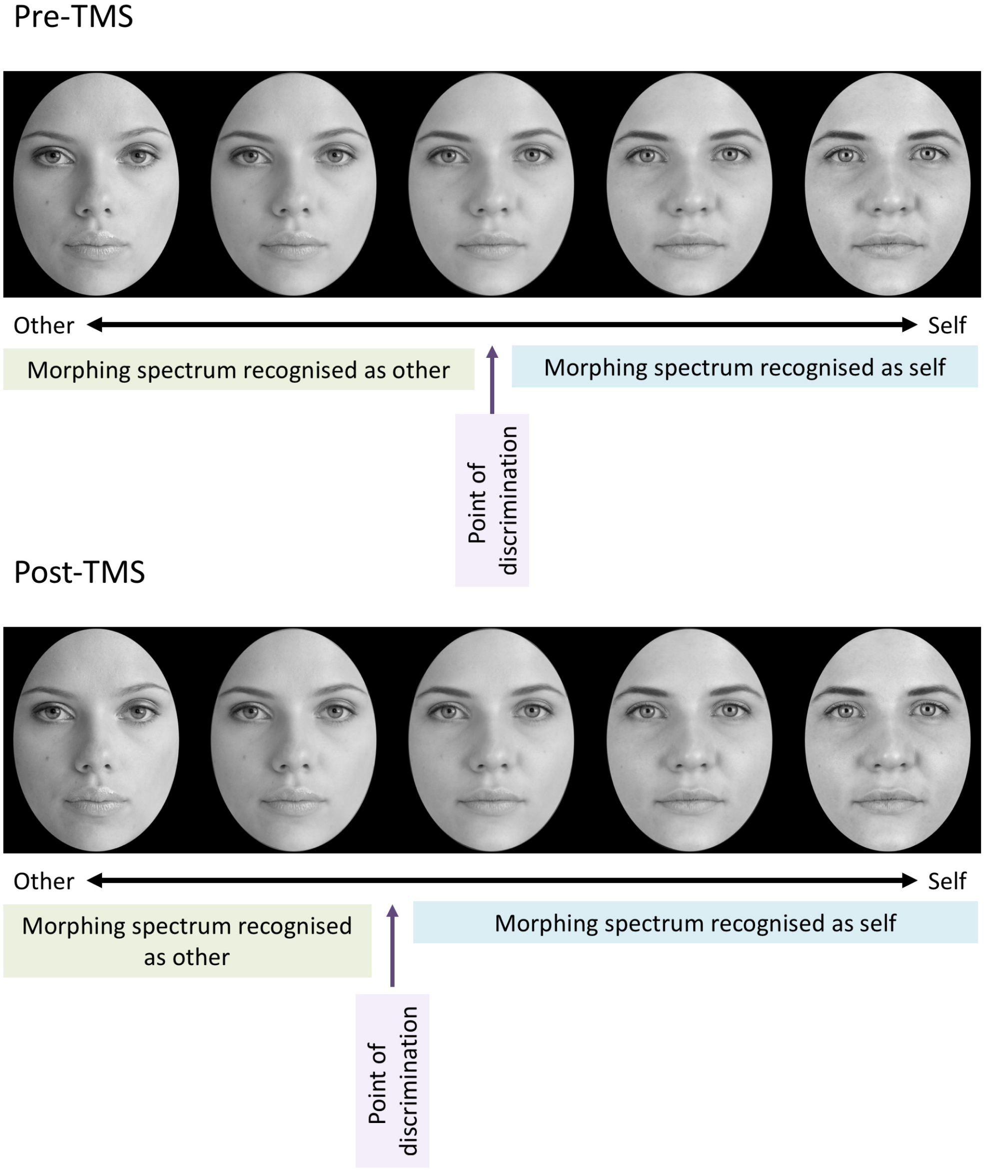

Figure 3.1: The point of discrimination on the self-other morphing spectrum before and after TMS to the right TPJ. Following TMS, participants discriminated between self and other at a point where less of the self-face was actually visible, resulting in more of the spectrum being recognized at 'self'.

The temporoparietal area has also been extensively implicated in wider self-body processing (Blanke, 2012). Lesions to the temporoparietal areas are often reported in patients suffering from body identification disorders such as asomatognosia and somatoparaphrenia, in which patients lose awareness of a body-part, or attribute ownership of their body-part to another person (Feinberg, Venneri, Simone, Fan, & Northoff, 2010). Furthermore, out-of-body experiences, in which patients experience their body as being located away from its true location, have been associated with processing in temporoparietal areas (Blanke & Arzy, 2005). Accordingly, direct cortical stimulation over the right angular gyrus has been shown to disrupt accurate processing of one's body by inducing out-of-body illusory experiences (Blanke, Ortigue, Landis, & Seeck, 2002). The temporoparietal area has also been implicated in higher-level social cognitive processes such theory of mind, engaged during the classic Sally-Anne theory of mind task (Baron-Cohen, Leslie, & Frith, 1985), explicit and implicit mentalizing (Frith & Frith, 2003), and visual perspective taking (Aichhorn, Perner, Kronbichler, Staffen, & Ladurner, 2006; Keysar, Barr, Balin, & Brauner, 2000; Ramsey, Hansen, Apperly, & Samson, 2013; Shibata & Inui, 2011). Because of the wide-ranging involvement of TPJ in body-related processing as well as social-cognition, there is growing support for the idea that self-other discrimination is not only a prerequisite for complex social cognitive processes to develop, but that the low-level computational mechanisms that discriminate signals arising from the self from signals arising from the environment may be crucial to higher-level social cognitive processes (Decety & Lamm, 2007).

Decety and Lamm (2007) have proposed that higher-level forms of social cognition such as theory of mind, in which one must simultaneously represent and discriminate between one's own perspective and someone else's perspective, may rely on the same mechanisms that allow for the discrimination of self and other at a lower-level in social cognitive processing, such as the discrimination of the self-face from the faces of others. .They also speculate that the rTPJ may underpin this mechanism. In support of this, Santiesteban et al. (2012) found that increasing neuronal excitability in rTPJ led to enhanced performance on two social cognitive perspective taking tasks. However, to date there is no research that has investigated how lower-level forms of self-other discrimination are affected when cortical excitability is increased in the right temporoparietal area. Research addressing this question will not only contribute to our understanding of this area's involvement in low-level self-other discrimination, but also has the potential to provide insight into how low-level mechanisms may contribute to meta-cognition.

Experiment 1 aimed to investigate the role of the right temporoparietal area in lower-level self-other discrimination by targeting this region with anodal tDCS. An established face morphing task (Heinisch et al., 2011, 2012; Tajadura-Jiménez, Grehl, & Tsakiris, 2012; Keenan, Freund, Hamilton, Ganis, & Pascual-Leone, 2000) was adapted to investigate the extent to which anodal stimulation over the right temporoparietal area would affect the ability to discriminate self from other. Participants watched videos of their face morphing into the face of a familiar other, and a familiar face morphing into their own face (before and after 20 minutes of tDCS) and responded when they detected a change in identity of the face in the video. The pre-tDCS block of videos acted as a baseline measure of self-other discrimination, and changes in performance from pre-tDCS to post-tDCS were compared. Based on the results of Uddin et al. (2006) and Heinisch et al. (2011, 2012), which showed that impaired functioning of rTPJ facilitated self-recognition by reducing the amount of self-face required to discriminate between self and other, it was hypothesised that an increase in cortical excitability in this area would have the opposite effect: anodal tDCS over the right temporoparietal area would cause an inhibition of self-recognition, by requiring more of the self-face to be visible to discriminate between self and other.

3.2 Materials and Methods

3.2.1 Participants

Sixty (44 female, mean age 21.54 years) participants volunteered to take part in the study and were reimbursed for their time. All participants were screened for possible contraindications to tDCS, and provided signed and informed consent for their participation. Once recruited, participants were randomly assigned to the anodal (n = 20, 15 female), cathodal (n = 20, 15 female), or sham (n = 20, 14 female) stimulation group. We chose this number of participants per condition based on the reported N size in recent, similar tDCS studies (see Enticott et al., 2012; Santiesteban et al., 2012). All participants were naïve to the purpose of the study and were unaware of the type of stimulation they received until after the experiment. The study was approved by the Royal Holloway, University of London Ethics Committee.

3.2.2 Design

The study was a double-blind, sham-controlled, mixed design, with a within subjects factors of Timing of the Video Morphing Task (Pre vs. Post-stimulation), and a between groups factor of tDCS Group (anodal vs. cathodal vs. sham). We chose a between-groups design to avoid learning effects on the Video Morphing Task across several sessions of stimulation. Participants took part in one experimental session in which they completed two blocks of the Video Morphing Task, separated by 20 minutes of tDCS.

3.2.3 Stimuli and Tasks

3.2.3.1 Self-Recognition Video Morphing Task

The study used a modified version of Keenan, Freund, et al.'s (2000) video morphing task (see also Heinisch et al., 2011, 2012; Tajadura-Jiménez, Grehl, & Tsakiris, 2012). First, a photograph was taken of each participant's face with a neutral expression. Participants with glasses or facial hair did not take part in order to control variation in the morphing videos. All photographs were converted to greyscale, flipped horizontally so as to reflect the orientation of the self-face that participants would be most accustomed with (from mirror exposure), and a template was applied around the face to remove hair and non-facial features. All photo manipulation was completed using Adobe Photoshop

CS6. Every participant was then paired with a familiar, gender- and skin-tone-matched, famous individual (following the procedure of Heinisch et al., 2011, 2012, participants indicated the name of a famous individual with whom they were highly familiar), and the same procedure was applied to a photograph of the famous face. Famous faces were used following the finding that rTMS over rTPJ only affects discrimination of the self from familiar, but not unfamiliar faces (Heinisch et al., 2012). The face morphing software Abrasoft Fantamorph (www.fantamorph.com) was used to create a morphing continuum between the two faces, and 100 images representing 1% steps of morphing between the two faces were exported. Adobe Premier Pro was used to convert the image series into two directions of video (self-to-other and other-to-self), with three durations (10, 15 and 20 seconds), resulting in six videos for each participant. The three durations, and two directions of video were created in order to make the videos less predictable, and required participants to make a conscious choice regarding when the face in the video started to look more like the individual it was morphing into, rather than responding at the same temporal point in each video.

During the Experiment, each of the six videos was presented five times per block in a randomised order, resulting in 30 trials per block. Before each video a fixation cross was presented on screen for 1-2.5sec. The video was then presented, and participants watched the video and made their response. Participants were told to respond with a button press as soon as they detected a change in the identity of the face in the video, such that, when the video morphed from self to other, participants responded when the face started to look more like the familiar other, and when the video morphed from other to self, participants responded when the face started to look more like their own (see Figure 3.2). All participants responded with their right index finger. The pre-stimulation video morphing trials provided a baseline measure of the 'point of discrimination' between self and other, and we compared performance in the post-tDCS block with baseline performance to investigate the effect of tDCS on self-other discrimination.

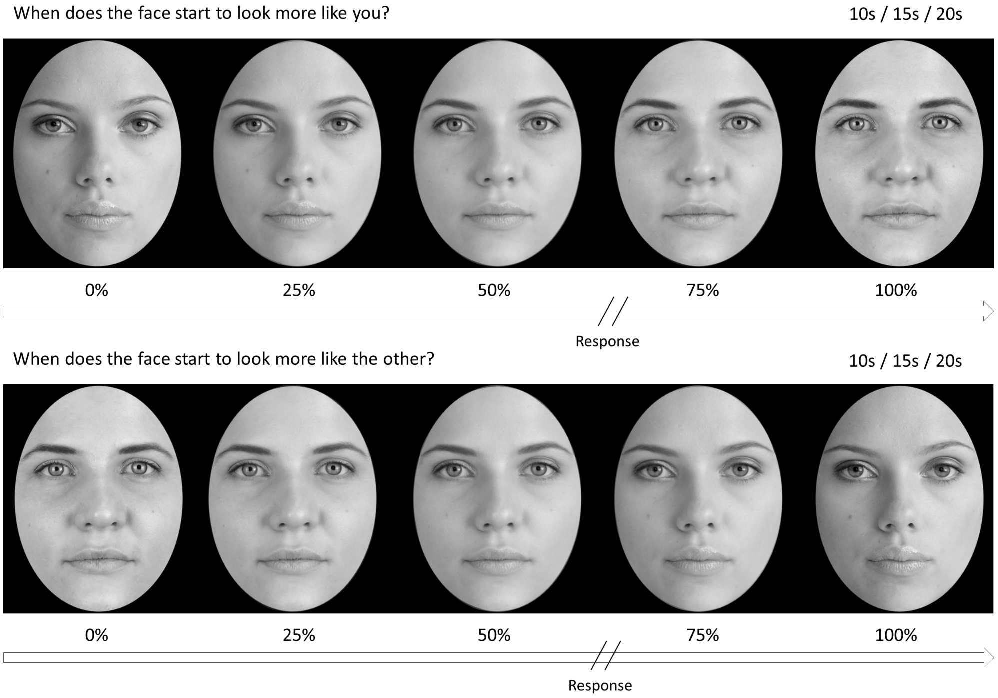

FIGURE 3.2: An example of the two directions of morphing video used in the experiment. Videos were 10, 15 or 20 seconds in length, and morphed either from a familiar face into the participant's own face, or from the participant's face to a familiar face.

3.2.4 tDCS Parameters

Participants were stimulated with either the anode or cathode electrode placed over the right temporoparietal area (electrode position CP6: electroencephalography (EEG) 10/20 system; Herwig, Satrapi, & Schönfeldt-Lecuona, 2003) and the reference electrode over the Vertex (measured individually for each participant). Stimulation was delivered via two 3.5 electrodes, placed within saline-soaked sponges, for 20 minutes at the intensity of 1mA (30 seconds ramp up, 20 seconds ramp down). The set-up for the sham stimulation was identical, with the anode electrode position counterbalanced across participants, except that the stimulator was only switched on for the first 15 seconds of stimulation. Participants were asked following the experiment if they were aware of the type of stimulation they received, with the majority being unaware. The electrode montage and tDCS parameters were identical to those used previously to successfully modulate cortical excitability of rTPJ (Santiesteban et al., 2012).

Table 3.1: Experiment 1 Demographic Data by tDCS Group

	Demographic Data					
	Age	Gender		Handedness		
	M (SD)	Female	Male	Right	Left	Ambidextrous
Anodal	19.6 (1.23)	15	5	18	2	-
Cathodal	22.25 (5.97)	14	6	20	-	-
Sham	22.45 (4.41)	12	5	14	2	1

3.2.5 Data Analysis

Preceding analysis, the raw RT data were converted into % of self-face present in the morphing video at the point at which participants judged a change in identity. As past research has shown that brain stimulation (i.e. TMS) affected self-other discrimination ability independently of the direction of morphing video (self-to-other vs. other-to-self; Heinisch et al., 2011, 2012), and because the experiment was not interested in the directions themselves but rather in the amount of the self-face required to discriminate between the two faces, the data were averaged across direction of video to create a point of discrimination before and after tDCS, reflecting the amount of self-face needed to discriminate between the self and another's face [2]. Following this, data were cleaned by identifying participants with responses outside 2 SD +/- *M* response. Three participants were excluded from analysis, leaving a total of 57 data points for analysis. See Table 3.1 for demographic data.

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[2] Analysis including the factor of Direction of Morphing was conducted, to ensure that tDCS Group did not interact with self-other discrimination depending on the direction of the video. While there was a main effect of Direction of Morphing: $F(1, 54) = 309.49$, $p < .001$, $\eta^2 = .851$, this was expected based upon the amount of each face required to recognise each identity. Direction of Morphing did not interact with tDCS Group: Direction of Morphing * tDCS Group: $F(2, 54) = 2.07$, $p = .14$, $\eta^2 = .071$, Direction of Morphing * tDCS Group * Timing: $F(2, 54) = .58$, $p = .57$, $\eta^2 = .021$. There was a significant interaction between Timing and tDCS Group: $F(2, 54) = 5.18$, $p = .009$, $\eta^2 = .161$, for which further analysis would collapse across Direction of Morphing. Therefore, the main analysis presented in this Chapter collapses across Direction of Morphing.

3.3 Results

Before conducting analysis on the experimental tasks, independent t-tests were used to check whether the tDCS groups differed significantly on age. The t-tests revealed no significant differences between any of the groups: anodal and cathodal, $t(38) = 1.943$, $p = .059$; anodal and sham, $t(35) = 1.989$, $p = .056$; cathodal and sham, $t(35) = .418$, $p = .69$.

Pre-tDCS and post-tDCS self-other discrimination performance was entered into a repeated measures ANOVA with tDCS group as a between subjects factor and Timing of Task (Pre- vs. Post-tDCS) as a within subjects factor. There was no significant effect of Timing of Task, $F(1, 54) = 2.337$, $p = .132$, $\eta^2 = .041$, or tDCS Group, $F(2, 54) = .692$, $p = .505$, $\eta^2 = .025$. However, the interaction between Timing of Task and tDCS group was significant, $F(2, 54) = 5.178$, $p = .009$, $\eta^2 = .161$. Paired-samples t-tests split by tDCS Group, with Bonferroni correction applied for multiple comparisons, highlighted a significant increase in the percent of self-face present at the point of discrimination following anodal tDCS: $t(19) = -3.896$, $p = .001$ (Pre-tDCS $M = 50.46$, Post-tDCS $M = 52.88$). There was a slight increase following cathodal stimulation, and a slight decrease following sham stimulation, however, neither or these differences approached significance. Cathodal: $t(19) = -.414$, $p = .683$ (Pre-tDCS $M = 50.11$, Post-tDCS $M = 50.42$); sham: $t(16) = 1.064$, $p = .303$ (Pre-tDCS $M = 50.36$, Post-tDCS $M = 49.54$). See Figure 3.3.

3.4 Discussion

Previous research has investigated the effect of low-frequency rTMS over rTPJ on self-other discrimination. Experiment 1 sought to expand the understanding of the role of the right temporoparietal area in this process by observing the effects of excitatory anodal tDCS over this region on a self-other face discrimination task. Participants watched videos that morphed between their own and a familiar other's face, and responded when they judged a change in identity of the face. The amount of the participant's own face in the video at

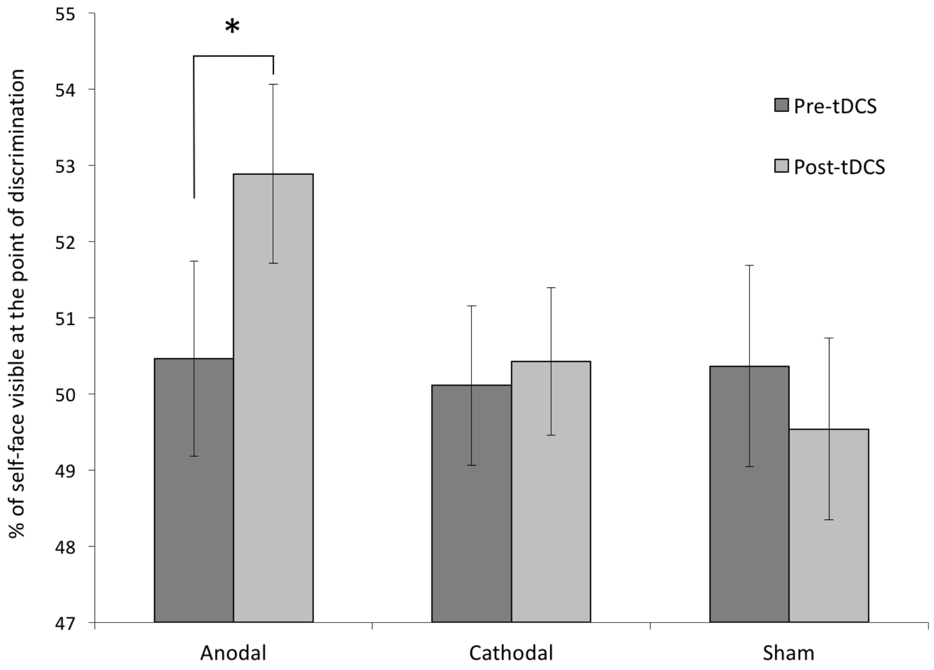

FIGURE 3.3: Mean % of self-face visible at the point of discrimination before and after tDCS. Error bars represent SE.

the point of response was used to reflect the 'point of discrimination' between the participant and the familiar other. Participants performed this task before (baseline) and after a 20 minute session of tDCS in which they received anodal, cathodal, or sham stimulation targeted over the right temporoparietal area. Following anodal stimulation, but not cathodal or sham, there was a change in the participants' ability to discriminate between self and other. Specifically, following stimulation participants required more of their own face to be visible in order to discriminate between self and other. In effect, self-recognition was inhibited as participants recognised fewer frames of the morphing video as resembling themselves.

Three previous studies have applied repetitive TMS over rTPJ to investigate this area's functional role in self-other discrimination. Following rTMS, participants were more likely to judge images containing 60% of the other and only 40% of the self as 'self' (Uddin et al., 2006), and judged a change in identity in videos morphing between the self and the other at a point that contained more of the other's face than before stimulation (Heinisch et al., 2011, 2012).

In essence, there was a facilitation of self-recognition, as more frames of the morphing video were recognised as self (rather than other) following rTMS to rTPJ (Uddin et al., 2006; Heinisch et al., 2011, 2012). The finding that self-recognition is facilitated when activity in rTPJ is disrupted with rTMS, and inhibited when neural excitability in the right temporoparietal area is enhanced with tDCS as the results of Experiment 1 suggest, may seem surprising when considering the right hemisphere's involvement in self-recognition. However, these results are in line with the idea that the right temporoparietal area is involved in a mechanism which distinguishes between representations of self and other, underpinning higher-level social cognition (Bird & Viding, 2014; Decety & Lamm, 2007), as explained below.

In recent years, the neural underpinnings of self-other discrimination have been extensively investigated as part of the larger social neuroscience programme. In particular, the study of self-other distinction was extended from the field of self-awareness to that of social cognition as it became clear that the process whereby the self is represented as distinct from others is a prerequisite for fundamental social cognitive processes, such as empathy (Bird & Viding, 2014; Decety & Lamm, 2007). Neuroimaging evidence highlights an overlap between regions within the right temporoparietal area involved in performing high-level social cognitive tasks, including theory of mind (Frith & Frith, 2006), empathy (Jackson, Brunet, Meltzoff, & Decety, 2006) and perspective taking (Aichhorn et al., 2006), with those involved in lower-level self-other processing (Decety & Lamm, 2007). This has led to the suggestion that a domain general computational mechanism associated with low-level agency processing (comparing signals arising from the self with externally produced signals) may support higher-level social cognitive processes (Decety & Lamm, 2007). Such a mechanism would allow an individual to distinguish between their own and another's perspective, thus supporting processes such as empathy and theory of mind. For example, the outcome of a low-level agency judgement, i.e. whether or not an observed action is attributed to the self or another, could be applied in a more abstract sense to attribute a mental state to either the self or another (see Brass, Ruby, & Spengler, 2009). In a similar vein, this mechanism could also extend to the sharing and understanding of other's emotional states. In Bird and Viding's (2014) Self to Other model of empathy, a crucial step in empathizing is the 'Self-Other Switch': an active process in which the empathizer switches from focusing on the signals arising from the self, to focusing on the state of the target individual. This idea is consistent with evolutionary views that higher-order processes operate on the framework of preceding levels of processing (see also Decety & Lamm, 2007). Bird and Viding speculate that the location of such a mechanism may be TPJ, due to its involvement in the control of self and other representations. If higher order social cognition relies, at least in part, on the same basic computational mechanisms as low-level discriminatory processes, the active role of rTPJ in this process may be to inhibit representation of the self, in order to enhance representation and recognition of another.

This is in line with the idea that the default state of the cognitive representational system appears to be 'self', while switching to a state in which representation of another is enhanced is an active process (Bird & Viding, 2014; Gusnard, Akbudak, Shulman, & Raichle, 2001). Research suggests that the state of the self often influences judgements about others – an 'egocentricity bias' - whether these be judgements about another's beliefs (Nickerson, 1999), affective state (Silani, Lamm, Ruff, & Singer, 2013), or visual perspective (Surtees & Apperly, 2012). In order to accurately represent the state of another, online representations of the self must be inhibited. Santiesteban et al. (2012) demonstrated that anodal tDCS over rTPJ reduced the extent to which the participant's own perspective interfered with taking the incongruent visual perspective of another person. In essence, the participant's own perspective was inhibited, while the perspective of the other was enhanced. This finding may reflect the facilitation of such a representational switching mechanism. The results of Experiment 1 may reflect the operation of this same mechanism at a lower-level, resulting in enhanced recognition of a familiar other's face, while inhibiting recognition of the self, lending weight to the idea that low-level computational mechanisms may support higher-level meta-cognition.

While it may have been expected to observe in the cathodal group the opposite effect to the anodal group, the lack of an effect from cathodal stimulation is not entirely surprising. In a recent meta-analysis of tDCS studies, Jacobson et al. (2012) report that, while in the motor-domain the majority of anodal stimulation leads to a facilitation, and cathodal stimulation leads to an inhibition, cathodal stimulation in the cognitive domain is unlikely to result in a decrease of function in cognitive processing. This has been attributed to compensatory processes in the complex neuro-networks involved in cognitive processes. In line with this, we did not find any differences in self-other discrimination following cathodal stimulation of the temporoparietal area, but observed a selective effect of anodal stimulation.

The stimulation site in Experiment 1 was localised using the EEG 10/20 system. While the preferable approach would be to use fMRI-guided neuronavigation to individually target the right temporoparietal area for each participant, localisation with the EEG 10/20 system is considered acceptable with this type of stimulation (Herwig et al., 2003). Future studies should also consider including an active control stimulation site, such as the left temporoparietal area, to ensure that any effect of stimulation is site specific. However, while this approach is considered acceptable to localise the stimulation site, it is important to note that it is unlikely that modulation of only neural activity in the right temporoparietal area was affected by the tDCS in the current experiment. Datta et al. (2009) has shown that tDCS delivered by rectangular sponge electrodes (such as those used in the current experiment) result in diffuse modulation of neural activity that is not specific to the site targeted. Future research employing a ring electrode configuration, shown to provide superior spatial focality, would provide valuable insight into the specificity of the effect observed in the current experiment to the modulation of neural activity in right temporoparietal junction.

There is also a possibility that the effect observed in the current experiment was influenced by uncontrolled variables such as baseline neural excitability. A between-groups design was chosen to avoid practice effects on the video morphing task across several sessions, however, this introduces the possibility the effect that is observed post-stimulation could be due to differences in baseline neurological features between the three stimulation groups. While the current experiment attempted to control for differences between the groups on baseline self-other discrimination ability with the pre-tDCS video morphing task, the effect of tDCS on modulating neuronal excitability may have varied between the groups, despite the random allocation of participants to tDCS groups. However, it is unlikely that the baseline neural excitability of the individuals in the anodal group was consistently different from those in the other two group.

To conclude, the results of Experiment 1 suggest that anodal tDCS over the right temporoparietal region affects self-other face discrimination by inhibiting recognition of the self while facilitating recognition of a familiar other. The results of Experiment 1 supports previous research indicating a functional involvement of the right temporoparietal area in self-other discrimination, and provides insights into the active role of this region in this process. It is speculated that the right temporoparietal area may support higher-order social cognitive processes including mentalising and empathy, and Experiment 1 suggests that this region may support these processes by enhancing the representation of others, and inhibiting the representation of the self.

4 The right temporoparietal area: beyond self-face recognition

4.1 Introduction

Experiment 1 found that anodal tDCS over the right temporoparietal area facilitated recognition of a familiar face, over recognition of one's own face. Participants recognised more frames of a video morphing between their own face and a familiar other's face as representing the other person's face following anodal stimulation of right temporoparietal area. This was suggested to reflect interference with a mechanism that distinguishes between representations of the self-face and the faces of others, biasing perception of self-other morphed face stimuli towards recognition of the other. Chapter 4 describes an initial exploratory experiment investigating whether tDCS over the right temporoparietal area affects discrimination between one's own bodily perspective and the perspective of another person.

The ability to imagine ourselves in another person's spatial location with a corresponding altered perspective is one that we use often in everyday life. For example, when giving directions you may imagine yourself in the other person's location and describe the necessary steps to take from their point of view. This process requires an imagined transformation of one's egocentric perspective, and an adoption of a disembodied self-location. This ability to take another's spatial perspective, while simultaneously distinguishing it from our own, may contribute to conceptually similar, higher level social cognitive processes such as theory of mind and empathy (Decety & Lamm, 2007), and so understanding the neural structures that support this process could have wider implications for our understanding of social cognition processes.

Research into mental body transformations (MBT) typically presents participants with line drawings of human bodies, of which they are required to make left-right judgements about a particular body part (Parsons, 1987). Reaction times are generally longer for figures presented facing the participant (or inverted), than figures facing away from the participant (or upright), reflecting the longer time required to imagine oneself in a position which is far removed from one's actual position in space (Blanke et al., 2005; Parsons, 1987; Zacks, Rypma, Gabrieli, Tversky, & Glover, 1999). Neuropsychological evidence suggests that the temporoparietal junction (TPJ) supports imagined changes in egocentric perspective and position. Functional magnetic resonance imaging (fMRI: Zacks, Ollinger, Sheridan, & Tversky, 2002; Zacks et al., 1999) magnetoencephalography (MEG: Wang, Callaghan, Gooding-Williams, McAllister, & Kessler, 2016), and electroencephalogram (EEG: Arzy, Thut, Mohr, Michel, & Blanke, 2006; Blanke & Arzy, 2005) studies all highlight the involvement of TPJ during the performance of MBTs. While there is no clear lateralisation of this task-related activity, with reports of both left and right temporoparietal activation in response to egocentric perspective transformations, two studies have provided causal evidence for the involvement of rTPJ by showing that the application of single- and double-pulse TMS over rTPJ impairs MBTs (Wang et al., 2016; Blanke & Arzy, 2005). However, no study to date has directly compared, using brain stimulation methods, the specific involvement of left and right TPJ in egocentric perspective transformations.

As well as a lack of clear lateralisation of TPJ in MBT, there is little research investigating whether the identity of the figure which the transformation is aimed towards affects MBTs. The stimuli used in earlier MBT studies were typically not photographs of real individuals, and were cartoonish in nature, often presented in unrealistic positions such as upside down. Given the well reported involvement of rTPJ in self-other discrimination as well as MBT (Heinisch et al., 2011, 2012; Uddin et al., 2006), it seems prudent to investigate whether egocentric transformations of one's body differ depending on whether the target of those transformations is the self, or another individual. One study that the author knows of has investigated MBT towards images of one's own body in contrast to images of another's body. Ganesh, van Schie, Cross, de Lange, and Wigboldus (2015) found that egocentric MBTs towards the self recruited higher activation of bilateral TPJ compared with egocentric MBTs towards a stranger (when self-related awkwardness was taken into account), suggesting that the TPJ may discriminate between self and other during the performance of MBTs. However, no reaction time data was collected for body transformations towards either identity, so it is unclear whether MBTs towards the self and others differ behaviourally.

Experiment 2 investigates the causal involvement of right and left temporoparietal area in MBT performance using tDCS. Previously, stimulation of rTPJ with anodal tDCS has led to enhanced performance on two social cognitive tasks involving the control of imitation and perspective taking (Hogeveen et al., 2014; Santiesteban et al., 2012), leading to the suggestion that this region is involved in the control of self and other representations. Subsequently, Santiesteban et al. (2015) used tDCS to investigate the lateralisation of self-other control and found that anodal tDCS over both the left and right TPJ improved performance on the same imitation inhibition and perspective taking tasks, suggesting bilateral involvement of TPJ in these social cognitive abilities. Anodal tDCS over rTPJ has also led to improved performance on a lie-detection task (Sowden et al., 2015), and increased the use of belief information in moral judgements of others' actions (Sellaro et al., 2015), suggesting that rTPJ is also involved in processing others' beliefs and intentions. These studies highlight the potential of tDCS as a methodological tool for investigating social functioning. To date, no study has applied tDCS to investigate egocentric perspective transformations in a mental body transformation task.

The aims of the current experiment are threefold: firstly, Experiment 2 will investigate whether MBTs performed towards one's own body differ from transformations towards the body of a gender-matched other. Secondly, Experiment 2 aims to disambiguate the involvement of the left temporoparietal area and the right temporoparietal area in MBT. To the author's knowledge, no study has yet compared directly the effect of excitatory stimulation of right and left temporoparietal areas on MBT. Finally, Experiment 2 will investigate the potential interaction between tDCS and identity of the transformed perspective. Previously reported stimulation of rTPJ with TMS has impaired not only MBT (Wang et al., 2016; Blanke & Arzy, 2005), but has also affected self-other discrimination processes (Heinisch et al., 2011, 2012; Uddin et al., 2006). Therefore, the modulation of right temporoparietal area cortical excitability may have an important interaction effect on MBT, affecting transformations towards one's own body differently than transformations towards another's body. To answer these questions, Experiment 2 will measure the effect of tDCS across two tasks (MBT task and a control 'Lateralisation' task). In both tasks participants will be presented with photos of their own body, and a friend's body (to control for familiarity), facing towards or away from the camera. Participants will judge the lateralisation of a gloved hand, either from the perspective of the person on the screen: by transforming their body position to match that of the photo (MBT task); or in relation to a fixation cross, requiring no transformation (Lateralisation task). It is hypothesised, based on the effect of TMS over rTPJ on MBT (Blanke & Arzy, 2005), and the excitatory effect of anodal tDCS over cortical brain areas (Nitsche & Paulus, 2000b; Santiesteban et al., 2012), that anodal tDCS over an area involved in MBT should result in shorter RTs when performing the MBT task (as opposed to the control Lateralisation task). The effects of anodal tDCS over the right temporoparietal area will be contrasted with anodal tDCS over the left temporoparietal area, and sham stimulation.

4.2 Materials and Methods

4.2.1 Participants

Due to the exploratory nature of the exeriment, 30 (26 female, mean age 21.71 years, SD = 3.56) participants volunteered to take part in the study and were reimbursed for their time. All participants were screened for possible contraindications to tDCS, and provided signed and informed consent for their participation. Participants were assigned randomly to one of three stimulation groups: Anodal-right temporoparietal area (n = 10, 9 female), Anodal-left temporoparietal area (n = 10, 8 female), or sham (n = 10, 9 female). All participants were unaware of the aims of the study. The study was approved by the Departmental Ethics Committees, Department of Psychology, Royal Holloway, University of London.

4.2.2 Design

The study was a single-blind, sham-controlled, mixed design, with a within subjects factors of Identity (self vs. friend), Orientation (front-facing vs. back-facing) and Task (MBT vs. Lateralisation), and a between groups factor of tDCS Group (right temporoparietal area-anodal vs. left temporoparietal area-anodal vs. sham). Participants took part in one experimental session in which they experienced 20 minutes of tDCS, followed by performing the Mental Body Transformation task and Lateralisation task (the order of which was counterbalanced across participants). The Lateralisation task was introduced to control for any general effects of tDCS on RTs, as the task was similar in nature to the MBT task but required no transformation of egocentric perspective. Participants were blind to the type of stimulation that they received until after the end of the experiment.

4.2.3 Stimuli

Before the experimental session, all participants attended a photo session along with a close, same-gender friend. A friend was chosen rather than an unfamiliar person to control for the effects of familiarity. Two full body photographs of each participant (and their friend) were taken to use in the MBT and Lateralisation tasks. The participants were asked to wear a pair of black shorts and a white sleeveless top to create uniformity, and avoid any effect of distinctive clothing. The participants held their arms out to the side, and two photographs were taken, facing towards (front-facing) and away from (back-facing) the camera. The photographs were all converted to greyscale, and a grey background was applied. For the photographs of the participant, each picture was also mirror reversed to reflect how participants are used to seeing themselves in the mirror. The images were then edited to create a set of stimuli showing each individual wearing a glove on one of their hands. During the tasks, participants judged which hand the glove was on, either from the perspective of the person on the screen (MBT task), or in relation to a central fixation cross (Lateralisation task). In total, four images were created of both the participant and their friend (eight in total): front-facing left hand, front-facing right hand, back-facing left hand, back-facing right hand (see Figure 4.1A for example stimuli).

4.2.4 Procedure

At the beginning of the session participants received 20 minutes of tDCS, which was either left temporoparietal area-anodal stimulation, right temporoparietal area-anodal stimulation, or sham stimulation. Following the tDCS participants performed the MBT task and the Lateralisation task. The order of these tasks was counterbalanced across participants.

4.2.4.1 tDCS Parameters

The stimulation parameters used in this experiment follow those of previous research which has successfully used tDCS to investigate the role of TPJ in social cognition (see Santiesteban et al., 2012; Payne & Tsakiris, 2016). Stimulation was applied through two square 3.5cm^2 electrodes, inserted in saline-soaked sponge sleeves. Participants in the right temporoparietal area-anodal stimulation group had the anodal electrode placed over CP6 (electroencephalography 10/20 system) and the cathodal electrode placed over the Vertex (measured individually for each participant). Participants in the left temporoparietal area-anodal stimulation group had the anodal electrode placed over CP5, and the cathodal over the Vertex. For participants in the sham group, the site of the anodal electrode was counterbalanced between CP6 and CP5, with the location of the cathodal electrode held constant over the Vertex. Stimulation was delivered for 20 minutes at an intensity of 1mA (30 seconds ramp up, 20 seconds ramp down). For the sham stimulation, the stimulator was only switched on for the first 15 seconds of stimulation in order to mimic the initial itching sensation felt by participants in the active stimulation groups. During the stimulation period, participants in all three groups were told to sit quietly and relax.

4.2.4.2 Mental Body Transformation Task

Each trial began with the presentation of a fixation cross for 1000ms, followed by one of the eight body stimuli for 400ms, which was followed by a blank screen until participants made their response (see Figure 4.1B). Participants were instructed to imagine themselves in the position of the person on the screen, and respond with a button press to indicate whether the glove in the photo was on the person's left or right hand. Participants were instructed to respond as quickly and accurately as they could, but to ensure that they performed an egocentric perspective transformation before giving their response. Once participants had made their response, the next trial began. Participants performed half of the task with their right hand, and half with their left, the starting hand was counterbalanced across participants. The task was divided into four blocks of 64 trials, with each image repeated eight times. Participants performed a short block of eight practice trials at the beginning to familiarise themselves with the task.

4.2.4.3 Lateralisation Task

The Lateralisation task was exactly the same at the MBT task, except that participants were not required to imagine themselves in the position of the person on screen, and merely indicated which side of the fixation cross the glove appeared on.

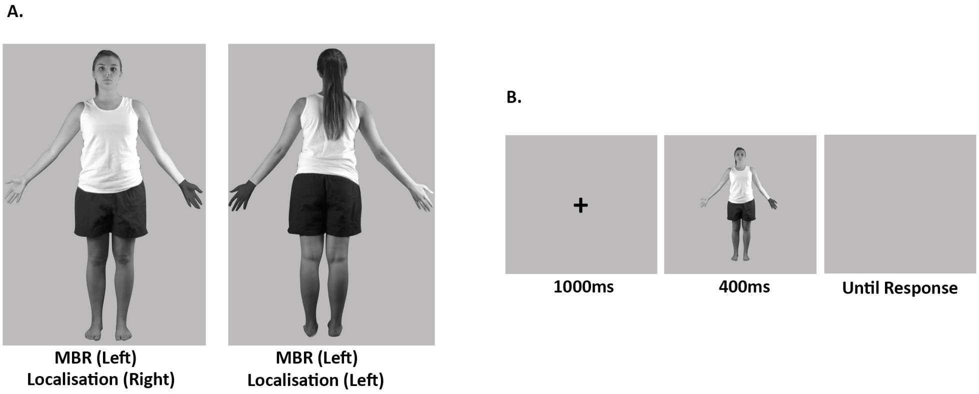

Figure 4.1: Stimuli and trial procedure. (A) An example of the type of stimuli seen by participants in the MBT task and the Lateralisation task. The captions underneath the full body photos show the correct response to the stimuli for the MBT and Lateralisation tasks. (B) Each trial begins with a fixation cross, followed by presentation of the body stimuli, followed by a blank screen until the participant's response is recorded.

4.2.5 Data Analysis

The average RTs from correct trials were used as the dependent variable in our statistical analysis. Two participants were excluded for making incorrect responses on over 25% of trials. Of the remaining 28 participants, the average error rate was 7.76%.

4.3 Results

A 2 x 2 x 2 x 3 ANOVA was conducted on the RT data, with within-subjects factors of Task (MBT vs. Lateralisation), ID (Self vs. Friend) and Orientation (Front-facing vs. Back-facing), and a between subjects factor of tDCS (right temporoparietal area-anodal vs. left temporoparietal area-anodal vs. sham). There was no main effect of ID on RTs: $F(1, 25) = 2.626$, $p = .118$, $\eta^2 = .095$, nor any significant interactions involving ID. However, the analysis revealed main effects of Task, $F(1,\ 25) = 132.731$, $p < .001$, $\eta^2 = .842$, Orientation: $F(1,\ 25) = 40.385$, $p < .001$, $\eta^2 = .618$, and tDCS: $F(2,\ 25) = 5.01$, $p = .015$, $\eta^2 = .286$, which were superseded by significant interactions between Task and tDCS: $F(2,\ 25) = 8.263$, $p = .002$, $\eta^2 = .398$, and Task and Orientation: $F(1,\ 25) = 40.817$, $p < .001$, $\eta^2 = .62$. No other interaction effects reached significance.

To investigate these interactions, further analysis was split by task and collapsed across ID. Firstly, performance on the control Lateralisation task was analysed. As expected, the ANOVA indicated that tDCS had no effect on the performance of simple lateralisation judgements: $F(2,\ 25) = 2.456$, $p = .106$, $\eta^2 = .164$, with no difference between performance of the three tDCS groups (right temporoparietal area $M = 360.89$, left temporoparietal area $M = 380.89$, sham $= 437.44$). Again, as expected there was no effect of Orientation on RTs in the Lateralisation task: $F(1,\ 25) = 2.022$, $p = .167$, $\eta^2 = .075$. The interaction between tDCS and Orientation was not significant: $F(2,\ 25) = .319$, $p = .730$, $\eta^2 = .025$.

Next, RT data from the MBT task was analysed to explore the effect of tDCS on mental body rotation. There was a main effect of Orientation on RTs in the MBT task: $F(1, 25) = 40.74$, $p < .001$, $\eta^2 = .62$, reflecting longer RTs when participants made judgements about front-facing figures ($M = 987.68$), compared to back-facing figures ($M = 767.26$). Importantly, the effect of Orientation was specific to the MBT task, indicating that participants were performing the egocentric perspective transformations in this task, and not in the Lateralisation task. There was also a main effect of tDCS: $F(2,\ 25) = 6.255$, $p = .006$, $\eta^2 = .334$. Bonferroni corrected t-tests (with a corrected alpha level of .016) revealed that stimulation of right temporoparietal area resulted in significantly shorter RTs (M = 628.09) than left temporoparietal area (M = 1060.05, p = .002), while the difference between right temporoparietal area and sham stimulation approached significance (M = 944.27, p = .02). Performance between the left temporoparietal area and sham groups did not differ ($p = .38$). The interaction between tDCS and Orientation in the MBT task was not significant: $F(2,\ 25)$

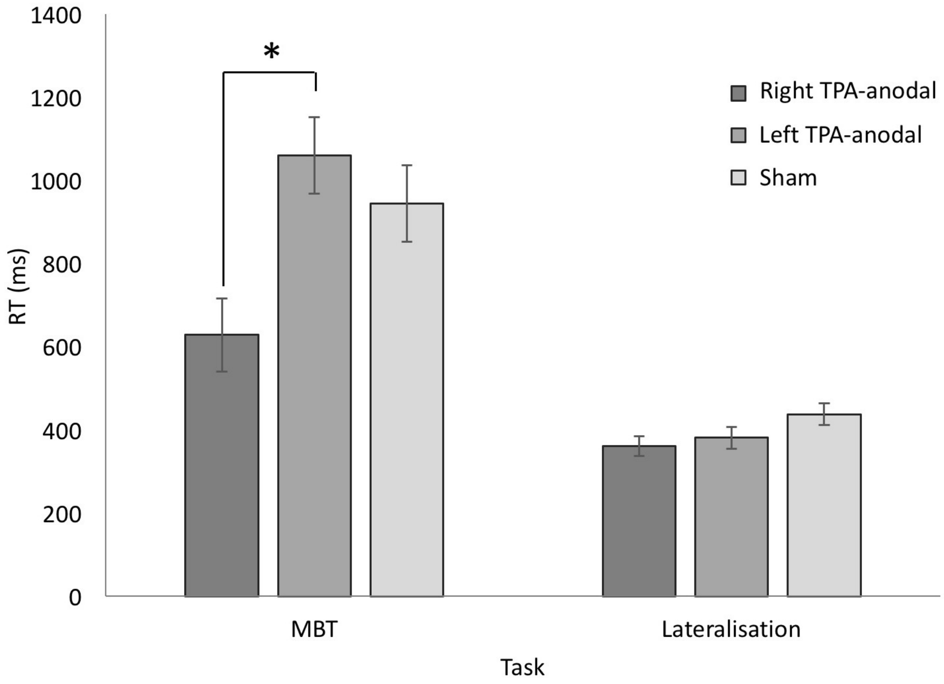

FIGURE 4.2: Mean RTs by tDCS group in the MBT and Lateralisation tasks, averaged across Identity and Orientation. Error bars represent standard error. TPA = temporoparietal area.

= 2.953, p = .071, η^2 = .191. See Figure 4.2. See Table 4.1 for means, SDs and 95% confidence intervals for all trial types by tDCS condition.

Error rates were analysed to check that tDCS over right temporoparietal area did not increase RT at the cost of accuracy. The % of errors made on each task was entered into a 2 x 2 ANOVA with factors of Task (MBT vs. Lateralisation) and tDCS (right temporoparietal area-anodal vs. left temporoparietal area-anodal vs. sham). There was a main effect of Task: F(1, 25) = 46.63, p < .001, = .65, reflecting more errors in the MBT relative to the Lateralisation task (MBT M = .08, Lateralisation M = .03). There was no main effect of tDCS: F(2, 25) = .17, p = .84, = .01, nor an interaction between tDCS and Task: F(2, 25) = 1,11, p = .34, = .08, suggesting that tDCS over right temporoparietal area improved speed of response on the MBT task without sacrificing accuracy.

Table 4.1: Means, SDs and 95% confidence intervals for all trial types in the right temporoparietal area, left temporoparietal area, and sham groups

		Mental Body Rotation				Lateralization			
		Self		Friend		Self		Friend	
		Front-facing	Back-facing	Front-facing	Back-facing	Front-facing	Back-facing	Front-facing	Back-facing
Right TPA	M (SD)	669.909 (247.725)	564.656 (156.195)	703.072 (250.222)	574.74 (180.662)	358.412 (57.007)	359.286 (51.408)	364.047 (48.597)	361.821 (55.045)
	95% CI	[492.698, 847.121]	[452.922, 676.391]	[524.074, 882.07]	[445.503, 703.978]	[317.632, 399.192]	[322.511, 396.061]	[329.283, 398.811]	[322.444, 401.198]
Left TPA	M (SD)	1212.267 (420.183)	890.353 (182.278)	1228.018 (404.838)	909.572 (187.476)	382.234 (49.977)	374.747 (42.3)	383.97 (45.879)	382.611 (45.123)
	95% CI	[889.286, 1535.248]	[750.242, 1030.464]	[916.832, 1539.204]	[765.465, 1053.678]	[343.818, 420.65]	[342.232, 407.262]	[348.704, 419.236]	[347.927, 417.296]
Sham	M (SD)	1059.495 (385.697)	821.824 (259.774)	1053.322 (402.896)	842.436 (301.248)	441.074 (112.326)	433.366 (114.709)	437.767 (126.13)	437.551 (114.764)
	95% CI	[763.023, 1355.968]	[622.144, 1021.505]	[743.628, 1363.015]	[610.877, 1073.996]	[354.733, 527.416]	[345.193, 521.539]	[340.815, 534.719]	[349.336, 525.767]

TPA = temporoparietal area.

4.4 Discussion

The current study aimed to investigate the involvement of the left and right TPJ in egocentric perspective transformations using the modulatory effect of tDCS. Anodal tDCS over right temporoparietal area, but not left temporoparietal area, led to an enhanced ability to perform MBTs. Participants who received tDCS over right temporoparietal area were faster to make egocentric perspective transformations than those who received anodal tDCS over left temporoparietal area. tDCS over right temporoparietal area did not appear to significantly affect performance on a similar control task in which participants were not required to perform egocentric perspective transformations, suggesting that the effect of the stimulation was specific to MBTs, rather than a general improvement in speed of response. Although there did seem to be a slight improvement in RT on the Lateralisation task in the right temporoparietal area group compared with left temporoparietal area and sham, this difference was far greater in the MBT task, suggesting that even if anodal tDCS over right temporoparietal area were having a general effect on RTs, it was having a greater impact on MBT above general speed of response. This finding is supported by previous research demonstrating causal involvement of rTPJ in egocentric perspective transformations (Blanke & Arzy, 2005), and indicates that the involvement of the temporoparietal area in egocentric MBTs may be heavily lateralised to the right hemisphere.

The results of Experiment 2 corroborate previous reports of TPJ activity during egocentric perspective transformations, and add to the understanding of the causal involvement of the right temporoparietal area in this process. Previously, Blanke and Arzy (2005) demonstrated that disrupting activity in rTPJ impaired mental body transformations. The results of Experiment 2 have expanded upon this by highlighting the excitatory effect of anodal tDCS over right temporoparietal area, which led to an enhanced ability to mentally rotate one's body. Taken together, these findings highlight the causal role of the right temporoparietal area in performing egocentric body transformations, and suggest that processes of self location, agency and egocentric perspective, vital for a sense of belonging in one's body, may be enhanced by tDCS of right temporoparietal area, but not of left temporoparietal area.

One of the aims of Experiment 2 was to provide evidence to directly compare the effects of anodal stimulation of the right and left temporoparietal areas on MBTs. Interestingly, there was no effect of anodal stimulation over the left temporoparietal area on MBTs. This is surprising when considering that activity in this area has been previously reported in response to imagined shifts in egocentric perspective and position (Arzy et al., 2006; Zacks et al., 2002, 1999). However, while neuroimaging studies have highlighted lTPJ activity associated with the performance of MBT, no study has provided causal evidence for this region's involvement. Increased BOLD activity in both left and right temporoparietal areas correlated with MBT may reflect distinct cognitive processes engaged when performing MBT tasks, of which left temporoparietal area activity contributes to, but is not necessary for, egocentric perspective transformations. The results of Experiment 2 support a reliance on the right hemisphere for MBT, rather than the left.

Experiment 2 also investigated whether MBTs are affected by whether they are directed towards an image of one's own body, or an image of another individual's body. The results showed no difference between MBTs directed towards an image of the self and an image of a friend. Nor did the results indicate that identity interacted with the effect of the tDCS at either site. This is interesting when considering the literature on self biases in perception (Keenan et al., 1999; Ma & Han, 2010; Tong & Nakayama, 1999), which indicates that the self elicits prioritised processing. However, the results of Experiment 2 suggest that the right temporoparietal area does not distinguish between taking the spatial perspective of one's own body over that of another person's, suggesting that at least in the case of spatial body transformations, the functional involvement of the right temporoparietal area goes beyond body- or person-identity. Furthermore, the lack of a main effect of identity, independently of the tDCS stimulation, corroborates the hypothesis that egocentric perspective transformations do not depend on identity.

It is important to note that Experiment 2 had a number of limitations. Firstly, the sample size, while similar to previous brain stimulation research investigating MBT (Blanke et al., 2005) is small, meaning that the results may be statistically underpowered and should be interpreted with caution. As the current experiment was an exploratory experiment to investigate the further involvement of the temporoparietal junction in social cognition, future research is needed to replicate the current results. Furthermore, owing to the between subjects design of the experiment, it cannot be ruled out that the three groups were affected differently by the tDCS based on individual features, such as differences in anatomy impacting upon current flow, and baseline differences in neural excitability (Benwell, Learmonth, Miniussi, Harvey, & Thut, 2015; Sellaro, Nitsche, & Colzato, 2016; Truong, Magerowski, Blackburn, Bikson, & Alonso-Alonso, 2013). It is also important to consider that the location of the control electrode in the current experiment (over Cz) may have introduced a potential confound, when considering the proximity of Cz to the primary motor cortex (M1), and thus its proximity to areas of the human mirror neuron system. The human MNS is heavily implicated in the observation of other's bodies and actions, and so may be involved in a task in which one must take another's spatial perspective. However, as the position of the reference electrode remained constant across both right temporoparietal area and left temporoparietal area conditions, regardless of whether it had an impact on task performance there was still a difference between anodal stimulation of right temporoparietal area and left temporoparietal area on MBT performance, suggesting a differential involvement of the left and right hemisphere in this ability.

Activity in TPJ has been widely reported in response to egocentric perspective transformations. Experiment 2 extends the knowledge of the right temporoparietal area's inolvement in this function by demonstrating that excitatory anodal tDCS over the right temporoparietal area leads to an enhanced ability to perform MBTs. This finding has implications for a wide range of social cognitive processes which may rely in part on mental imagery of bodies. It has been suggested that ability to take someone else's spatial perspective may contribute to higher-level social cognitive processes, such as mental state understanding (Decety & Sommerville, 2003), and that the rTPJ underpins a general self-other discrimination mechanism which is involved in both low-level and high-level social cognition (Decety & Lamm, 2007). In line with this, Santiesteban et al. (2012) found that anodal tDCS over rTPJ improved performance on two social cognitive tasks which required control over self and other representations. MBTs and high-level sociocognitive processes may share neural underpinnings, and future research may wish to explore whether improvement in MBT abilities through training can lead to improvements in social cognition.

In conclusion, the results of Experiment 2 suggest that the right temporoparietal area is not only involved in controlling representations of the self-face, but also postural and spatial representations of the self-body. Experiment 2 provides further evidence that the mechanisms underpinning self-other discrimination in the right temporoparietal area may support other processes involved in producing a coherent sense of self.

5 The role of intraparietal sulcus in self-identification and self-updating

5.1 Introduction

Chapter 3 of this thesis explored the involvement of the right temporoparietal area in *self-recognition*: the process by which a mental representation of the self-face is maintained. Chapters 5 and 6 will focus on the processes of *self-identification* and *self-updating.* The introductory chapter of this thesis defined *self-identification* as the process by which a mental representation of the self-face is initially acquired, and *self-updating* as the process by which the mental self-face representation is updated to reflect changes in physical appearance over time. Both self-identification and self-updating rely on the integration of multisensory stimulation, and the experiments in the following two chapters will investigate, using tDCS, the involvement of two brain areas in multisensory integration during the Enfacement Illusion.

As indicated in Chapter 1 of this thesis, a central element of self-identification and self—updating is the integration of multisensory information relating to the body. Research has shown that the interaction of information from multiple modalities can have a powerful effect on the experience of one's body (e.g. Botvinick & Cohen, 1998; Tsakiris, 2008), as well as perception of external stimuli. For example, in the classical McGurk effect, the integration of a seen lip-movement with a temporally congruent speech sound alters the way the sound is perceived (McGurk & Macdonald, 1976). Similarly, visual detection can be enhanced by the presentation of an auditory stimulus at a temporally and spatially congruent location (Frassinetti, Bolognini, & Làdavas, 2002). While these studies demonstrate how the convergence of unimodal information can affect the perception of external stimuli, the current Chapter will investigate how multisensory integration can affect the mental representation of one's own body.

In 1998, Botvinick and Cohen elegantly demonstrated how the impact of multisensory integration extended to the process of self-identification. Participants sat at a table with their left hand resting on the table but hidden from view. A rubber left hand was placed on the table in front of the participant. Participants were instructed to fixate on the rubber hand, while the experimenter stroked the rubber hand and the participant's hand with two paintbrushes. When the stroking was synchronised, such that touch occurred on the participant's real hand at the same time as the rubber hand, participants reported feeling as if the touch they felt was that observed on the rubber hand. Botvinick and Cohen (1998) also reported a distortion in proprioception following the illusion. Participants' own judgements about the position of their left hand following the illusion were displaced towards the position of the rubber hand (relative to pre-illusion judgements). The RHI shows how the integration of felt and observed touch is able to change proprioceptive information, and elicit a sense of body ownership over an object not a part of one's body. Since the initial studies on the RHI, researchers have adapted and extended the paradigm to show how multisensory integration is also implicated in the formation, and updating, of mental body-representations at the level of the whole body: in the full body illusion (Petkova et al., 2011), and faces in the Enfacement Illusion (Tsakiris, 2008, see Chapter 1 for a full discussion of multisensory bodily illusions). These findings provided evidence for the growing idea that the processes of identification with a body-part may be driven by specific forms of multisensory integration.

FMRI studies of the RHI implicate premotor cortices, intraparietal cortices and the cerebellum in the illusory experience of ownership over a fake hand (Ehrsson, Holmes, & Passingham, 2005; Ehrsson et al., 2004). Ehrsson et al.

(2005, 2004) suggested that activity in these areas reflected the detection and integration of multisensory information during the illusion. Activity in premotor and intraparietal cortices has also been found to correlate, along with activity in the left putamen, with the experience of ownership over a whole body in the multisensory body-swap illusion (Petkova et al., 2011). In Apps et al.'s (2013) study of the neural correlates of the Enfacement Illusion, they identified activity in multimodal TPJ and intraparietal sulcus (IPS) which varied parametrically with the strength of the illusion. Interestingly, there was a reduction in activity in TPJ during the experience of the illusion. As TPJ has been shown to be involved in processing the perspectives of self and other, reduction in this area during the experience of enfacement may reflect a merging of self with other. TPJ is also thought to underpin a 'test for fit' process, discriminating objects as either body or non-body related (Tsakiris, 2010). TMS to rTPJ during the RHI reduced the proprioceptive drift experienced towards a rubber hand, and increased proprioceptive drift towards a non-hand object, reducing the discrimination between body related and non-body related objects in body-ownership (Tsakiris, 2008).

The IPS on the other hand is thought to integrate multisensory information during the Enfacement Illusion (Apps et al., 2013). IPS is a multimodal area, with studies in monkeys and humans showing that IPS receives both vestibular and somatosensory input (Grefkes & Fink, 2005; Lopez & Blanke, 2011; Matsuzaki, Kyuhou, Matsuura-Nakao, & Gemba, 2004; Seltzer & Pandya, 1980, 1986), suggesting that this area is involved in integrating proprioceptive and tactile information relating to the body. Furthermore, bimodal neurons that have topographically aligned somatosensory and visual receptive fields have been identified within IPS in both monkeys and humans (Duhamel, Colby, & Goldberg, 1998; Avillac, Denève, Olivier, Pouget, & Duhamel, 2005; Sereno & Huang, 2006). This has led to the suggestion that the IPS is involved in integrating incoming sensory, vestibular, and visual information, contributing to the process of self-updating. In support of this, Makin, Holmes, and Zohary (2007) manipulated sensory information about hand position while participants were inside an MRI scanner, and analysis of IPS activity showed that anterior IPS was sensitive to both visual information about hand location and tactile stimulation applied to the hand, suggesting that the anterior IPS combines multisensory information about the hand to produce hand representations in peripersonal space. IPS activity has also been linked with the illusory sense of ownership over a rubber hand (Ehrsson et al., 2005) and whole body (Petkova et al., 2011). Furthermore, Apps et al. (2013) reported that activity in the IPS during the Enfacement Illusion was modulated by the synchronicity and specular congruency of the stroking received by participants, and that the activity varied parametrically with the extent to which participants experienced the illusion. Taken together, these findings suggest that the IPS is involved in updating body representations and producing the sense of ownership during multisensory integration.

If IPS is involved in integrating multisensory information to update and produce coherent body representations, then it is critical for the processes of self-identification and self-updating. Experiment 3 aimed to investigate the involvement of right IPS in self-updating, by observing the effects of anodal tDCS over this region on the Enfacement Illusion. Participants took part in three experimental sessions which were distinguished by the type of stimulation received. In one session participants received anodal tDCS to the right IPS region, while the remaining two served as an active control (anodal-PFC) and a baseline (Sham) condition. After receiving the tDCS, participants completed a typical enfacement paradigm consisting of two self-recognition tasks separated by an IMS session. The first self-recognition task served as a baseline while the second measured changes in self-recognition following the IMS session. It was expected that the typical enfacement effect: an inclusion of the IMS face in the self-face representation, would be observed in the two control conditions (anodal-PFC and sham); but also that in the IPS session this effect would be enhanced. It was hypothesised that if IPS contributes to the self-updating process by integrating incoming multisensory signals, then increasing cortical excitability in this region would enhance the effect of the Enfacement Illusion.

5.2 Materials and Methods

5.2.1 Participants

Twenty-five participants were recruited to take part in the study. Twenty-three participants (12 female, 11 male, mean age = 20.7 years, SD = 3.72) completed all three experimental sessions and were reimbursed for their time. All participants were screened for possible contraindications to tDCS before they took part in the study, and were unaware of the aim of the study until they had completed their participation. All participants were self-reportedly right handed. The study was approved by the Department of Psychology Ethics Committee, Royal Holloway, University of London.

5.2.2 Design

The study was a double-blind, sham-controlled, repeated measures, within-subjects design with factors of tDCS Type (anodal-IPS vs anodal-PFC vs Sham), Timing of the self-recognition task (pre-IMS vs post-IMS), Synchronicity of IMS (synchronous vs asynchronous), and direction of the morphing video ("self-to-other" vs "other-to-self").

5.2.3 Tasks and Scales

5.2.3.1 Self-Recognition Video Morphing Task

The self-recognition task used in the current experiment was the same as that used in Experiment 1, except for the inclusion of a practice task before the first instance of the self-recognition task. For a full description of the stimuli and procedure see Section 3.2.3.1. Prior to the study a photograph was taken of each participant's face, which was then morphed separately with two unfamiliar faces (IMS-A and IMS-B). Six morphing videos were created for each unfamiliar face identity (10, 15 and 20sec for each direction of morphing), resulting in 12 videos per participant. All photo manipulation, morphing, and video creation was carried out using Adobe Photoshop CS6, Abrasoft Fantamorph, and Adobe Premier Pro.

Preceding the beginning of the task, participants were able to view the photo of their own face and the unfamiliar person's face used to create the videos. During the self-recognition task participants viewed the morphing videos presented in a randomised order, and responded with their right index finger when they judged a change in identity of the face. Each of the six videos was played five times (30 trials total). Between each video a fixation cross was presented for between 1-2.5 seconds. Each video ended once the participant made their response, and the next trial began.

Before the first block of the first session, participants took part in a practice video morphing task in which they saw videos morphing between the faces of two famous individuals (Emma Watson and Jennifer Lawrence). The instructions given were the same as for the actual self-recognition task, such that participants were instructed to respond when they thought that the face in the video started to look more like the person it was morphing into.

5.2.3.2 Interpersonal Multisensory Stimulation Session

Two IMS videos were recorded, one with each of the unfamiliar individuals (IMS-A and IMS-B). In the videos the model looked directly into the camera with a neutral expression while they were stroked on the cheek with a cotton bud. The videos lasted two minutes with a stroke occurring approximately every 3 seconds (Cardini, Tajadura-Jiménez, Serino, & Tsakiris, 2013; Tajadura-Jiménez, Longo, et al., 2012; Tajadura-Jiménez, Lorusso, & Tsakiris, 2013).

During the IMS session participants were instructed to sit as still as possible while watching the video of one of the unfamiliar individuals (IMS-A or IMS-B) being stroked on the cheek with a cotton bud. While watching the video the participant was stroked on the same place on their own cheek with a cotton bud by the experimenter. The stroking was always applied in a specularly congruent location to the video, as if the participant were looking into a mirror. The participants were stroked either in synchrony or asynchrony with the stroking in the video.

5.2.3.3 Interpersonal Multisensory Stimulation Questionnaire

The Interpersonal Multisensory Stimulation (IMS) questionnaire can be used to assess the subjective strength of the enfacement experience. The scale was adapted from (Tajadura-Jiménez, Longo, et al., 2012). Participants answered ten questions assessing four different aspects of the enfacement experience (Control, Similarity, Ownership and Touch Referral), making four subsscales. The Control sub-scale focuses on the sense of control and imitation of the IMS face. The Similarity sub-scale focuses on the subjective sense of similarity between the participant's own face and the IMS face. The Ownership sub-scale contains questions about the sense of body-ownership over the IMS face, and the Touch Referral sub-scale asks about the experience of touch during IMS. Items are scored on a 7-point Likert scale from "Strongly Agree" (3) to "Strongly Disagree" (-3), with positive scores representing stronger subjective effects of the illusion. Scores were recoded to a scale of 0 to 6 for the analysis. See Table 5.1 for the full list of items in the IMS questionnaire.

Table 5.1: Items in the Interpersonal Multisensory Stimulation Questionnaire.

Item	During the IMS session...	Sub-scale
1	"I felt like the other's face was my face"	Ownership
2	"It seemed like the other's face belonged to me"	Ownership
3	"It seemed like I was looking at my own mirror reflection"	Ownership
4	"It seemed like the other's face began to resemble my own face"	Similarity
5	"It seemed like my own face began to resemble the other person's face"	Similarity
6	"It seemed like my own face was out of my control"	Control
7	"It seemed like the experience of my face was less vivid than normal"	Control
8	"I felt that I was imitating the other person"	Control
9	"The touch I felt was caused by the cotton bud touching the other's face"	Touch Referral
10	"The touch I saw on the other's face was caused by the cotton bud touching my own face"	Touch Referral

5.2.3.4 Inclusion of Other in Self Scale

The Inclusion of Other in Self Scale (IOS) is a single-item, pictorial measure of self-other closeness (Aron, Aron, & Smollan, 1992). Participants are presented with a series of images showing increasingly overlapping circles, representing themselves and another person (see Figure 5.1). Participants choose which of the images best represents their relationship with a named person.

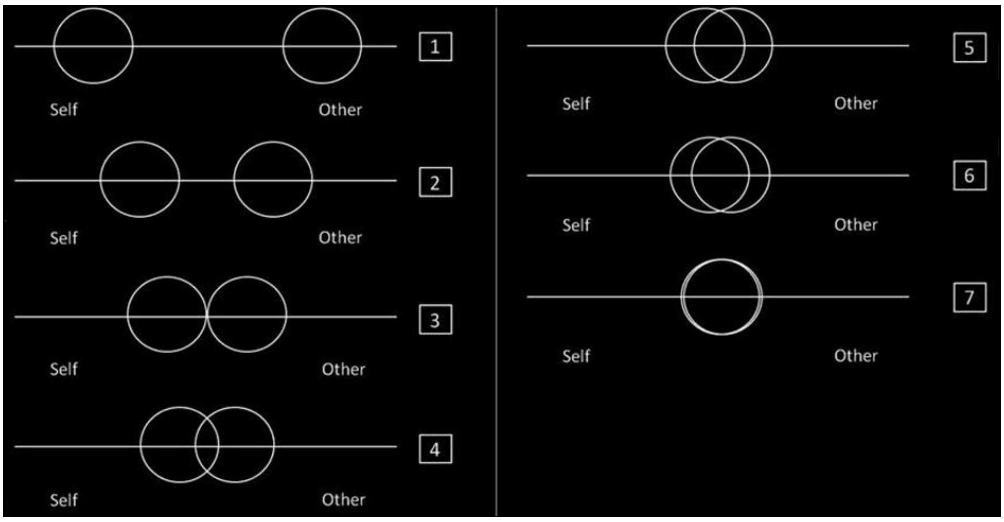

Figure 5.1: The single-item Inclusion of Other in the Self Scale. Participants choose which of the Venn-like diagram images best represents their relationship with a named person.

5.2.4 tDCS Parameters

Two square electrodes, placed inside saline soaked sponge sleeves were used for the stimulation. Two rubber straps held the electrodes in place on the participant's head. For Anodal-IPS, the anodal electrode was placed over electrode position P4, corresponding to right IPS (electroencephalography 10/20 system: Herwig et al., 2003; Jacobson et al., 2012; Klein et al., 2013) while the Cathodal electrode was placed on the forehead. For Anodal-PFC stimulation the anodal electrode was placed over F3, corresponding left PFC (Herwig et al., 2003), and the Cathodal electrode was placed on the vertex (individually measured for each participant). For the Sham stimulation, either the Anodal-IPS or Anodal-PFC electrode set-up was used, counterbalanced across participants. The stimulation duration was 20 minutes, with an intensity of 1.5 mA (30 seconds ramp up, 20 seconds ramp down). For the Sham stimulation, the stimulator was switched on only the first 15 seconds of stimulation, to mimic the initial itching sensation experienced in the active stimulation sessions, after which it only conducted periodic impedance checks.

5.2.5 Procedure

Each participant took part in three stimulation sessions, separated by at least 24 hours. In each session the participant received a different type of stimulation at the beginning of the session (Anodal-IPS, Anodal-PFC, and Sham-IPS/PFC). The order of the stimulation type received was counterbalanced across participants. Participants received 20 minutes of stimulation before starting the experimental tasks.

Following 20 minutes of stimulation, the participant took part in two experimental blocks. Each block consisted of a Pre-IMS self-recognition task, followed by a two minute IMS session, followed by the post-IMS self-recognition task, and finally the IMS questionnaire and IOS scale. Within each block participants saw the same unfamiliar face (IMS-A or IMS-B) across both self-recognition tasks and the IMS session. The other unfamiliar face (IMS-A or IMS-B) was used in the second experimental block. Between the two blocks participants rested for five minutes, and looked at their face in a mirror for 60 seconds to abolish the effect of the IMS. In each session, participants experienced synchronous IMS in one block, and asynchronous IMS in the other. The order of synchronicity and the identity of the unfamiliar face used in each IMS session was counterbalanced across participants. See Figure 5.2 for an illustrated procedure.

5.2.6 Data Analysis

Preceding analysis, the raw RT data from the self-recognition task was converted into '% of self visible at time of response'.

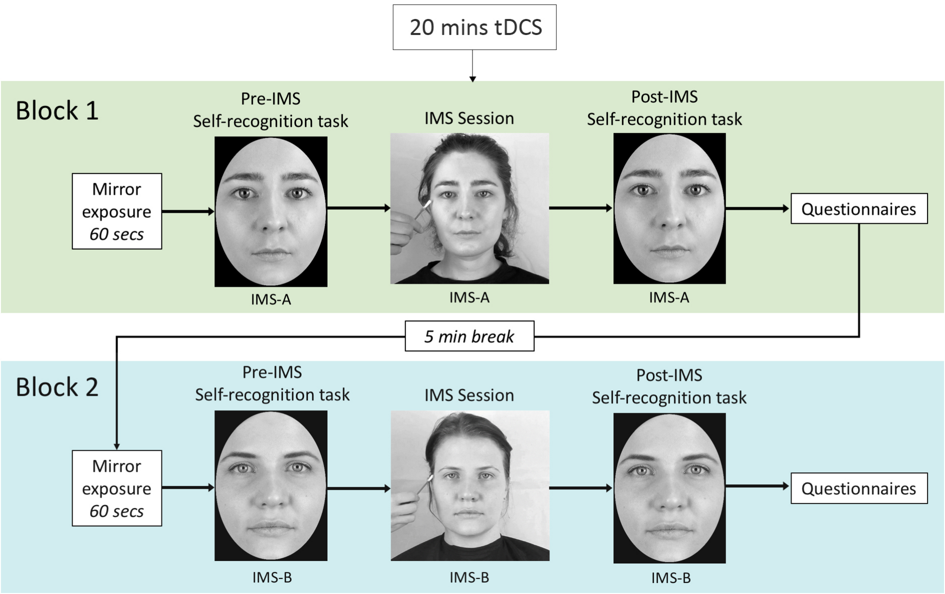

FIGURE 5.2: An illustrated procedure of one experimental session. Each session started with 20 minutes of tDCS, followed by two blocks. Each block started with 60 seconds of mirror exposure, followed by a pre-IMS self-recognition task, an IMS session, a post-IMS self-recognition task, and lastly the IMS and IOS questionnaires. In one of the blocks participants experienced synchronous IMS, and in the other block they experienced asynchronous IMS.

5.3 Results

5.3.1 Self-Recognition Task Analysis

3 x 2 x 2 x 2 repeated measures ANOVA with factors of tDCS (anodal-IPS vs. anodal-PFC vs. sham), synchronicity of IMS (synchronous vs. asynchronous), timing of self-recognition task (pre-IMS vs. post-IMS) and direction of morphing (self-to-other vs. other-to-self). The ANOVA revealed a predictable main effect of direction of morphing: $F(1, 22) = 47.30$, $p < .001$, $\eta^2 = .68$, reflecting that in the self-to-other direction of morphing, when participants indicated the point at which they recognised the other's face, there was significantly less of the self-face-visible than in the other-to-self direction when participants indicated the point at which they recognised their own face (self-to-other $M = 41.28$, other-to-self $M = 65.88$). There was also a significant main effect of timing: $F(1, 22) = 35.36$, $p < .001$, $\eta^2 = .62$, reflecting a reduction in the %-of-self-face visible at the point of discrimination following IMS, regardless of synchronicity of the IMS, tDCS or direction of morphing (pre M

= 54.81, post M = 52.35). These main effects were eclipsed by a significant interaction between timing and direction of morphing: $F(1, 22) = 4.42$, $p = .047$, $\eta^2 = .17$.

To explore the interaction, four new variables were created by collapsing across tDCS and synchronicity, to create values reflecting the % of self-face visible at the pre-IMS self-recognition task for self-to-other and other-to-self directions of morphing, and the post-IMS self-recognition task for self-to-other and other-to-self directions of morphing. Paired samples t-tests (with a corrected alpha level of .016) revealed significant differences in both directions of morphing following IMS: self-to-other pre vs. post-IMS [$t(22) = 5.229$, $p < .001$] (pre M = 42.97, post M = 39.59)., other-to-self pre vs. post-IMS [$t(22) = 5.743$, $p = .012$] (pre M = 66.65, post M = 65.12. See Figure 5.3. Means, SDs and 95% confidence intervals for all conditions can be seen in Table 5.2.

Figure 5.3: There was a significant reduction in the amount of self-face visible following IMS in both directions of video, regardless of synchronicity of the IMS or the type of tDCS received. Error bars represent standard error.

A further two variables were created to explore whether the change following IMS was different between directions of morphing. These variables represented the difference between the post-IMS and pre-IMS scores for each direction of morphing separately. A paired-samples t test (with corrected alpha level of .016) revealed that there was no significant difference in the change following IMS between the two directions of morphing: $t(22) = 2.102$, $p = .047$ (self-to-other $M = 3.383$, other-to-self $M = 1.531$).

5.3.2 Interpersonal Multisensory Stimulation Questionnaire Analysis

The potential effects of tDCS on the subjective experience of the Enfacement Illusion were analysed by comparing reports on the IMS questionnaire across the different stimulation sessions and the IMS blocks. The four sub-scales of the IMS questionnaire were entered into a repeated measures ANOVA with factors sub-scale (ownership vs. similarity vs. touch referral vs. control), tDCS (anodal-IMS vs. anodal PFC vs. sham) and synchronicity of IMS (synchronous vs. asynchronous). There was a significant main effect of sub-scale: $F(3, 66) = 8.951$, $p < .001$, $\eta^2 = .289$, reflecting that participants agreed more strongly with the Similarity and Control sub-scales than the Ownership and Touch Referral sub-scales (Similarity $M = 2.681$, Control $M = 2.644$, Ownership $M = 2.012$, Touch Referral $M = 1.761$). Bonferroni corrected t-tests comparing each sub-scale against every other sub-scale revealed significant differences between scores on the Ownership and Similarity sub-scales ($p = .004$), Ownership and Control sub-scales ($p = .028$), Touch Referral and Similarity sub-scales ($p = .019$), and Touch Referral and Control sub-scales ($p = .003$). There was also a main effect of synchronicity of IMS: $F(1, 22) = 26.94$, $p < .001$, $\eta^2 = .55$, reflecting a stronger subjective experience of the Enfacement Illusion following synchronous IMS ($M = 2.79$), rather than asynchronous IMS ($M = 1.76$). The main effect of tDCS was not significant, nor were any interaction effects. See Figure 5.4.

5.3.3 Inclusion of Other in Self Scale Analysis

The scores from the IOS scale were analysed, to compare the subjective experience of the inclusion of other in self following IMS across the tDCS conditions. Scores from the IOS scale were provided as input in a 3 x 2 repeated

Table 5.2: Means, SDs, and 95% confidence intervals for all trial types in the IPS, PFC and Sham tDCS sessions

		% of Self-face at Response during Self-recognition Task							
		Synchronous				Asynchronous			
		Pre-IMS		Post-IMS		Pre-IMS		Post-IMS	
		Self-to-other	Other-to-self	Self-to-other	Other-to-self	Self-to-other	Other-to-self	Self-to-other	Other-to-self
IPS	M (SD)	43.647 (11.911)	64.874 (8.825)	38.045 (13.23)	63.333 (9.592)	43.442 (11.566)	66.665 (11.156)	40.525 (11.001)	65.001 (11.073)
	95% CI	[38.496, 48.798]	[61.058, 68.69]	[32.324, 43.765]	[59.186, 67.481]	[38.441, 48.444]	[61.841, 71.489]	[35.767, 45.283]	[60.213, 69.79]
PFC	M (SD)	42.237 (13.074)	68.738 (11.287)	40.587 (11.953)	66.162 (10.868)	44.021 (12.585)	67.403 (10.316)	40.064 (13.12)	65.806 (11.763)
	95% CI	[36.584, 47.891]	[63.857, 73.619]	[35.419, 45.756]	[61.463, 70.862]	[38.579, 49.463]	[62.942, 71.864]	[34.39, 45.738]	[60.72, 70.893]
Sham	M (SD)	42.971 (11.326)	66.981 (10.586)	40.505 (12.245)	64.857 (9.418)	41.521 (12.086)	65.215 (9.063)	37.811 (13.596)	65.53 (10.341)
	95% CI	[38.076, 47.867]	[62.403, 71.559]	[35.210, 45.800]	[60.784, 68.93]	[36.295, 46.748]	[61.295, 69.134]	[31.932, 43.691]	[61.058, 70.001]

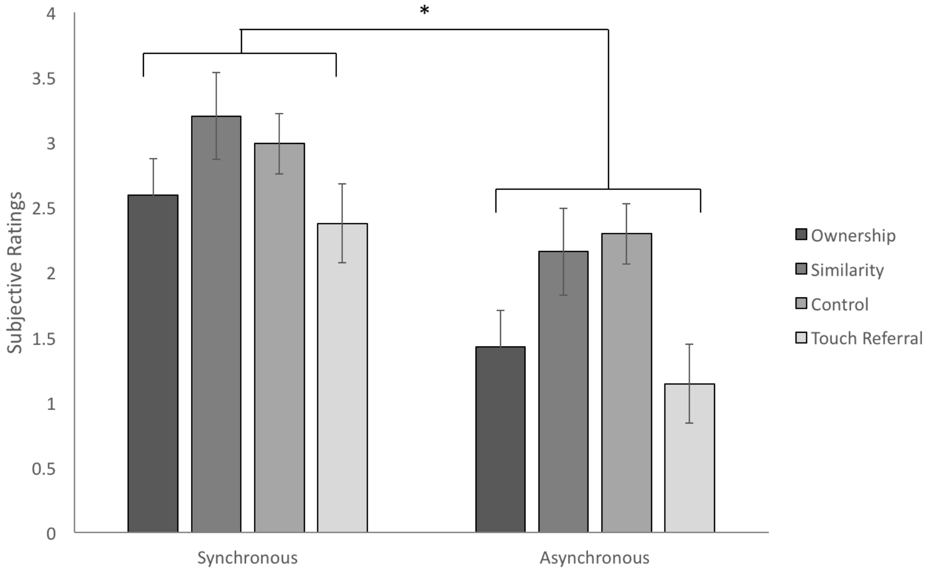

FIGURE 5.4: Scores on the IMS questionnaire were significantly highly across all sub-scales and tDCS sessions for the synchronous IMS block, relative to the asynchronous IMS block. Error bars represent standard error.

measures ANOVA with factors of tDCS (anodal-IMS vs. anodal PFC vs. sham) and synchronicity of IMS (synchronous vs. asynchronous). There was a main effect of synchronicity of IMS: $F(1,\ 22) = 19.186$, $p < .001$, $\eta^2 = .466$, indicating a stronger subjective inclusion of other into self following synchronous IMS ($M = 3.2$), as opposed to asynchronous IMS ($M = 2.33$). No other main or interaction effects reached significance. See Figure 5.5.

5.4 Discussion

Experiment 3 aimed to investigate the involvement of IPS in multisensory integration during the process of self-updating. It was hypothesized that Anodal tDCS over IPS would facilitate the integration of multisensory signals during the Enfacement Illusion, resulting in a stronger behavioral and subjective Enfacement effect (relative to anodal-PFC and Sham stimulation). It was predicted that the results of the self-recognition task would show more inclusion of the IMS in the self-face representation following synchronous IMS in the anodal-IPS condition than synchronous IMS in both the anodal-PFC and

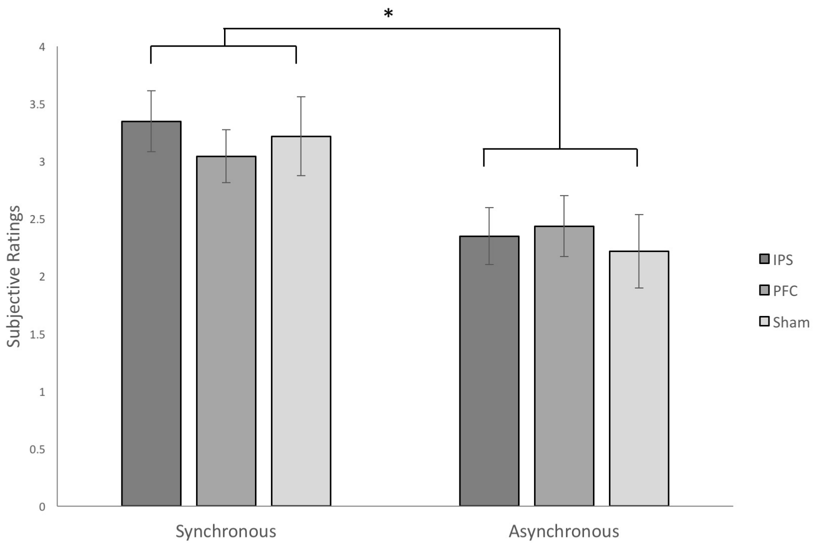

Figure 5.5: Subjective ratings on the IOS scale were significantly higher across all tDCS conditions following synchronous IMS, as opposed to asynchronous IMS. Error bars represent standard error.

Sham conditions. No change in the self-face representation was expected following asynchronous IMS in any tDCS condition, akin with the typical Enfacement effect. It was also expected that the subjective experience of Enfacement, measured with the IOS scale and IMS questionnaire, would be stronger following synchronous IMS in the anodal-IPS condition relative to following synchronous IMS in both the anodal-PFC and Sham conditions. As with the behavioural results, it was expected that the overall subjective experience of Enfacement would be stronger following synchronous IMS compared with asynchronous IMS across all tDCS conditions.

Firstly, analysis of the questionnaire data (IMS and IOS scales) indicated that the synchronous IMS session successfully elicited a subjective 'enfacement' experience across all tDCS conditions. Agreement with all sub-scales of the IMS questionnaire was stronger following synchronous IMS, in comparison with asynchronous IMS. This indicates that participants identified more with the IMS face, and felt that the IMS face and their own face were more similar, following synchronous IMS. The same pattern was also found for the IOS scale: participants reported feeling closer to the IMS individual following synchronous IMS in comparison with asynchronous IMS. Interpretation of the IMS questionnaire results would suggest that the manipulation of synchronicity was successful at inducing the introspective experience of enfacement, that is: participants identified with the face in the video, and participants felt that the face more closely resembled their own. This subjective experience during synchronous IMS mirrors two of the key processes involved in producing a mental self-face representation – self-identification and self-recognition.

However, although the synchronous IMS session appeared to have induced a subjective 'enfacement' effect, the same pattern was not reflected in the results of the self-recognition task. The results indicated that, following both synchronous and asynchronous IMS, participants discriminated between their own and the other's face at a point where less of their own face was visible than before the IMS session. This was apparent in both directions of morphing video. Previous research investigating self-updating using the Enfacement Illusion and video morphing self-recognition tasks has found a specific effect of synchronous IMS on self-other recognition (Tsakiris, 2008), with one study finding an effect only in the other-to-self direction of morphing (Tajadura-Jiménez, Longo, et al., 2012). Specifically, following synchronous IMS, participants responded during the video to indicate recognition of their own face at an earlier point, when more of the other's face was visible than before the IMS session. This has been interpreted as reflecting an inclusion of the other's face in the mental self-face representation, induced by the multisensory integration of seen and observed touch during the IMS session.

Considering the results of the questionnaire analysis, suggesting that an 'enfacement' effect was induced during synchronous IMS, it is surprising that such an effect was not reflected in the self-recognition data. This disparity between subjective and objective measures of the illusion may suggest that the video morphing task used to measure self-recognition is sensitive to practice effects, and not able to capture the subtle changes in self-face representation following a successful induction of the ‘enfacement’ illusion. A review of studies that used the ‘enfacement’ paradigm, and objectively measured changes in self-recognition between synchronous and asynchronous IMS, shows that five studies used a static photo task to measure self-recognition (Cardini et al., 2013; Maister, Banissy, & Tsakiris, 2013; Sforza, Bufalari, Haggard, & Aglioti, 2010; Tajadura-Jiménez, Longo, et al., 2012; Tajadura-Jiménez et al., 2013), while two used a morphing video task (Tajadura-Jiménez, Longo, et al., 2012; Tsakiris, 2008, for a full review see Chapter 1). Of the two that used a morphing video task, both paradigms differed to that used in the current study. Firstly, the videos were of a longer length than those used in the current study (50sec and 100sec: Tajadura-Jiménez, Longo, et al., 2012; Tsakiris, 2008). Secondly, participants responded to the videos in short blocks, consisting of one video, an IMS session, and a second video (within each block only one direction of video was shown). These differences between the paradigms used by previous research and the experiment in this chapter could go some way to explaining the results of the current experiment. Specifically, the current study had a larger number of trials than previous enfacement research using a video morphing self-other recognition task, and these were intermixed before and after only one session of IMS.

The results of the current experiment may reflect a learning effect, as participants become more familiar with what the IMS face looks like throughout the video morphing tasks and the IMS session. Before taking part in the experiment, participants had never seen the face of the IMS individual, but through exposure to the IMS face during the video morphing task and the IMS sessions, participants would have come to recognise the face. The results of the current study showed that regardless of synchronicity of the IMS, the direction of the morphing video, or the type of tDCS received, participants always responded following IMS at a point in the video when more of the other’s face was visible. This might reflect a more stringent criterion for recognising the other’s face, following increased familiarity with what the other looked like throughout the experiment. As participants became more familiar with the other’s face, they may have started to respond at a point where more of the other's face was visible, to match with their newly formed concept of what the other's face looked like. The video task used in this experiment would be far more susceptible to this type of learning effect than static image tasks used in other enfacement research due to the fact that participants repeatedly, and knowingly, saw the endpoint of the self-other morph representing 100% the other's face at the beginning of the other-to-self direction of morphing videos. Therefore, on half of the trials, participants began by seeing what the other's face actually looked like. In static image tasks, the images are randomised so that participants are unaware of which image truly represents 100% other, and are therefore less likely to produce up an accurate representation of the other's face during the self-other recognition task. It is important to make a comparison here between the video morphing task used in Experiment 1 and the task used in the current Chapter. In Experiment 1, participants only performed the video morphing task twice: once before and once after tDCS, compared with six times in the current Experiment (with each IMS face). Furthermore, in Experiment 1 participants were already familiar with the other's face in the videos as they themselves had chosen a famous person with which they were highly familiar. Therefore, the same learning effect would not have been present in the video morphing task in Experiment 1.

Because of the potential practice effects of the morphing video task, it is difficult to conclusively tell whether there was an effect of anodal tDCS over IPS on multisensory integration. Analysis of the questionnaire data did not indicate a difference in the subjective experience of the illusion between tDCS types, but it is unclear whether this would indicate that there was no effect at all of the tDCS on multisensory integration, or whether different brain areas are involved in producing the subjective experience of ownership over a seen face, from those involved in integrating visual and tactile experiences in order to produce coherent representations of the body. Apps et al. (2013), in their brain imaging study of the Enfacement Illusion, found that the IPS, IOG and TPJ all showed activity that varied parametrically with the extent to which the illusion was experienced. IPS is thought to be involved in updating representations of the body via the integration of multisensory information, which then result in predictions being formed about upcoming somatosensory input to the body (Blanke, 2012). The TPJ also integrates multisensory information and is important in processing of the first person perspective (Ionta et al., 2011), but additionally, TPJ has also been implicated in the processing of other's mental perspectives (Decety & Lamm, 2007; Frith & Frith, 2006; Santiesteban et al., 2012). This indicates that activity in TPJ may reflect the extent to which both self, and other people's perspectives are being processed. Interestingly, Apps et al. (2013) observed a reduction in TPJ activity during synchronous IMS, scaled with the experience of enfacement, which they suggest could indicate that participants were representing and experiencing the other's face as their own during synchronous IMS, rather than a separate individual. It could be that the subjective experience of identifying with the IMS face relies more closely on processing within the TPJ, and thus was not affected by the tDCS manipulation of the current study. Although, it is important to note that the TPJ is connected to the ventral IPS (reference), and therefore it may be expected that the extent to which the illusion is experienced subjectively – if this is dependent on activity in TPJ – would also be linked to the functioning of IPS during multisensory integration.

It is also possible that the current study found no effect of tDCS on the magnitude of the Enfacement Illusion because the tDCS targeted only one area of a wider network that contributes to the updating of body-representations through multisensory integration. As previously stated, activity within TPJ, IPS and IOG has been shown to vary parametrically with the extent to which the Enfacement Illusion is being experienced (Apps et al., 2013). The experience of the illusion therefore is likely to rely on the interplay between, at least, these three brain regions. It may not be possible to influence the strength of the illusion by manipulating neuronal excitability in just one part of this network (IPS). If the effects of multisensory integration on self-updating and self-recognition reply on processing in a wider network of areas, increasing excitability in one area may not have an overall effect on the illusion while the excitability of neuronal populations in other areas remains unchanged, leading to a bottleneck processing effect.

In conclusion, it is difficult to interpret from the results of the current study whether tDCS over IPS affected self-recognition when viewing the self-other morphing videos following synchronous IMS. However, it did not appear to affect the subjective experience of the synchronous IMS, as measured by the IMS questionnaire and IOS scale, which may suggest that anodal tDCS of IPS did not increase the magnitude of multisensory integration on self-face updating. It is speculated that this could be due to IPS's role as a part of a wider network involved in integrating multisensory stimulation during the Enfacement Illusion, in which the interplay between different areas produces the enfacement experience. Increasing excitability in one area may not be able to enhance the effect of synchronous IMS as other brain areas also critically contribute to the processes of updating one's face representation and identifying with a new face.

6 The role of primary somatosensory cortex in self-identification and self-updating

6.1 Introduction

In the previous Chapter, Experiment 3 investigated the invovlement of IPS in *self-identification* and *self-updating* during the Enfacement Illusion. In this Chapter, Experiment 4 will investigate how the primary somatosensory area (S1), as part of the somatosensory mirror system, may contribute to these two processes by representing observed and experienced tactile stimulation.

Chapter 1 of this thesis introduced the idea that *self-identification* and *self-updating* rely on mechanisms of multisensory integration, by coupling unimodal visual and tactile information about the body in order to update existing mental body representations (Tajadura-Jiménez, Grehl, & Tsakiris, 2012). Touch on the skin is conveyed to the primary somatosensory cortex, which is then mapped onto a stored mental representation of the body – localising the touch to a particular body part. This tactile information then converges with visual information in multisensory brain areas, i.e. the intraparietal sulcus and rTPJ (Apps et al., 2013). Here, the tactile and visual information is integrated, leading to an updated self-face representation. Thereby the process of self-recognition is not simply a comparison of what is seen in the mirror with a stored representation of one's face, but relies on a complex network of brain regions which integrate incoming sensory information about the body with pre-existing and continually updated body representations. The role of multisensory integration in body updating can be observed experimentally with bodily illusions (e.g. RHI and Enfacement Illusion), which manipulate sensory inputs under experimental conditions to induce changes in body ownership and representation. Neuroimaging research combined with bodily illusions has highlighted a number of brain regions that may be involved in multisensory integration during self-updating (Apps et al., 2013). However, to date there has been little research employing the techniques of noninvasive brain stimulation to provide causal evidence of the involvement of specific regions in this process. The current chapter aims to investigate the role of the primary somatosensory area (S1) in the perception of touch and its contribution to self-updating. Specifically, Experiment 4 will combine a well reported bodily illusion (the Enfacement Illusion) with non-invasive brain stimulation (tDCS) to explore the causal involvement of S1 in self-updating.

The conscious experience of touch depends on a close link between somatic sensory receptors on the skin and activation of a specific population of neurons in S1 (Serino & Haggard, 2010). When the body is touched, peripheral signals from the skin are conveyed by the dorsal column-medial lemniscus pathway to S1 of the contralateral hemisphere. The neurons in S1 code the spatial properties of the tactile stimulation relative to the body. Within S1, the neurons comprise a topographically organised map of the contralateral side of the human body. Thus, tactile stimulation to a body part will elicit activation in a specific part of S1. The relationship between localisation of touch on the body and activation of the corresponding part of the somatosensory homunculus has been reported in both humans and animals (Penfield & Boldrey, 1937; Kaas, Nelson, Sur, Lin, & Merzenich, 1979; Yang, Gallen, Schwartz, & Bloom, 1993). However, evidence for reorganization of this 'map' following peripheral (e.g. amputation), or central (e.g. lesion) modifications, suggests that there is not a hard-wired link between the perception of touch on the body and activation of a specific part of S1 (Medina & Coslett, 2010). In line with this, it is suggested that the localisation of physical touch to the body is a two-step process. Firstly, the tactile stimulus is localised within the somatotopic map within S1, which codes its location relative to other locations within the map. Secondly, the location of the touch within the somatotopic map is mapped onto structural and postural representations of the body (Longo, Azañón, & Haggard, 2010; Medina & Coslett, 2010; Serino & Haggard, 2010). Following the mapping of the somatotopic touch onto the pre-existing body models, the physical experience of touch is localised to the corresponding body part.

Under certain conditions, the human somatosensory system can also be activated in the absence of tactile stimulation. In a somatosensory analogue of the human mirror neuron system that represents both executed and observed actions (Rizzolatti, 2005), the human somatosensory system appears to reflect the tactile experiences of others (Keysers, Kaas, & Gazzola, 2010). SII, and parts of SI, have been shown to be vicariously activated during the perception of touch being delivered to other people (Schaefer, Xu, Flor, & Cohen, 2009; Blakemore, Bristow, Bird, Frith, & Ward, 2005; Keysers et al., 2004). Crucially, BA3 (within SI) is never activated during the observation of touch to others, but only when we are touched ourselves (Keysers et al., 2010). This lack of vicarious BA3 activation may be the crucial factor that accounts for the fact that we can neurally represent others' tactile experiences but do not consciously experience them as qualia on our own body (Keysers et al., 2010). In support of this, vicarious activation of BA3 has been observed in a sub-set of synathestic individuals (mirror-touch synathetes) who experience the sensation of touch on their own bodies when viewing other people being touched (Blakemore et al., 2005).

Blakemore et al. (2005) provided the first report of an individual with vision-touch, or 'mirror-touch' synesthesia (MTS). When 'C' observed another person being touched on their body, she experienced the sensation of tactile stimulation on the same part of her body. Blakemore et al. (2005) used fMRI to compare activation in C's brain during the observation of touch with non-synesthetic controls. In C, the observation of another person being touched was associated with heightened activation of the somatosensory system, and additional activation in the central sulcus (roughly corresponding to BA3). A recent tDCS study in neurotypical individuals supports the idea that the experience of synaesthetic touch in MTS may be in part due to overactivity in the somatosensory system. Bolognini, Miniussi, Gallo, and Vallar (2013) induced MTS-like effects in non-synesthetic participants by applying anodal tDCS over S1 while the participants performed a vision-touch interference task (specifically designed to test MTS). The increase in cortical excitability in S1 caused participants to become slower at localising a tactile stimulus delivered to their hand when they viewed a video of the opposite hand being touched, similar to typical task performance for individuals with MTS.

Maister et al. (2013) tested whether the remapping of observed touch in individuals with MTS could lead to changes in the self-face representation. Participants took part in a modified enfacement paradigm in which they performed a self-recognition task before and after watching a typical enfacement video, except that during the video they did not receive any touch to their own face (neither synchronous nor asynchronous). In a control group of participants without synesthesia, no change in self-recognition was observed following the enfacement video. However, the participants with MTS reported feeling tactile stimulation on their own face when they watched the other person being touched; showed corresponding subjective reports of self-other blurring; and demonstrated behavioural change in self-recognition akin to the typical Enfacement effect. The results show that synesthetic touch, in the absence of physical touch, is able to update the mental representation of the self-face, reflecting the typical process of self-updating during the Enfacement Illusion. Taken together with theories of MTS, this suggests that activity in S1 contributes to self-updating during multisensory integration by representing the experienced physical touch in the brain.

Experiment 4 aimed to explore the involvement of S1 in self-updating by using tDCS to enhance cortical excitability in S1 in an attempt to induce MTS-like somatosensory mirroring effects. The experiment compared the effect of anodal tDCS over S1 with a control condition of sham stimulation. Participants took part in two experimental sessions, on separate days, which were the same except for the type of tDCS delivered at the beginning of each session. In one session, participants received 20 minutes of anodal tDCS over S1, while in the control session they received 20 minutes of sham stimulation. Following stimulation, participants performed a self-recognition task before and after watching an IMS video in which an unfamiliar person was stroked on the cheek but, unlike in the typical Enfacement Illusion, the participant did not receive touch to their own face. Performance on the self-recognition task before IMS was compared to the performance following IMS. The interaction between the timing of the self-recognition task and the type of tDCS received was explored. It was hypothesised that there would be a change in self-recognition performance following IMS in the anodal condition, as the enhanced cortical excitability of S1 would lead to above threshold vicarious activation in this area in response to the observation of the other's face being touched in the IMS video. This would result in the conscious experience of touch, and lead to the integration of the visual information in the video with the tactile sensation, resulting in a change in the stored self-face representation. It was further hypothesised that the magnitude of the change would be positively related to individual differences in empathic traits because previous research has reported of higher levels of empathic ability in individuals with MTS (Banissy & Ward, 2007), as well as a positive relationship in neurotypical individuals between empathic ability and the vicarious recruitment of S1 while observing touch delivered to others (as measured by the Perspective Taking sub-scale of the Interpersonal Reactivity Index) (Schaefer, Heinze, & Rotte, 2012).

6.2 Materials and Methods

6.2.1 Participants

30 participants volunteered to take part in the study. Two participants did not complete the second session of the experiment and so were not included

in the analysis, leaving 28 complete data points. All participants were female and had normal or corrected-to-normal vision (Mean age = 21.5 years, SD = 2.5; Right-handed = 23, Left-handed = 5). All participants were screened for contraindications to tDCS before taking part, and provided signed informed consent before the experiment began. The study was approved by the Royal Holloway, University of London Ethics Committee.

6.2.2 Design

The study employed a sham-controlled, double-blind, repeated measures, within-subjects design, with factors Type of Stimulation (anodal vs. sham) and Timing of self-recognition task (Pre-IMS vs. Post-IMS). All participants took part in two sessions, separated by at least 24 hours, in which they received active stimulation in one session and sham stimulation in the other. The order of the stimulation sessions was counterbalanced across participants.

6.2.3 Procedure

All participants took part in two experimental sessions. At the beginning of the first session, participants filled out the Interpersonal Reactivity Index (IRI) as a measure of empathy. Each session started with 20 minutes of tDCS (either anodal or sham stimulation) over right S1. Participants then performed a self-recognition task both before and after watching an IMS video in a no-touch IMS session session (where they watched a face being stroked but were not touched themselves). Both experimental sessions were identical, except for the type of stimulation received (Active or sham), and the identity of the face seen in the self-recognition task and IMS video. The identity of the face in the self-recognition task and IMS video was held constant within each stimulation condition, but differed between stimulation conditions. The identitiy of the IMS face was not a factor in the design, but a different face was used for each session to avoid carry over effects from the previous session. See Figure 6.1C.

FIGURE 6.1: (A) An example of the morphed images presented to participants in the self-recognition task. (B) A frame from the IMS video. (C) The experimental procedure.

6.2.4 tDCS Parameters

In the anodal session, participants received anodal stimulation to the right S1, contralateral to the side of the face that would have received tactile stimulation during the IMS session. The electrode positions were localised using the EEG 10/20 system, with the anodal electrode placed centrally over the point 2cm posterior from EEG electrode position P4 to stimulate S1, and the reference electrode over the contralateral supraorbital area (Bolognini et al., 2013). Participants received stimulation for 20 minutes at an amplitude of 1.5mA (fade in time: 30sec; fade out time: 30sec).

6.2.5 Stimuli and Tasks

6.2.5.1 Self-Recognition Task

Before the experimental session a photograph was taken of each participant's face with a neutral expression. All photographs were converted to greyscale, flipped horizontally so as to reflect the orientation of the self-face that participants would be most accustomed with (from mirror exposure), and a template was applied around the face to remove hair and non-facial features. All photo manipulation was completed using Adobe Photoshop CS6. The same procedure was also applied to photographs of two gender-matched unfamiliar individuals. The participant's face was then morphed with each of the two unfamiliar faces separately, creating two sets of morphed images images (one for use in each session - anodal/sham). The face morphing software Abrasoft Fantamorph (www.fantamorph.com) was used to create a morphing continuum between each pair of faces. 25 images representing 4% steps of morphing between the two faces were exported. See Figure 6.1A.

In each session, one of the sets of morphed images was used for both the pre-IMS and post-IMS self-recognition task. Each trial of the self-recognition task began with a central fixation cross, presented for 500-1500ms. One of the 25 morphed face images was then presented for 2000ms, replaced by a sliding scale consisting of a vertical line marked with 100 at the top and 0 at the bottom. Participants used a mouse to rate on the scale how much the presented face resembled their own face. Participants had as much time as they required to give their response, but were encouraged to go with their initial instincts about the photos and respond quickly. Images were presented in a randomised order. Each of the 25 images was repeated four times per block (pre-IMS and post-IMS), resulting in a total of 100 trials per block. The identity of the face morphed with the participant's face for the self-recognition task matched the face seen in the IMS video within the same session. The order of the morphing face identities (first session or second session) and the pairing between each identity and each type of stimulation (anodal and sham) was counterbalanced across participants.

6.2.5.2 No-touch Interpersonal Multisensory Stimulation Session

Following the first block of the self-recognition task, participants took part in a 'no-touch' IMS session. For two minutes participants watched a typical IMS video in which the face in the video was stroked on the cheek approximately every 2 seconds, however, participants received no touch themselves during this time.

The person in the video was always touched on their right cheek, which was contralateral to the tDCS site (right S1) from a specular perspective. The rationale for this was that when looking at a pair of hands from a first-person perspective, the induction of mirror-touch synesthesia in non-synaesthetes through tDCS was only effective when visual touch was contralateral to tDCS (Bolognini et al., 2013), suggesting the use of an anatomical frame of reference. As for observed touch to faces, Blakemore et al. (2005) provide functional MRI support for an anatomical reference frame as well. In non-synesthetes viewing videos of faces being touched, S1 activation was observed contralateral to the side of the face being touched, such that touch to the left side of a face activated right S1. However, one's own face is only ever viewed in the mirror, which supports the relative bias among mirror-touch synesthetes towards a specular frame of reference when observing touch to a face (Banissy, Cohen Kadosh, Maus, Walsh, & Ward, 2009). When mirror-touch synaesthetes experience the Enfacement Illusion in a no-touch condition (Maister et al., 2013), they must be using a specular reference frame – and experiencing touch on the same side of their face as the touch in the video (from a specular perspective, not anatomically) – otherwise the illusion would not work. Therefore, for the illusion to work through the inducement of mirror-touch synesthesia by tDCS, the observed touch must be contralateral to the tDCS site (from a specular perspective), and ipsilateral anatomically. See Figure 6.1B.

6.2.6 Scales

6.2.6.1 Interpersonal Multisensory Stimulation Questionnaire

The IMS Questionnaire was used to measure the subjective experience of the Enfacement Illusion. For a full description of the questionnaire see Section 5.2.3.3. One adaption was made to the Touch Referral sub-scale of the questionnaire, removing the item "The touch I saw on the other's face was caused by the cotton bud touching my own face", leaving nine items.

6.2.6.2 Inclusion of Other in the Self Scale

The IOS Scale was used to measure the subjective sense of overlap between the participant and the IMS individual. See Section 5.2.3.4 for a full description of the scale.

6.2.6.3 Interpersonal Reactivity Index

In their first experimental session, before receiving tDCS, participants completed the Interpersonal Reactivity Index (IRI) as a measure of empathic ability. The IRI is a 28-item measure, answered on a 5-point likert scale, from “Does not describe me well” to “Describes me very well”. The items in the scale are split up into 4 sub-scales, containing 7 items each: Perspective Taking, Fantasy, Empathic Concern and Personal Distress (Davis, 1983). Higher scores on the scale represent better empathic ability.

6.2.7 Data Analysis

The participants’ ratings of the morphed-face stimuli in the self-face recognition task were fitted into a sigmoid statistical model to determine the percentage of morphing at which participants judged the amount of their own face and the other face to be equal – the ‘point of subjective equality’ (PSE; Sforza et al., 2010). This resulted in four PSE values per participant, i.e. the baseline and post-IMS self-recognition tasks for both the anodal and sham tDCS sessions. These values were used in the analysis to investigate the effect of tDCS over S1 on self-updating.

6.3 Results

6.3.1 IMS Questionnaire and IOS Scale Analysis

First, the subjective effect of the IMS video was investigated by analysing data from the IMS questionnaire and IOS scale. A two-way within-subjects ANOVA was conducted with factors Type of Stimulation (anodal vs. sham) and sub-scale (4 sub-scales: Similarity, Ownership, Control and Touch Referral). There was no main effect of Type of Stimulation, indicating that the subjective experiences of the IMS session did not differ depending on whether participants received tDCS to S1 or sham stimulation: $F(1, 27) = 1.761$, $p = .196$, $\eta^2 = .061$. For both the main effect of sub-scale, and the interaction between Type of Stimulation and sub-scale, Mauchly’s test of Sphericity was

Table 6.1: Mean scores on the sub-scales of the IMS Questionnaire and the IOS Scale across both tDCS conditions.

	Sub-scale				
	Ownership	Similarity	Control	Touch Referral	IOS
Anodal	1.7 (1.61)	2.13 (1.74)	2.38 (1.44)	1.39 (1.99)	2.5 (1.26)
Sham	1.57 (1.38)	2.41 (1.72)	2.67 (1.32)	2.39 (2.15)	2.75 (1.27)
Sig.*	0.65	0.38	0.26	0.04*	0.45

*Comparisons are significant at alpha level of .05.

significant, indicating that the assumption of Sphericity was not met (both *p*s < .001). Therefore, Greenhouse-Geisser corrected p-values were applied for the main effect of sub-scale and the interaction between Type of Stimulation and sub-scale. There was a significant main effect of sub-scale: $F(1.787,\ 48.24) = 4.13$, $p = .026$, $\eta^2 = .133$. Bonferroni corrected pairwise comparisons indicated that scores on the Ownership sub-scale were significantly lower than both the Similarity and Control sub-scales ($p = .01$, $p < .001$ respectively). There was also a significant interaction between sub-scale and Type of Stimulation: $F(1.854,\ 50.065) = 4.071$, $p = .026$, $\eta^2 = .131$. Paired samples t-tests indicated that there were no significant differences between anodal and sham stimulation on the Ownership: $t(27) = .462$, $p = .648$, Similarity: $t(27) = -.9$, $p = .376$, and control sub-scales Control, $t(27) = -1.151$, $p = .26$. There was a significant difference between anodal and sham stimulation on the Touch Referral sub-scale, $t(27) = -2.16$, $p = .04$, indicating a stronger experience of touch referral following sham tDCS compared with anodal tDCS. Average responses on all sub-scales in both stimulation conditions can be seen in Table 6.1.

Responses on the IOS scale were compared across both experimental sessions using a paired-samples t-test. There was no significant difference in self-other overlap between S1 tDCS and sham stimulation as measured by the IOS scale: $t\ (27) = -.893$, $p = .38$.

6.3.2 Self-Recognition Task Analysis

Next, the analysis explored whether tDCS over S1 (relative to sham stimulation) elicited a change in self-recognition when participants watched the IMS video but did not receive touch to their own face. The PSE values were entered into a 2-way repeated measures ANOVA with factors Type of Stimulation (anodal vs. sham) and Timing (pre-IMS vs. post-IMS). There was a significant main effect of Type of Stimulation: $F(1,\ 27) = 8.372$, $p = .007$, $\eta^2 = .237$, reflecting that, regardless of Timing, PSE values were lower in the sham session than the anodal session (sham $M = 48.70$, anodal $M = 51.56$). There was also a main effect of Timing: $F(1,27) = 16.574$, $p < .001$, $\eta^2 = .38$, reflecting the fact that in both anodal and sham sessions, the PSE was lower after watching the IMS video (Pre-IMS $M = 51.79$, Post-IMS $M = 48.54$). The interaction between Type of Stimulation and Timing was not significant, indicating that the effect of tDCS to S1 on self-updating did not differ from the control condition of sham stimulation. See Figure 6.2.

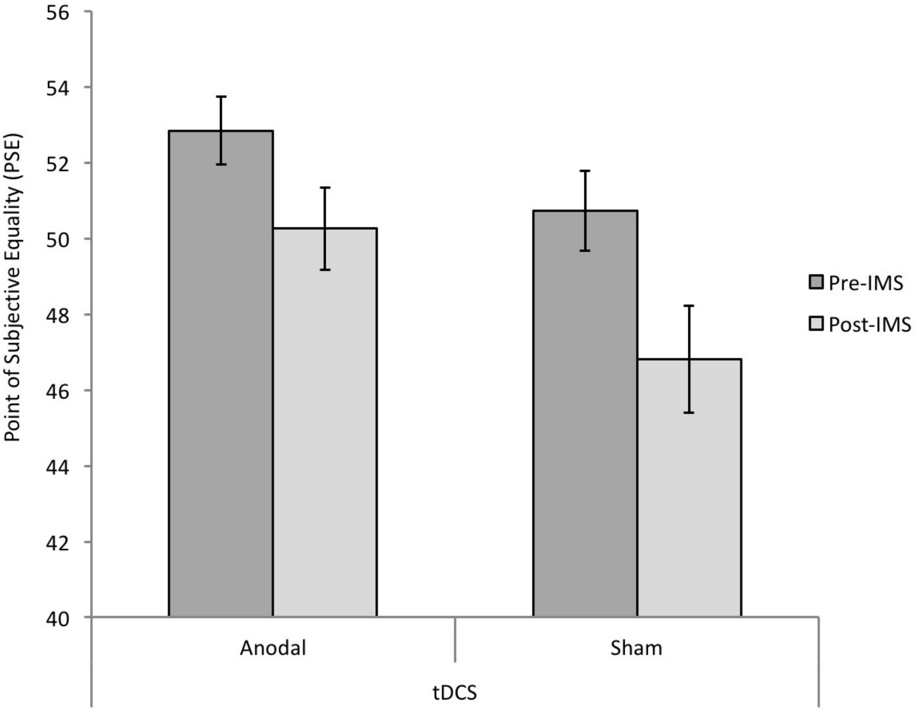

Figure 6.2: PSE scores for the anodal and sham stimulation sessions, before and after the no-touch IMS session. There was a main effect of Timing, and a main effect of tDCS.

6.3.3 Interpersonal Reactivity Index Analysis

To investigate whether changes in PSE were related to empathic traits, change scores were calculated to reflect the magnitude of the change in self-recognition. These were calculated as Post-IMS minus Pre-IMS, such that a negative value would indicate a lower PSE following the IMS video, reflecting less of the self-face visible at the PSE. The change score for the anodal and sham sessions were entered as the outcome variables into two separate multiple regressions with the sub-scales of the IRI (Perspective Taking, Fantasy, Empathic Concern, Personal Distress) as predictor variables.

In the anodal condition, scores on the IRI explained 13.5% of the variance of the PSE change between post- and pre-test. The overall model was not significant in predicting the change in PSE score: $F(4,\ 21) = 1.98$, $p = .135$. Individually, Fantasy ($\beta = .403$, $t = 1.703$, $p = .103$), Empathic Concern ($\beta = -.256$, $t = -1.144$, $p = .266$) and Personal Distress ($\beta = .295$, $t = 1.374$, $p = .184$) did not significantly predict PSE change score. However, scores on the Perspective Taking sub-scale did significantly predict PSE change score ($\beta = -.581$, $t = -2.226$, $p = .037$). Higher scores on the Perspective Taking sub-scale (reflecting better cognitive empathic ability), predicted more of a reduction in PSE following the IMS video (reflecting more of an inclusion of the other's face in the self-face representation). See Figure 6.3.

For the regression on PSE change score in the sham condition, the overall model was not significant: $F(4,\ 21) = .86$, $p = .504$. Individually, none of the sub-scales significantly predicted PSE change score: Perspective Taking: $\beta = -.102$, $t = -.265$, $p = .794$; Fantasy: $\beta = -.413$, t = -1.184, $p = .25$; Empathic Concern: $\beta = -.188$, $t = -.57$, $p = .575$; Personal Distress: $\beta = .173$, $t = .546$, $p = .591$.

6.4 Discussion

Experiment 4 aimed to induce mirror-touch synesthetic-like symptoms in non-synesthetic participants through the modulation of cortical excitability in

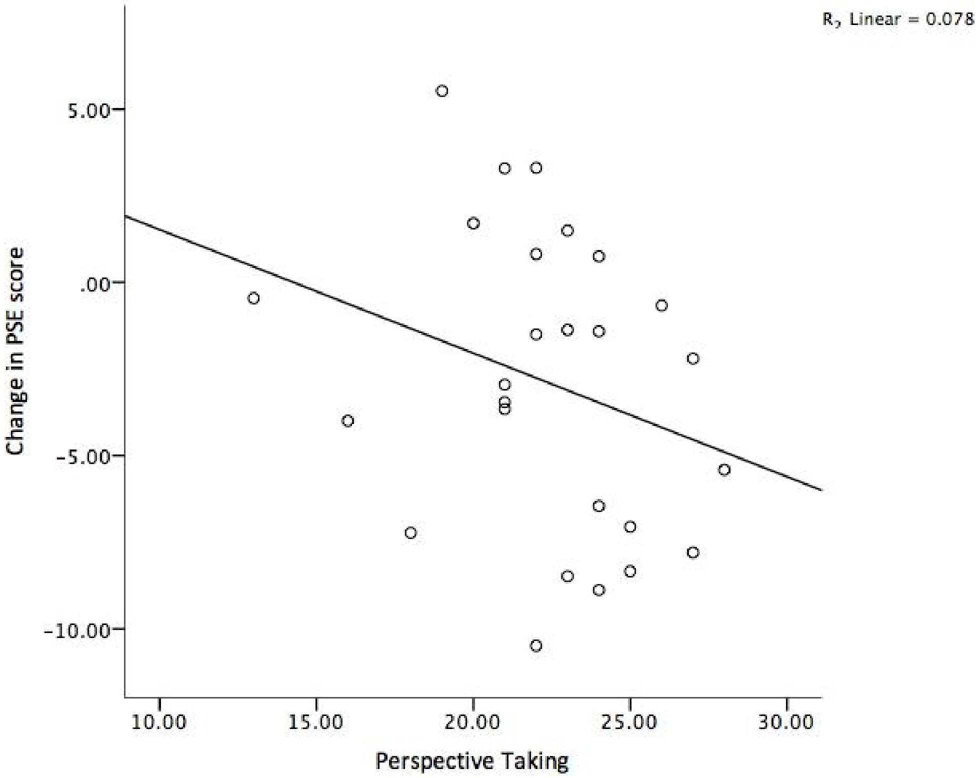

Figure 6.3: Higher Scores on the Perspective Taking sub-scale of the Interpersonal Reactivity Index predicted larger decreases in PSE score following the no-touch IMS session in the anodal tDCS session.

S1, using anodal tDCS as a means to investigate self-identification and self-updating in neurotypical individuals. Following 20 minutes of tDCS, participants took part in a typical enfacement paradigm, except that during the IMS session the participants did not receive any touch to their own face. It was hypothesised that after receiving anodal tDCS over S1, a change in self-recognition akin to the typical enfacement effect would be observed following the IMS session. This would result from the integration of the observed tactile stimulation (in the IMS video) with synesthetically experienced touch induced through tDCS of S1. This would be in line with theories of body-representation and body-ownership which suggest that S1 plays a role in maintaining and updating current representations of the body (Tsakiris, 2010). The results of Experiment 4 indicated that anodal tDCS over S1 did not facilitate self-updating following the no-touch IMS session. The analysis of the change in PSE following the non-touch IMS session indicated that there was no difference in changes in PSE between the anodal and sham tDCS session. The following discussion will consider possible explanations for the lack of a specific effect of tDCS on self-recognition following the no-touch IMS video

Firstly, the lack of a specific behavioural effect of anodal tDCS over S1 suggests that the manipulation may not have been effective at inducing overactivity in the somatosensory mirror system. Agreement with the statement 'I felt touch on my face when I saw the other being touched' (from the Touch Referral sub-scale of the enfacement questionnaire) did show a significant difference between anodal and sham sessions, but it was in the sham session that participants reported higher subjective experiences of touch referral. Despite this difference between anodal and sham session, it is important to note that the mean responses on the touch referral sub-scale indicated that participants did not consciously experience touch on their own face when they observed the other being touched in either session. Mean scores for both sessions reflected disagreement with the statement 'I felt touch on my face when I saw the other being touched'. This suggests that the modulation of cortical excitability in S1 with anodal tDCS did not induce the conscious experience of tactile stimulation when observing another person being touched. It is important to note that a previous application of anodal tDCS over S1 did not elicit differences in explicit subjective reports of synesthetic touch, but did induce synesthetic-like effects that manifested at the level of reaction time differences (Bolognini et al., 2013). As such, a lack of conscious experience of synesthetic touch does not mean that 'sub-threshold' synesthetic symptoms were not induced by anodal tDCS in the current experiment. However, given that the results indicated that there was a similar change in PSE following the IMS video in both the anodal and sham stimulation conditions, they suggest that any effect of the tDCS manipulation did not play a specific role in updating stored self-face representations. Despite this, it is interesting that any change in at all in PSE was observed following the no-touch IMS session, as during the session there was no conscious experience of tactile stimulation to be integrated with the observed touch. Explanations for the lack of a specific effect of tDCS, as well as the finding of a change in PSE in both tDCS sessions, will be discussed below.

Firstly, there may be brain areas other than S1 that are critically involved in the experience of synesthetic touch during observation of tactile stimulation. Blakemore et al. (2005) showed that individuals with MTS showed increased activity in BA3 corresponding to the observation of touch on other peoples' bodies and the experience of synesthetic touch. In neurotypical individuals, BA3 is never vicariously activated by the observation of touch to other people, suggesting that BA3 may maintain boundaries between the sensory experiences of the self and others (Keysers et al., 2010). Banissy et al. (2009) suggested that overactivity in the somatosensory system in MTS is mediated by mechanisms involved in the process of self-other discrimination, causing a blurring of self-other boundaries and the misattribution of another's experience of touch to the self. Banissy et al. (2009) speculate that areas involved in self-other discrimination, including the IPL and IFG, are overactive in MTS and cause other's bodies to be incorporated into the representation of the synaesthetes body. Interestingly, the studies by Heinisch et al. (2011, 2012) and Uddin et al. (2006) as well as Experiment 1 in this thesis, provide causal evidence that disruption of typical functioning in the temporoparietal area and the encompassing IPL can cause a blurring between representations of the self and other. It may be the case that, without disruption to the mechanisms of self-other discrimination, vicarious activation of the somatosensory cortices will not be attributed to the self. Therefore, even in the case of heightened neuronal excitability in S1 induced by anodal tDCS, vicarious activation during the observation of touch to another would not be experienced as synesthetic touch to the self.

With regard to the finding that there was a change in PSE following the no-touch IMS session in both tDCS sessions, firstly, the change in PSE could have been a result of increased familiarity with the IMS face. Research suggests that familiar others can become integrated within our own self-concept, altering cognitive processing of the other (Aron, Aron, Tudor, & Nelson, 1991; Aron & Aron, 1996; Aron & Fraley, 1999). Observing the other's face for two minutes immediately preceding the second self-recognition task may have made the face sufficiently familiar as to change the perception of the boundary between self and other. However, the inclusion of others into the self-representation tends to reflect the level of personal closeness, rather than merely familiarity with another (Symons & Johnson, 1997). Furthermore, in previous research using the Enfacement Illusion, when the participants received tactile stimulation that was asynchronous with the touch observed in the IMS session, there was no change in self-recognition performance despite the fact that participants saw the IMS face during the session and thus also became more familiar with it (e.g. Tajadura-Jiménez, Grehl, & Tsakiris, 2012; Tajadura-Jiménez et al., 2013; Tsakiris, 2008). Taken together, these results could suggest that the familiarity developed with the other's face during the IMS-session is not sufficient to induce an inclusion of the IMS-face into the self-face representation. To control for this possibility, a follow-up study should compare changes in self-recognition following an IMS session in which the IMS face is not touched at all, with an IMS session in which only the participant does not receive touch (such as the IMS session in the current experiment). This would create the same level of familiarity between the participant and the IMS individual, and thus provide evidence to clarify the question of whether a mere increase in familiarity with a face is sufficient to change one's self-face representation.

Alternatively, the results of the current study could suggest that vicarious, sub-threshold somatosensory resonance with another individual is ever-present (i.e. even in the sham condition), and under certain conditions, is able to elicit a change in self-recognition. Research on the human mirror neuron system (MNS) has shown that during action observation, areas of the brain involved in the execution of the observed action are activated (Rizzolatti, 2005). This vicarious activation of the motor system during the observation of action can have measurable effects on behavioural. For example, vicarious activation of the motor plan of an observed action can facilitate performance of that action (Brass, Bekkering, Wohlschläger, & Prinz, 2000; Craighero, Bello, Fadiga, & Rizzolatti, 2002). More recently the idea of a somatosensory mirror system has been proposed, following evidence of vicarious activation of S1 during the observation of touch to another person (Blakemore et al., 2005; Keysers et al., 2004; Schaefer et al., 2012). Along the same lines of action facilitation during action observation in the mirror neuron system, evidence shows that vicarious somatosensory activity in response to the observation of another person being touched can also affect behaviour. For example, the detection of near-threshold touch to one's own face can be enhanced by watching another person's face being touched in a congruent location (Serino, Pizzoferrato, & Làdavas, 2008). Similarly, somatosensory areas show vicarious activation when observers view emotional faces (Winston, O'Doherty, & Dolan, 2003). Moreover, when this activity is disrupted by TMS or brain injury, emotional recognition suffers (Adolphs, Damasio, Tranel, Cooper, & Damasio, 2000; Pourtois et al., 2004), suggesting that neurological mirroring of other's facial expressions in somatosensory areas contributes to emotional detection. In summary, past research implies that automatic, vicarious activation of the somatosensory system occurs in response to the observation of other peoples' tactile experiences (or emotional facial expressions), and that this activation can facilitate the sharing of that experience in the observer. Considering this, watching the IMS video in the current Experiment is likely to have elicited vicarious activation of the participants' somatosensory cortices, mirroring the experience of the person in the video, regardless of whether participants received anodal tDCS or sham stimulation. This activation, while sub-threshold for the physical experience of touch, may have had an effect on the stored representation of the self-face in a similar way to activation elicited through actual touch.

Although multisensory bodily illusions rely on the integration of both observed touch and physically experienced tactile sensations, in the current study, while participants did not receive touch to their own face that was congruent with the touch they observed during the IMS session, they did not receive incongruent touch either. In the classical enfacement paradigm, the typical control condition consists of touch being delivered to the participant's face at a temporally incongruent location to the touch observed in the IMS video. The temporal discrepancy between the observed and the felt touch ensures that these will be processed as discrete events, and will not be combined in multisensory brain areas. Thus, the touch in the IMS video is not judged to be the same touch as that felt on the body. Therefore, the self-face representation is not updated. In the current study, although participants did not receive temporally congruent touch during the IMS session, they also did not receive conflicting tactile stimulation (as asynchronous stroking provides) which would have indicated to them that the face they were observing was not their own. Evidence suggests that vision can have powerful effects on the perception of touch. Pavani, Spence, and Driver (2000) have demonstrated a 'visual capture of touch' effect, in which the perceived location of touch to one's hidden hand was drawn towards a seen rubber hand in an anatomically plausible location, despite being in conflict with proprioceptive information. Therefore, evidence shows that when sensory modalities (visual and proprioceptive) are in conflict, visual information can dominate over proprioception. In the current experiment, the observed touch to the IMS face may have taken precedent over the lack of felt touch on the participant's own body, leading to a remapping of the body schema to include the IMS face, resulting in a change in PSE.

To investigate this possibility further, it would be beneficial for future research to directly compare the effects of synchronous IMS, asynchronous IMS, a no-touch IMS session (where the participant receives no touch), and an IMS session in which neither the participant nor the IMS individual receives touch. It is unlikely that the same magnitude of change in PSE would be observed between the synchronous and no-touch IMS sessions, as the effect of integrated multisensory stimulation on updating one's face representation would certainly be stronger than that of vicarious somatosensory activation experienced alongside observed touch. However, if a difference were found between the asynchronous and no-touch conditions this would provide support for the idea that somatosensory mirroring of touch is able to induce a change in self-recognition which was previously thought to require both physical touch and observed touch.

7 Investigating Novel Mechanisms of Self-Updating

7.1 Introduction

[1] The mental representation of the self is a complex construct, containing both perceptual information (such as information about the physical appearance of the body, e.g. facial appearance), and conceptual information, which is comprised of varied semantic and episodic knowledge relevant to the self. So far in this thesis, Chapters 3-6 have investigated mechanisms involved in the maintenance and updating of the perceptual self-representation. Interestingly, there appears to be modulatory links between the conceptual and perceptual self-representations. Changes in the bodily self-representation have been shown to elicit changes in the way the self is conceptualised (Banakou et al., 2013) and to also elicit changes in social cognition (Maister et al., 2014). However, it is unclear whether changes to the conceptual self can elicit corresponding changes in the perceptual self-representation. In this Chapter, Experiment 5 will investigate whether the mental representation of the self-face can be changed as a consequence of changes to the conceptual self-representation. Experiment 5 will use a recently developed perceptual matching paradigm (Sui, He, & Humphreys, 2012) to create an association between a novel face and the conceptual self-representation, and investigate whether the self-face representation has changed to incorporate the novel face.

The study of self-representations can be split into perceptual and conceptual. The perceptual representation of the self, the main focus of this thesis,

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constitutes information about the physical appearance and proprioceptive information about one's body. The conceptual self-representation encompasses varied semantic information about the self, including personality traits, demographic information and episodic memories (Gillihan & Farah, 2005). Research on the processing of conceptual aspects of self highlights that processing of conceptual self information often benefits from a 'self-reference effect', in which self-relevant information receives prioritised processing relative to information relating to other people, corresponding with research on the processing of the self-face as described in Chapter 1. For example, trait words referring to the self are remembered more accurately than trait words referring to other people (Rogers, Kuiper, & Kirker, 1977). Furthermore, self-relevant stimuli are more likely to grab attention when presented as distractor stimuli, suggesting that self-relevant information may be processed in a highly automatic fashion. Bargh (1982) used a dichotic listening task, in which participants are presented with two streams of auditory information, one in each ear, and attend to only one, to investigate the automatic processing of self-relevant information. It was found that information in the unattended stream only entered conscious awareness when it contained words relating to the conceptual self-representation, and that this information was processed more efficiently than non-self relevant information. Information relating to the conceptual-self also appears to differentially engage neural regions in comparison with information about others. Areas spanning the frontal (medial frontal gyrus) temporal (bilateral superior temporal gyrus) and parietal cortices (inferior parietal lobule) have all shown activity during processing of self-relevant information in contrast with information about other people (Hu et al., 2015), and EEG research suggests that self-information benefits from selective attention (Gray, Ambady, Lowenthal, & Deldin, 2004).

Evidence suggests that conceptual and bodily aspects of self-representation are closely linked, and that changes to the perceptual self-representation can lead to changes to conceptual self-representations (Banakou et al., 2013; Maister et al., 2014; Paladino, Mazzurega, Pavani, & Schubert, 2010). For example, Banakou et al. (2013) demonstrated that after embodying a child-sized body in a virtual reality environment, participants showed implicit associations between themselves and child-like concepts. In another study, Paladino et al. (2010) demonstrated that after experiencing IMS with an unfamiliar face, not only did participants report an increase in perceived physical similarity between themselves and the unfamiliar actor, but the IMS also led them to represent themselves as conceptually closer and more similar to the embodied other (see also Mazzurega, Pavani, Paladino, & Schubert, 2011). However, it remains unknown whether this link is bidirectional; whether a change in conceptual self-representation could lead to a change in the perceptual self-representation. Recent evidence suggests that a bidirectional link may exist. Farmer et al. (2013) report an experiment in which the manipulated trustworthiness of an unfamiliar individual impacted upon perceived similarity between the participant's face and the unfamiliar face. Participants played a trust game with two unfamiliar individuals whose faces were shown on screen. One of the individuals was trustworthy, while the other always betrayed the participant's trust. Before and after the game, participants performed a self-other discrimination task using morphed images (the same task as used to measure the increased perceptual similarity after the Enfacement Illusion; Tajadura-Jiménez, Grehl, & Tsakiris, 2012), to measure the perceived similarity between their own face and the faces of both players. Following the trust game, participants perceived their face to be more similar to the trustworthy individual than the untrustworthy player. This evidence may suggest that changes to the conceptual self-representation can have a modulatory effect on the bodily self-representation, however, as of yet such a link between the conceptual and perceptual self-representations has yet to be properly investigated.

In a series of recent experiments, Sui et al. (2012) elegantly demonstrated the malleability of the conceptual self-representation. Participants first associated geometric shapes with labels for themselves, familiar or unfamiliar others, and then performed a perceptual matching task in which they judged whether subsequent label-shape pairings were correctly matched. Self-associated shapes benefitted from faster reaction times (RT) and increased accuracy, compared to both familiar and unfamiliar shape associations. The authors suggest that the self-associated shape was incorporated into the 'self-template', a rich and well developed schema of the self based on self-knowledge, enabling "fast same" responses (participants are faster to identify when two pieces of information are the same, rather than different; Krueger, 1978). In support of this interpretation, they found that neutral shapes which had been associated with the conceptual self activated brain regions involved in self-representation and self-attention (Sui & Humphreys, 2013), suggesting that the newly-associated shape had been incorporated into the conceptual self-representation.

Experiment 5 will modify the simple paradigm reported by Sui et al. (2012) to investigate whether a bidirectional link between conceptual and bodily aspects of self exists. In this paradigm, Sui et al. (2012) established a rapid association between the self and a previously neutral shape. Robust attentional and perceptual biases in the processing of this newly self-associated shape suggested that the conceptual self-representation was extended to include it. The experiment in this chapter will firstly: develop this paradigm to test whether an unfamiliar face, rather than shape, can be associated with the conceptual self-representation. RT and accuracy data will be analysed to measure for perceptual biases towards the newly self-associated face in order to assess whether it has truly acquired an association with the conceptual self-representation. Secondly, Experiment 5 will investigate whether the bodily self-representation will update correspondingly to incorporate the newly-associated face. The self-face representation will be measured before and after the perceptual matching task using the same self-recognition task as used in Experiment 4. Experiment 5 will therefore assess whether a change in the conceptual self-representation can lead to a change in the bodily self-representation (i.e the mental representation of one's own face).

7.2 Materials and Methods

7.2.1 Participants

28 participants (26 female, mean age 20.07 years, SD 1.12) volunteered to take part in the study. All had normal or corrected-to-normal vision, and were right-handed. Informed consent was given by all participants before their participation, and the study was approved by Psychology Department Ethics Committee, Royal Holloway, University of London.

7.2.2 Stimuli and Tasks

7.2.2.1 perceptual matching task

The current experiment employed an adapted version of Sui et al.'s (2012) shape-label matching paradigm with unfamiliar faces in place of neutral geometric shapes. Three photos of gender-matched unfamiliar faces were converted to greyscale, and a circular template was applied to remove the outer hairline. The faces were presented above a fixation cross, with an identity label presented below. Three identity labels were used: 'Self', 'Friend', and 'Stranger', following Sui et al. (2012). During the task participants were required to judge whether briefly-presented face-label pairings were correct, or incorrect. The same three unfamiliar faces were used throughout the experiment, with the identity label pairings assigned randomly for each participant. The task was run on Presentation (NeuroBehavioural Systems).

The task started with a learning phase, in which all three unfamiliar faces were presented on screen with their matching identity labels written below each one (face-label pairings were counterbalanced across participants). Participants were told that each of the three faces belonged to themselves, their closest friend, or a stranger. Participants had 60 seconds to learn the face-label pairings before starting the perceptual matching task. During the perceptual matching task, a fixation cross was presented at the beginning of each trial for 400ms, followed by a face-label pairing for 200ms. The face-label pairing either corresponded to a pairing seen by participants during the learning phase (match trial), or was a novel pairing (mismatch trial). Participants were then required to judge whether the pairing was correct or incorrect based on what they had learnt during the learning phase. Following presentation of the face-label pairing, participants had 1000ms to respond, using one of two buttons (one for correct, one for incorrect), as quickly and as accurately as possible. Visual feedback for the participant's response was then presented following each trial (correct or incorrect), lasting 500ms. The task lasted a maximum of 15 minutes and was split into three blocks of 80 trials (240 trials total), with 12 practice trials before the first block. At the end of each block participants received visual feedback detailing the accuracy of their performance in the preceding block. Each identity label was presented an equal number of times, with an equal number of match and mismatch pairings, such that there were 40 trials in each condition (self-match, self-mismatch, friend-match, friend-mismatch, stranger-match, stranger-mismatch). Trials were randomised for each participant. It is important to note that, although the Learning Phase and the Matching Phase are differentiated by name, participants continue to learn the associations throughout the Matching Phase as feedback is given on every trial. This procedure is illustrated in Figure 7.1A.

7.2.2.2 Self-Recognition Task

The self-recognition task was the same morphed photos task as that used in Chapter 6, except that 50 morphed images were created instead of 25, representing 2% steps through the self-other morphing continuum. For a full description see Section 6.2.5.1. Briefly: a photograph of each participant's face taken with a neutral expression was morphed separately with the self-associated face, and the stranger-associated face, creating two morphed image sets per participant. Fifty morphed images were created for each set, representing 2% steps from the participant's face to the self/stranger face . During the self-recognition task, each of the 100 images was presented once, and participants rated how similar they perceived the face to their own. The pre-perceptual matching task self-recognition task acted as a baseline measure of self-recognition, and changes

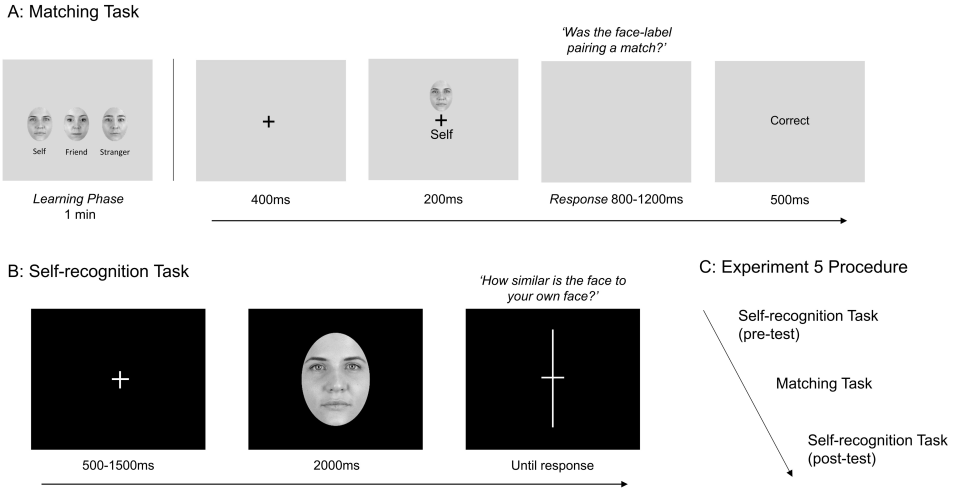

FIGURE 7.1: The experimental design and procedure for Experiment 5. A shows a visual representation of the perceptual matching task. In the Learning Phase all three unfamiliar faces and identity labels (self, friend and stranger) are presented on screen for 1 min. In the Matching Phase, each trial starts with a fixation cross (400ms), followed by a face-label pair (200ms), after which the participant has 1000ms to respond. Following the response, visual feedback is presented for 500ms before the start of the next trial. B shows a trial from the self-recognition task: a random interstimulus interval (ISI) with fixation cross is presented for 500-1500ms, followed by the presentation of one of the morphed images for 2000ms. The sliding response scale then appears until participants make their response. C shows the procedure for Experiment 5: participants complete the self-recognition task, followed by the perceptual matching task, and lastly the self-recognition task again.

from baseline were examined in the post-perceptual matching self-recognition task. We controlled for effects due to mere exposure to the self-associated face by including a control condition in which participants rated morphs between their own face and the stranger-associated face.

Each trial of the self-recognition task began with a central fixation cross, presented for 500-1500ms. One of the 100 morphed face images was then presented for 2000ms, replaced by a sliding scale consisting of a vertical line marked with 100 at the top and 0 at the bottom. Participants used a mouse to rate on the scale how much the presented face resembled their own face. Participants had as much time as they required to give their response, but were encouraged to go with their initial instincts about the photos and respond quickly. Images from both morphing sets ('self' and 'stranger') were intermixed and presented in a randomised order. The procedure is presented in Figure 7.1B.

7.2.3 Procedure

Participants performed the Self-Recognition Task first (lasting for approximately 8-10 minutes), followed by the perceptual matching task (lasting approximately 10 minutes), and lastly the Self-Recognition Task again. The procedure is illustrated in Figure 7.1C.

7.2.4 Data Analysis

7.2.4.1 perceptual matching task

Preceding analysis, responses shorter than 200 ms or longer than 1000 ms were excluded, eliminating 2.6% of trials.

7.2.4.2 Self-Recognition Task

The participants' ratings of the morphed-face stimuli in the self-recognition task were fitted into a sigmoid statistical model to determine the percentage of morphing at which participants judged the amount of their own face and the other face to be equal – the 'point of subjective equality' (PSE; Sforza et al., 2010). This resulted in two PSE values per participant: pre-perceptual matching task, and post-perceptual matching task.

7.3 Results

7.3.1 perceptual matching task Analysis

In line with Sui et al. (2012), a bootstrapping procedure was performed, combining accuracy (see Figure 7.2B) and RT data (see Figure 7.2A) in order to assess the overall training effect in each of the association conditions. RT and accuracy data for each condition, and each participant, were combined separately to create one data point. This data was then resampled with replacement, and the sample size was kept as the number of participants, creating a bootstrapped dataset. This procedure was repeated 2000 times, and the mean of the dataset from each instance was plotted, creating a visual representation of the estimated population mean and variation of each association condition.

The distributions across the three association conditions can be seen in Figure 7.2D. For matched trials, responses to self-associations follow a distinct RT-accuracy distribution, falling in the bottom right of the figure, while friend- and stranger-associations fall towards the middle and left respectively. For mismatch trials, responses in each condition tend to overlap (see Figure 7.2D).

Accuracy on the perceptual matching task was assessed using a signal detection approach. D', reflecting perceptual sensitivity to each face, was calculated by combining performance in each face identity condition across both match and mismatch trials. It was entered into a repeated-measures ANOVA with the within-subjects factor of Face Identity (Self vs. Friend vs. Stranger), and helmert planned contrasts were used to investigate any effects. There was a significant main effect of Identity, $F(2,\ 52) = 3.574$, $p = .035$, $\eta^2 = .121$. Self-associations benefited from a larger d' than both friend and stranger associations ($p = .026$). There was no difference between friend and stranger associations ($p = .411$).

To investigate the effect of Face Identity on RT, a repeated-measures ANOVA was run with factors of Face Identity and Match-type. Only trials in which participants made the correct response were included in the RT analysis. There was a main effect of Identity, $F(2,\ 52) = 3.677$, $p = .032$, $\eta^2 = .124$ reflecting faster RTs to self-associations relative to friend and stranger associations ($p = .018$). There was also a main effect of Match-type, $F(1,\ 26) = 105.769$, $p < .001$, $\eta^2 = .803$, reflecting faster RTs for matched pairs relative to mismatched pairs ($p < .001$). The interaction between Identity and Matching Judgment was also significant, $F(2,\ 52) = 11.339$, $p < .001$, $\eta^2 = .304$. Analysis was then run separately for matched and mismatched trials. There was no effect of Face Identity for mismatched trials, $F(2,\ 42) = .359$, $p = .7$, $\eta^2 = .014$. However, for Matched trials, Face Identity had a significant effect on RTs, $F(2,\ 52) = 8.542$, $p = .001$, $\eta^2 = .247$. Self-associations showed faster RTs than both friend and stranger associations ($p = .002$). Friend and stranger associations did not significantly differ ($p = .172$). See Table 7.1 for means, SDs and 95% confidence intervals for each trial type.

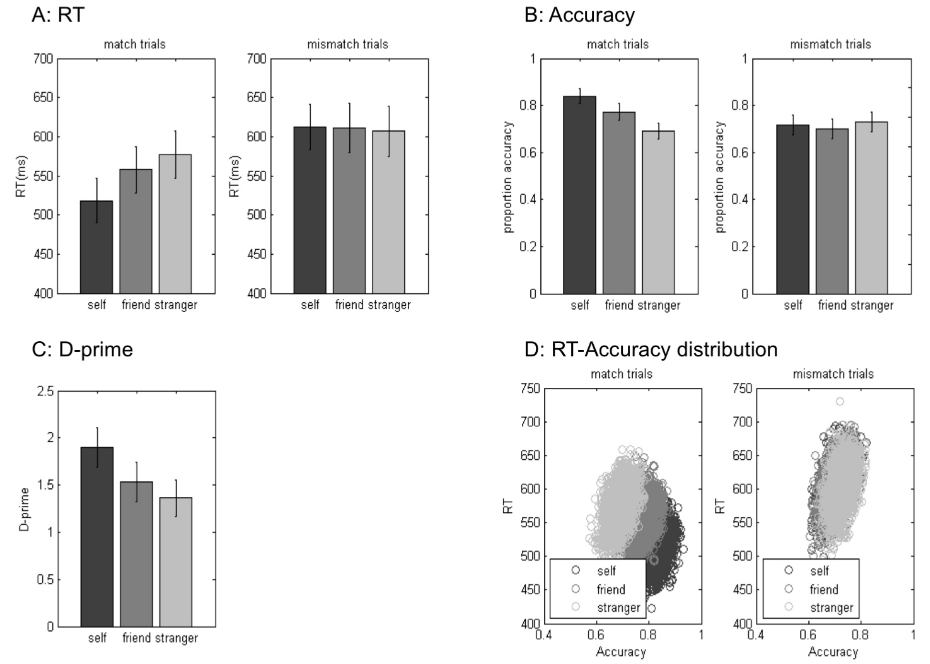

Figure 7.2: Behavioural results from the perceptual matching task. Mean RTs on correct trials (A), accuracy (B) and D-prime (C) to self, friend and stranger-associated faces for match trials (face and label were correctly matched) and mismatch trials (the label presented did not match the face). Error bars represent standard error. D shows the bootstrapped sample means (resampling with replacement repeated for 2000 samples) for match and mismatch trials. A bootstrapping procedure combining accuracy and RT was adopted to examine the distribution characteristics of each trial type.

7.3.2 Self-Recognition Task Analysis

Next the self-recognition task data was analysed. To check that baseline PSE values for self-associated morphs and stranger-associated morphs did not differ, baseline PSE scores for each morph set were analysed first in a repeated measures ANOVA with Morph Identity as a factor. There was no effect of morph identity on baseline PSE scores $F(1,\ 27) = .646$, $p = .429$, $\eta^2 = .023$, so then all of the PSE values were analysed in a repeated measures ANOVA

Table 7.1: Means, standard deviations and 95% confidence intervals for D' and RT measures (across match and mismatch trials) for each face-identity.

	Self-associated face		Friend-associated face		Stranger-associated face	
Variable	M (SD)	95% CI	M (SD)	95% CI	M (SD)	95% CI
D'	1.87 (1.13)	[1.42, 2.32]	1.51 (1.11)	[1.07, 1.94]	1.36 (1.04)	.95, 1.77]
RT Match Trials	511.68 (145.82)	[454, 569.37]	552.24 (154.36)	[491.18, 613.3]	569.59 (156.6)	[507.64, 631.54]
RT Mismatch Trials	605.58 (153.11)	[545.01, 666.15]	603.95 (164.62)	[538.83, 669.07]	598.32 (166.41)	[532.49, 664.15]

with factors Morph Identity (‘Self’ vs ‘Stranger’ morphs) and Timing of Task (pre- vs. post-perceptual matching task). There was no main effect of Morph Identity, $F(1,\ 27) = .506$, $p = .483$ $\eta^2 = .018$, or Timing of Task, $F(1,\ 27) = 2.89$, $p = .101$, $\eta^2 = .097$, nor an interaction between Morph Identity and Timing, $F(1,\ 27) = .249$, $p = .622$, $\eta^2 = .009$, indicating that PSE scores were not influenced by the timing of the task or the association of a new face with the self. See Figure 7.3.

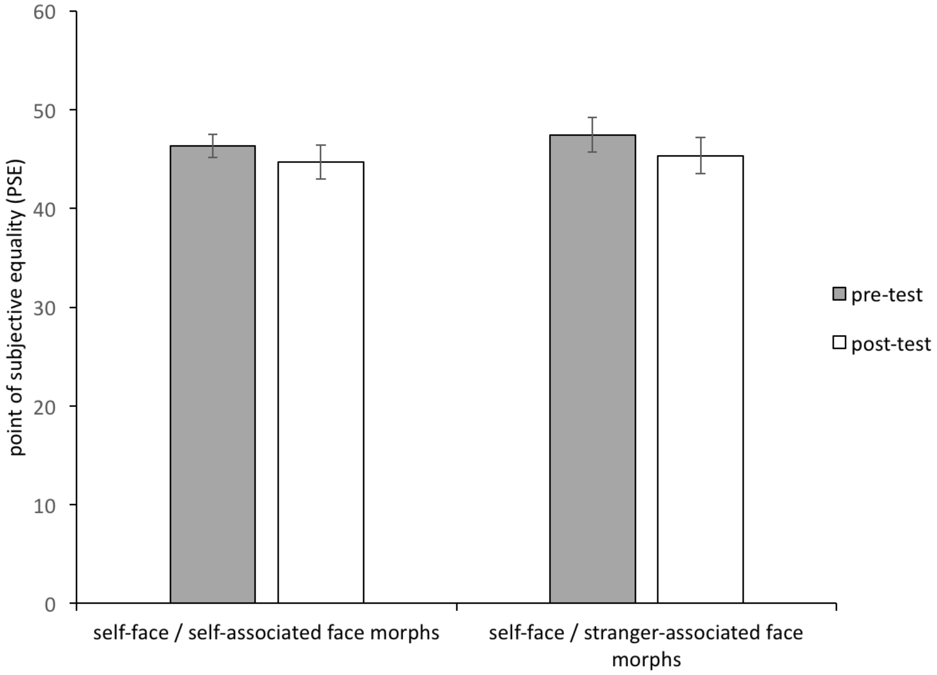

Figure 7.3: The bars represent the point in the morphing spectrum that participants perceived there to be an equal amount of their own and the other face (PSE). On the left are the mean PSEs for self and self-associated-face morphs, before and after the perceptual matching task. On the right are mean PSEs for self and stranger-associated face morphs, before and after the perceptual matching task. Positive changes from pre- to post-test would indicate an increased amount of the other’s face at the perceived PSE, while negative changes would indicate more of the self-face at the perceived PSE.

7.4 Discussion

The perceptual matching task used in Experiment 5 measured the effects of associating an unfamiliar face with the self on perceptual processing. The results showed a clear perceptual prioritisation effect towards the unfamiliar face after only a brief period of self-association, which manifested itself in faster reaction times and increased perceptual sensitivity to the self-associated face over faces associated with a friend or stranger. The pattern of results closely mirrored those reported by Sui et al. (2012), in an analogous task using neutral shapes instead of faces. This suggests that the conceptual self-representation can be rapidly extended to incorporate an unfamiliar face, and that correspondingly, perceptual and attentional processing of that face is prioritised as 'self-relevant'. The results indicate that the perceptual matching task was successful at eliciting a change in the self-concept, reflecting a change at a more abstract level of the self-representation that the previous Experiments in this thesis which targeted the perceptual self-representation.

Experiment 5 also aimed to investigate whether a change in the conceptual representation of the self could elicit a change in the perceptual, bodily representation of the self. A self-face recognition task was used to measure each participant's self-face representation by calculating the PSE between the participant's own face and both the self-associated and stranger-associated faces from the perceptual matching task (the stranger-associated face was used as a control condition). The self-recognition task was performed both before and after the perceptual matching task. It was hypothesised that a change in PSE would be observed following the perceptual matching task, reflecting that an incorporation of the self-associated face had occurred in the bodily self-representation, causing participants to perceive an increase in physical similarity between their own and the newly associated face. However, the results indicated that the incorporation of a novel face into the self-concept, while leading to the unfamiliar face becoming self-relevant, did not alter the perceptual self-representation. Following successful association of the self-concept with an unfamiliar face, participants did not perceive their own face as more similar to the unfamiliar face.

The self-face is the most salient aspect of one's body. One's own face automatically captures attention (Brédart, Delchambre, & Laureys, 2006) and demands preferential processing above all other faces (Sui & Humphreys, 2013; Tong & Nakayama, 1999). Yet despite this strong salience of our own face, the results of the current experiment demonstrate that we are able to rapidly associate a previously unfamiliar face with our conceptual self-representation. The results from the perceptual matching task show a distinct response pattern to self-associated faces compared to both friend and stranger associations, reflecting the perceptual processing bias afforded to self-relevant stimuli. This rapid modification of perceptual processing to newly acquired self-associations fits in with a growing understanding of plasticity in the self, both in the physical and conceptual domains (Paladino et al., 2010; Sforza et al., 2010; Tajadura-Jiménez, Grehl, & Tsakiris, 2012; Tsakiris, 2008; Banakou et al., 2013; Maister et al., 2014).

The association of a previously unfamiliar face with the conceptual self-representation did not affect the perception of one's own face. On one level, this is surprising as previous research has demonstrated the striking malleability of the self-face representation (Paladino et al., 2010; Sforza et al., 2010; Tajadura-Jiménez, Grehl, & Tsakiris, 2012), and has also suggested the existence of functional links between conceptual and bodily aspects of the self-representation. For example, Paladino et al. (2010) showed that the modulation of perceived facial-similarity through interpersonal multisensory integration affects the experience of conceptual 'closeness' with the IMS individual, increasing the perception of not only physical but also psychological similarity. There was also evidence to suggest that the converse relationship might be true; that the modulation of conceptual aspects of self may have a knock-on effect on the bodily self-representation. The modulation of trust with another individual has been shown to affect the perceived physical similarity between one's self and the other individual (Farmer et al., 2013). Based on this it was hypothesised that the association of the conceptual self with an unfamiliar face would affect the perceived physical similarity between the self and the self-associated face. However, the findings demonstrated no functional link between alterations to the conceptual self-representation and the bodily self-representation.

It could be suggested that the manipulation, while successful at creating an association between participants and an unfamiliar face, may have been ineffective at altering central aspects of the self-concept because of the transient nature of the task. However, there is evidence to suggest this is not the case. For example, using the same brief association task in combination with fMRI, Sui and Humphreys (2013) demonstrated that areas of the brain associated with self-representation, such as the ventromedial prefrontal cortex (vmPFC; Mitchell, Macrae, & Banaji, 2006; Northoff et al., 2006) were robustly activated in response to a self-associated shape. Similarly, Kim and Johnson (2014) found activation in mPFC even when participants observed objects that they merely transiently 'owned' in a non-self-referential task. Given that activation in mPFC is reliably observed when participants view well established, explicit self-relevant information such their own name (Moran, Heatherton, & Kelley, 2009), this evidence suggests that even transient links between the self and an object can lead to the incorporation of the object into one's sense of self, causing a change at the conceptual level (see also: Perkins & Forehand, 2012, for behavioural changes following implicit links between the self and neutral stimuli).

One explanation for the findings could be the lack of social interaction in the paradigm, given that evidence suggests that social interaction and body representations are highly linked (Maister et al., 2014). In contrast, Farmer et al.'s (2013) paradigm involved an interaction with another through a trust game, in which the other player actively rewarded or punished the participant. The effect of trustworthiness on increased perceived physical similarity may play a functional role, as it could induce kin-like behaviours in future interactions, benefitting the participant (DeBruine, Jones, Little, & Perrett, 2008). DeBruine et al. (2008) has shown that individuals are more likely to trust others who bear a physical resemblance to them, and so a modulation of the bodily-self representation to more closely resemble those who act prosocially towards one's self may reflect a functional role in driving future interactions. Therefore, the bodily self-representation in Farmer et al.'s (2013) task, and its relation to the other's body, was highly relevant, and likely to be strongly activated alongside conceptual aspects of self, enabling information in the conceptual self to change aspects of the perceptual self. In contrast, the current study was involved purely in 'self' representations, without any interaction with another individual. Because of this, the transient inclusion of a novel face into the self-concept may never have become relevant to the bodily self-representation, and so links between the novel conceptual aspects and existing perceptual aspects of self may not have been formed. Despite there being evidence for changes in body representation leading to changes in conceptual self- and other-processing (Banakou et al., 2013; Maister et al., 2014; Paladino et al., 2010), the results of Experiment 5 suggest that the converse relationship, whereby basic self-association at the conceptual level can alter body representations, does not hold. The results support a hierarchical model of the self with unidirectional connections flowing in a bottom-up direction, from bodily self-representations to conceptual self-representations. If this is the case, then it is important to investigate the effects of these basic associations with the conceptual self-representation on higher levels of interpersonal processing, as while these associations do not seem to alter self-other relations at the physical bodily level, they may have an effect on the self-other relationship further up the processing hierarchy. In this way, the incorporation of an unfamiliar face into the conceptual self-representation may have interesting effects in the social domain. For example, the perception of another individual as an out-group member, based only on facial characteristics, can have profound effects on a number of social cognitive processes, ranging from explicit (e.g. ratings of trustworthiness, intelligence, attractiveness) to implicit attitudes, as well as affecting interpersonal behaviours (Pavan, Dalmaso, Galfano, & Castelli, 2011; Ratner, Dotsch, Wigboldus, van Knippenberg, & Amodio, 2014). Crucially, research has suggested that the neurological correlates of face perception also differ depending on whether the face belongs to an in-group or out-group member (Golby, Gabrieli, Chiao, & Eberhardt, 2001), even when group membership distinctions are arbitrary (Ratner & Amodio, 2013). These studies show that in-group faces benefit from prioritised perceptual and attentional processing relative to out-group faces.

In the current study, a perceptual processing bias towards a minimally self-associated face affected basic identity processing (as measured by the perceptual matching task), but it might also result in prioritised processing of the self-associated face's social signals, such as emotional expressions and gaze cueing, in a similar way to that observed for established in-group members (Pavan et al., 2011). Our social lives are structured around categorising other individuals as either 'in-group' or 'out-group', and we show strong self-associations with people who we conceptualise as similar to ourselves. The findings of Experiment 5 have demonstrated, at a relatively pure and fundamental level, that rapidly formed self-associations with another individual can alter the way in which their face is processed, and this modulation of perceptual processing may have fascinating knock-on consequences for social cognition.

In conclusion, Experiment 5 firstly showed that the conceptual self-representation can be extended to include a previously unfamiliar face, and that this extension of the conceptual self to the newly associated face results in enhanced perceptual processing of the self-associated face. Experiment 5 also found that this modulation of the conceptual self-representation did not affect the perception of the bodily self, suggesting a hierarchical model of the self with unidirectional links between levels flowing in a bottom-up direction. In this case the results of the current experiment may reflect a mechanism that can affect higher-level self-other processing; the extension of prioritised perceptual processing to the self-associated face may extend to the processing of social signals belonging to the face, such as emotion expression, gaze cues or social group membership.

8 Investigating Associations with the Self-Representation

8.1 Introduction

Experiment 5 replicated and expanded Sui et al.'s (2012) perceptual matching paradigm in which a neutral shape is associated with the self, and subsequently benefits from prioritised processing. Experiment 5 replaced the neutral shape with an unfamiliar face, and the results indicated that participants were able to quickly associate this face with themselves, resulting in the face becoming self-relevant and benefitting from the same prioritised perceptual processing observed in the original experiments (Sui et al., 2012; Sui, Rotshtein, & Humphreys, 2013). Experiment 5 also investigated whether the association of this novel face with the self would change the stored mental representation of one's own face, such that the newly associated face would be incorporated into the self-face representation. Participants completed a self-face recognition task before and after the Perceptual Matching Task in which they judged morphed images between their own and the self-associated face. The point of subjective equality (PSE) between the two faces was calculated at both time points and compared. No change in PSE was found following self-association with the new face, suggesting that although the new face had become associated with the self, it had not been incorporated into the self-face representation.

The lack of inclusion of the newly-associated face into the self-face representation suggests that when the novel face is associated with the self, it is associated only with the conceptual self-representation, and not with the perceptual self-representation. If this is the case, then the results further suggest that changes to the conceptual self-representation do not lead to corresponding changes in the perceptual self-representation. Evidence suggests that modulatory links exist between the conceptual and perceptual self-representations, however, the research to date, including the resutls of Experiment 5, suggests that these links flow in a bottom-up direction, with changes to the perceptual self-representation leading to corresponding changes in the way the self is conceptualised (Maister et al., 2014). The results presented in Chapter 7 suggest that modulatory links do not exist in the opposite direction, in other words, changes to the conceptual self-representation do not lead to changes in the perceptual representation of the self-face. Chapter 8 aims to elucidate upon this theory by investigating the nature of the association created between the self and a novel face during the Perceptual Matching Task. Experiment 6 aims to understand in what way the newly-associated face has been incorporated with the self: is the face associated with both the conceptual and perceptual self-representations, or, as the results suggest, only associated with the conceptual self. To test this, Experiment 6 directly contrasts how assocaition with a new face affects recognition of conceptual and perceptual representations of the self.

To investigate the nature of the self-association formed during the Perceptual Matching Task, Experiment 6 will employ a semantic priming paradigm. In a typical semantic priming task a ‘prime’ stimulus is presented first, followed closely by a ‘target’ stimulus to which the participant responds. Meyer and colleagues reported the first semantic priming effect in a task in which words were presented as both primes and targets, and participants were required to make a lexical decision (word/nonword) about the target word (Meyer & Schvaneveldt, 1971; Meyer, Schvaneveldt, & Ruddy, 1975). Responses to the target were faster when the prime and the target were semantically similar (e.g. doctor / nurse) than when they were dissimilar (e.g. doctor / bread): this is known as the *semantic priming effect.* Since these initial lexical priming studies, research has shown that semantic priming can also occur between stimuli of different modalities, such as words and pictures (Bajo & Juan Canas, 1989; Irwin & Lupker, 1983; Vanderwart, 1984), suggesting that a single system of semantic representation exists, which is accessed by multimodal stimuli, rather than separate semantic systems for stimuli of different types.

Indeed, the system of semantic memory has been metaphorically compared by Hutchison (2003) to a dictionary, encyclopaedia, and thesaurus; semantic memory contains information about a concept's identity, meaning, and relation to other similar concepts. Concepts within semantic memory are proposed to be connected to other concepts, or 'nodes', that share similarities through learned associations (Collins & Loftus, 1975), or shared features (Moss, Hare, Day, & Tyler, 1994). Evidence suggests that semantic priming can occur as a result of both associative strength between concepts as well as featural similarities (Hutchison, 2003). In regards to associated concepts, semantic priming is thought to occur as a result of activation, by the prime stimuli, of neural regions involved in the semantic representation of that word/picture, which leads to the automatic activation of related notes, facilitating the recognition of subsequently presented semantically related stimuli (Neely, 1991). In regards to featural similarity, it is suggested that semantic priming occurs not because of the spreading of activation from one node to a related node, but because the prime and target share multiple overlapping features, facilitating the processing of the featurally similar target (Masson, 1995). When the interval between presentation of the prime and target (stimulus onset asynchrony; SOA) is small, semantic priming is thought to occur as a result of automatic processes facilitating the processing of semantically similar concepts (Neely, 1991). In contrast, when the SOA is larger, over 400ms, the semantic priming effect is proposed to occur as a result of expectancies developed by participants based on the nature of the prime stimulus, such that attention is directed to semantically related target stimuli (Neely, 1977).

In Experiment 6 participants complete the same Perceptual Matching Task from Experiment 5, followed by a semantic priming task. During the Perceptual Matching Task participants learn to associate three unfamiliar faces with three identities (self, famous and stranger). The semantic priming task is used to investigate the nature of the association formed between the self-associated face and the pre-existing self-representation. To investigate whether the self-associated face is associated with the conceptual self-representation only, or both the conceptual and perceptual self-representations, target stimuli in the priming task represent aspects of the conceptual (self-name) and perceptual (self-face) self. Prime stimuli are the unfamiliar face from the Perceptual Matching Task. As a control condition, the face and name of the famous individual chosen to represent the famous identity in the Perceptual Matching Task are also used as target stimuli, and the famous-associated face as a prime stimulus. Participants make a categorical decision to the target stimuli (self / famous), and response times were hypothesised to vary depending on the nature of the association between the novel face and the conceptual/perceptual self-representation. It was hypothesised that the self-associated face is associated only with the conceptual self-representation, and thus, faster responses to the self-name would be observed when it follows the self-associated face, in contrast with responses to the self-face when it follows the self-associated face.

8.2 Materials and Methods

8.2.1 Participants

21 participants (15 female, mean age 21.3 years, SD 3.54) volunteered to take part in the study. All had normal or corrected-to-normal vision, and were right-handed. Informed consent was given by all participants before their participation, and the study was approved by the Psychology Department Ethics Committee, Royal Holloway, University of London. Design

8.2.2 Design

The experiment was a within-subjects repeated-measures design, with factors of Prime ID (self-associated face vs. famous-associated face), Target ID (self vs. famous), and Target Type (face vs. name). Participants took part in one experimental session in which they completed the Perceptual Matching Task (as used in Experiment 5) followed by a Priming Task described below.

8.2.3 Stimuli and Tasks

8.2.3.1 Perceptual Matching Task

The adapted version of Sui et al.'s (2012) Perceptual Matching Task from Experiment 5 was used in the current study. For a full description of the task see Section 7.2.2.1. One change was made to the task procedure: the 'Friend' label was replaced by an 'Actor' label, and participants named a familiar, gender matched actor, and were instructed that the 'Actor' label and corresponding unfamiliar face belonged to the famous individual. The unfamiliar face-identity label pairings were assigned randomly for each participant. The task was run on Presentation (NeuroBehavioural Systems).

8.2.3.2 Priming Task

Stimuli for the Priming Task consisted of the 'Self' and 'Famous' associated faces from the Perceptual Matching Task, a photo of the participant's own face and the named famous individual's face, and the participant's and famous individual's names. Photos of the participant's face was taken with a neutral expression, converted to greyscale and mirrored horizontally (for the self-face only), and cropped with a circular template to remove the outer hairline. The same procedure was applied to an image of the famous person's face. The images were then resized to match the dimensions of the unfamiliar faces from the Perceptual Matching Task.

Each trial of the Priming Task began with a prime stimulus presented for 20ms, which was then replaced by a target stimulus, presented for 200ms, after which a blank screen was presented until response. The next trial started as soon as the participant responded, but only responses made within 1000ms of the target disappearing were used in the analysis. All primes were either the self-associated face or the famous-associated face, both of which were presented an equal amount of times as the prime. The target stimuli were the self-face, self-name, famous-face and famous-name. All targets were presented an equal amount of times and were preceded by both of the two primes an equal amount of times. Participants were instructed to respond to the target stimulus, and to indicate with a button press whether the target was 'self' or 'famous'. Participants responded with their right index and middle fingers, and the ascription of 'self' and 'famous' to either finger was counterbalanced across participants. Unlike the Perceptual Matching Task, participants did not receive feedback on their responses during the Priming Task. The Priming Task was split into three blocks, with 66 trials in the first block, and 67 trials in the second and third blocks. There were 25 trials in each of the eight conditions: self-associated face prime – self-face target; self-associated face prime – self-name target; self-associated face prime – famous-face target; self-associated face prime – famous-name target; famous-associated face prime – self-face target; famous-associated face prime – self-name target; famous-associated face prime – famous-face target; famous-associated face – famous-name target. For a visual representation of the task procedure see Figure 8.1.

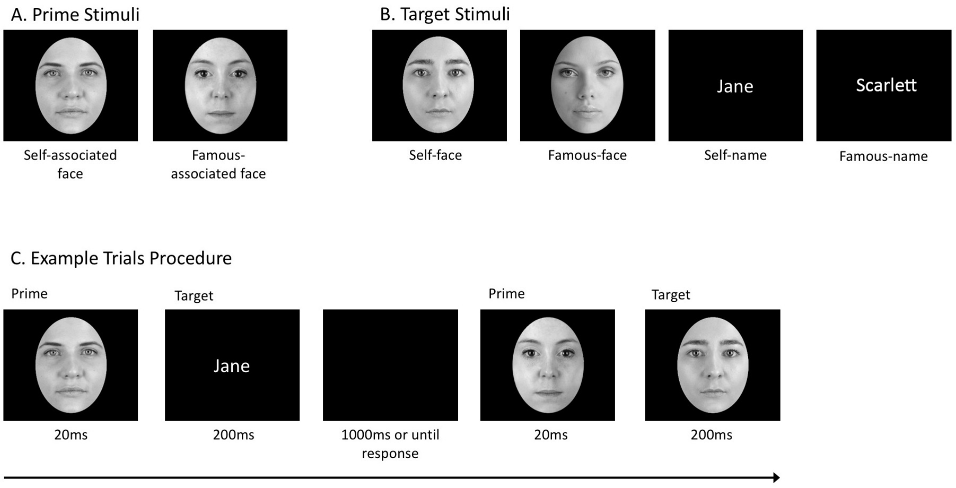

FIGURE 8.1: A) The Prime stimuli, the self-associated face and famous-associated face from the Perceptual Matching Task. B) The Target stimuli: actual self-face, actual famous-face, self-name and famous-name. C) An example of two consecutive trials in the semantic priming task. Each trial starts with the presentation of a prime stimulus for 20ms, followed by a target stimulus for 200ms. A blank screen is then shown for 1000ms or until the participant makes their response, at which point the next trial begins.

8.2.4 Procedure

Participants first completed the Perceptual Matching Task, and then the Priming Task. Participants were able to take short breaks in between the blocks of each of task.

8.2.5 Data Analysis

For both tasks, responses shorter than 200ms or longer than 1000ms were excluded from the analysis, eliminating less than 5% of trials. For the Priming Task, only correct trials were included in the analysis.

8.3 Results

8.3.1 Perceptual Matching Task Analysis

Accuracy on the Perceptual Matching Task was assessed using a signal detection approach. D' was calculated for each face by combining performance across match and mismatch trials, reflecting perceptual sensitivity. A repeated measures ANOVA with a within subjects factor of Face Identity (Self vs. Famous vs. Stranger) was used to compare sensitivity towards each face identity. There was a main effect of Face Identity: $F(2,\ 40) = 5.643$, $p = .007$, $\eta^2 = .22$. Helmert planned contrasts revealed a significant different between D' for the self-associated face compared with the famous-associated and stranger-associated faces ($p = .005$). There was no difference between D' for famous- and stranger-associated faces ($p = 87$). Means are displayed in Table 8.1. This finding replicates previous studies and confirms that the self-associated face had become self-relevant.

Next the effect of Face Identity on RT was assessed with a repeated-measures ANOVA with factors of Face Identity and Match Type (match vs. mismatch). Only trials in which participants responded correctly were included in the RT analysis. There was a significant main effect of Face Identity: $F(2,\ 40) = 9.594$, $p < .001$, $\eta^2 = .324$, reflecting faster responses to Self trials than Famous or Stranger trials ($p = .002$). Again there was no significant difference in performance between Famous and Stranger trials (p = .816). There was also a significant main effect of Match Type: $F(1,\ 20) = 10.415$, $p = .004$, $\eta^2 = .342$, reflecting faster RTs for Match trials compared with Mismatch trials (p

TABLE 8.1: Means, standard deviations and 95% confidence intervals for D' and RT measures (across match and mismatch trials) for each face-identity.

	Self-associated face		Famous-associated face		Stranger-associated face	
	M (SD)	95% CI	M (SD)	95% CI	M (SD)	95% CI
D'	1.589 (1.091)	[1.092, 2.086]	.988 (.94)	[.56, 1.416]	1.019 (.814)	[.648, 1.389]
RT Match Trials	498.533 (116.919)	[445.312, 551.754]	558.879 (105.189)	[510.997, 606.76]	591.281 (96.76)	[547.236, 635.326]
RT Mismatch Trials	582.457 (140.383)	[518.556, 646.359]	574.855 (104.615)	[527.234, 622.475]	604.041 (87.853)	[564.05, 644.031]

= .004). The interaction between Face Identity and Match Type did not reach significance. The means for each trial type are displayed in Table 8.1.

8.3.2 Priming Task Analysis

A 2 x 2 x 2 repeated-measures ANOVA was conducted on RT data from the Priming Task, with factors of Prime ID (self-associated face vs. famous-associated face), Target ID (self vs. famous), and Target Type (face vs. name). The ANOVA revealed a main effect of Target ID: $F(1, 20) = 11.198$, $p = .003$, $\eta^2 = .359$, reflecting faster responses to self targets regardless of Prime ID (self target $M = 493.815$; famous target $M = 514.877$). There was also a significant 3-way interaction between Prime ID, Target ID and Target Type: $F(1, 20) = 13.034$, $p = .002$, $\eta^2 = .395$. As the aim of the study was to compare semantic priming by the newly associated face across perceptual and conceptual aspects of self, further analysis to investigate the interaction was split by Target ID.

First, a repeated measures ANOVA was conducted on Self Target trials, with factors of Prime ID and Target Type. The ANOVA revealed no significant main effect of Prime ID: $F(1, 20) = .282$, $p = .602$, $\eta^2 = .014$, or Target Type $F(1, 20) = 2.639$, $p = .120$, $\eta^2 = .117$. Nor a significant interaction between the two factors: $F(1, 20) = 2.185$, $p = .155$, $\eta^2 = .098$. The means and SDs for each trial type can be seen in Table 8.2.

Next, a repeated measures ANOVA was conducted on Famous Target trials, with factors of Prime ID and Target Type. The ANOVA revealed a main effect of Prime ID: $F(1, 20) = 8.381$, $p = .009$, $\eta^2 = .295$, reflecting faster responses to targets preceded by famous-associated face trials. The main effect of Target Type was not significant: $F(1, 20) = .770$, $p = .391$, $\eta^2 = .037$, but the interaction between Prime ID and Target Type was significant: $F(1, 20) = 8.680$, $p = .008$, $\eta^2 = .303$. To investigate the interaction, paired samples t-tests were used to investigate whether RTs to face and name targets differed depending on the ID of the prime stimulus. The paired samples t-tests (with a corrected alpha level of .025) revealed no significant difference between RTs to famous-face targets primed by the self-associated face or famous-associated face: $t(20) = -.403$, $p = .691$. However, there was a significant difference between famous-name targets preceded by self-associated face or famous-associated face primes: $t(20) = 3.810$, $p = .001$. Specifically, famous-name targets preceded by famous-associated face primes benefitted from faster RTs than those preceded by self-associated face primes (self-associated primes $M = 527.357$, famous-associated primes $M = 492.333$), see Figure 8.2. Means and SDs for all trial types can be seen in Table 8.2.

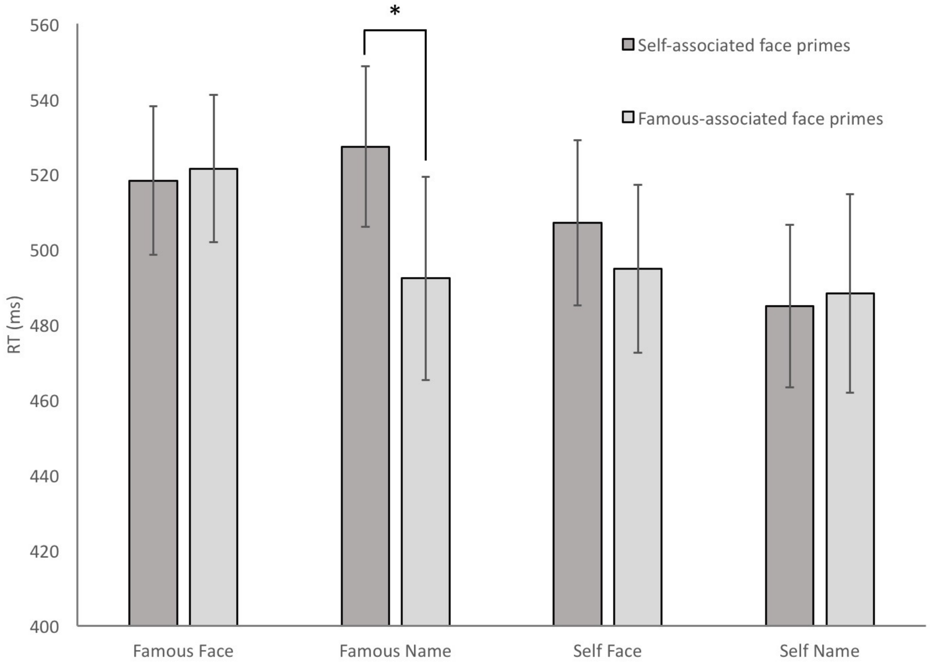

FIGURE 8.2: There was a significant difference in RTs between famous-name targets preceded by famous-associated primes and famous-name targets preceded by self-associated primes.

Table 8.2: Means (M), standard deviations (SD) and 95% confidence intervals for all trial types in the Semantic Priming task.

		Self-Face	Self-Name	Famous-Face	Famous-Name
SAF Primes	M (SD)	507.169 (100.634)	484.974 (98.828)	518.348 (90.773)	527.357 (97.628)
	95% CI	[461.361, 552.977]	[439.988, 529.959]	[477.028, 559.667]	[482.917, 571.797]
FAF Primes	M (SD)	494.833 (102.186)	488.283 (120.983)	521.471 (89.687)	492.333 (123.886)
	95% CI	[448.319, 541.348]	[433.213, 543.354]	[480.646, 562.297]	[435.941, 548.726]

SAF = self-associated face, FAF = famous-associated face.

8.4 Discussion

Experiment 6 aimed to investigate the nature of the association created between a previously unfamiliar face and the self-representation in the Perceptual Matching Task. Firstly, the Perceptual Matching Task was used to create an association between the participant and an unfamiliar, gender-matched face. Prioritised perceptual processing of the self-associated face, reflected in faster RTs and higher accuracy, suggested that the self-associated face had been incorporated into the self-representation, becoming self-relevant. Next, a semantic priming task was used to investigate the nature of the association created by the Perceptual Matching Task. It was hypothesized that the self-associated face, presented as the 'prime' stimulus in the semantic priming task, would facilitate recognition of self-related targets. The self-name and the self-face were used as targets to investigate whether the newly associated face had only been associated with the conceptual self-representation, as the results of Experiment 5 suggested, or also with the perceptual self-representation. The results of the analysis on the semantic priming task did not show a semantic priming effect between the self-associated face and either the self-face or the self-name. However, there was a semantic priming effect when the famous-associated face preceded the famous-name (but not the famous-face), suggesting that the famous-associated face had been incorporated into the conceptual representation of the famous individual.

It is surprising that the results of Experiment 6 show no semantic priming effect by the self-associated face on the conceptual self-target. The results of the Perceptual Matching Task in the current Experiment and the previous Chapter showed that the newly-associated face benefitted from prioritized processing, reflected in faster RTs and higher accuracy. Sui et al. (2012) suggest that prioritised processing is elicited for the self-associated stimuli once it has been incorporated into the 'self-template', a rich schema of the self, based on self-knowledge. Along these lines, self-prioritised processing of the self-associated face in the previous chapter was suggested to reflect an incorporation of the self-associated face into the conceptual self-representation. Furthermore, Sui et al. (2013) identified that activation in areas of the brain associated with self-representation, such as the ventromedial prefrontal cortex (vmPFC; Mitchell et al., 2006; Northoff et al., 2006) correlated with presentation of self-associated stimuli, providing further evidence that the perceptual matching paradigm leads to the incorporation of the associated face into the self-representation. Because of these previous results, in combination with the results of Experiment 5, which suggested that the associated face was not incorporated into the perceptual self-representation, Experiment 6 hypothesised that a semantic priming effect would be elicited for conceptual-self information (the self-name) when it was preceded by the self-associated face.

The results of Experiment 6 may suggest that the self-associated face was not incorporated into either the conceptual or the perceptual self-representations. They do, however, suggest that the famous-associated name was incorporated into the conceptual representation of that individual. Famous name targets were responded to significantly faster when preceded by famous-associated face primes than self-associated face primes. This dissociation may be explained by the differing nature of the conceptual representation of the self and the other. Specifically, the Perceptual Matching Task may not be able to establish a strong and lasting association between the self-associated face and the self-concept due to the rich nature of the self-representation. When thinking about the conceptual representation of the self compared with the representation of a famous individual, information within the conceptual self-representation is likely to be far more established, familiar, important, and reflect a far larger amount of information than the conceptual representation of any famous individual (Andersen, Glassman, & Gold, 1998) Within this context, it is unlikely that a face that has been seen for only a short period of time, with a very arbitrary connection to the self, would be able to prime such well-established aspects of the self-representation as the self-face and self-name. On the other hand, the depth of the semantic representation of the famous individual is likely to be far more shallow, reflecting a far smaller amount of information. Because of this, the famous-associated face may be more easily assimilated into the conceptual representation alongside the existing knowledge, able to semantically prime the existing information related to that identity.

In light of this, it would be illuminating for future research to investigate the longevity of the self-prioritisation effect observed for the stimuli associated with the self in the perceptual matching paradigm. To date, research has only investigated processing of the self-associated face during, and immediately following the perceptual matching paradigm (Sui et al., 2012; Sui & Humphreys, 2015), and there is no research to highlight how long the associated stimuli benefits from prioritized processing after the initial association is formed. The paradigm may result in a very transient and artificial association between the self and the associated stimuli, outside of the context of any other self-related information. If this is the case, it is less surprising that the self-associated face in Experiment 6 was unable to prime well-established components of the self-representation.

Further research could also benefit from designing a paradigm in which a novel piece of information can be robustly incorporated into the conceptual self-representation. Experiment 5 aimed to investigate, in part, whether changes to the conceptual self-representation could elicit changes in the perceptual representation of self. The results of Experiment 5 indicated that this was not the case, however, the lack of a change in PSE following association with the novel face may not have been due to a lack of modulatory links from the conceptual self-representation to the perceptual self-representation, but rather because the association created between the novel face and the conceptual self-representation was not strong enough to elicit such change. Investigating the modulatory links between conceptual and body representations of self is becoming increasingly relevant for self-recognition and social cognition, and this topic represents an area of study that would benefit from further empirical investigation.

9 General Discussion

9.1 Summary of Background and Aims

The self is a multifaceted entity comprising conceptual (e.g. attitudes, personality) and perceptual (bodily) representations (Gillihan & Farah, 2005). In light of the growing popularity of embodied accounts of social cognition (Gallese et al., 2004), research into the cognitive and neural mechanisms underpinning representations of the physical self is of importance not only for an understanding of the self, but also wider social cognition. This thesis focuses specifically on representations of the self-face, in light of the criticality of the self-face representation for identity and awareness (Zahavi & Roepstorff, 2011; Povinelli & Simon, 1998).

Currently within the literature there is not a clear understanding of the processes that underpin the acquisition, maintenance and updating of self-face representations. Studies of self-face recognition have typically focused on the process of *self-recognition*, involving a comparison of behaviour (or neural activity) between the visual recognition of the self-face and other faces. Neuroimaging research in particular has identified a large number of brain areas involved in the visual recognition of the self-face (see Devue et al., 2007). This introduces a number of gaps in the present literature. Firstly, there is little research that has used noninvasive brain stimulation methods to causally investigate the role of specific brain areas in self-face recognition (in comparison with using neuroimaging to investigate neural correlates). Secondly, the existing brain stimulation research has only focused on the process of *self-recognition*, while the neural underpinnings of *self-identification* and *self-updating* have yet to be explored with noninvasive brain stimulation. The present thesis aimed to fill these gaps by using tDCS to explore the causal involvement of specific brain areas in the processes of self-face recognition (self-identification, self-recognition and self-updating). Three studies to date have used rTMS to implicate rTPJ in the process of discriminating between one's own and another's face (Heinisch et al., 2011, 2012; Uddin et al., 2006), and research with tDCS has also implicated this area in higher-level self-other discrimination processes (Santiesteban et al., 2012). The present thesis aimed to expand upon this research by using tDCS to enhance cortical excitability in the right temporoparietal area, and investigate the effects on self-recognition and social cognition. Based on research investigating the neural correlates of self-identification and self-updating in the Enfacement Illusion (Apps et al., 2013), and an exploration of self-updating in mirror touch synesthesia (Maister et al., 2013), this thesis used tDCS to investigate the roles of IPS and S1 in self-identification and self-updating. Additionally, the focus of existing research into the mechanisms underpinning self-identification and self-updating has focused on the integration of multisensory information, informed by developmental research and bodily illusions. This thesis also aimed to explore whether the self-face representation could be updated via changes to the conceptual self-representation. Research suggests that changes to the way the bodily self is perceived can lead to corresponding changes in the way the self is conceptualised, but it is unclear whether modulatory links exist in the opposite direction, from conceptual to bodily. The present thesis aimed to investigate whether changes to the conceptual self-representation could elicit changes in the way the bodily self is perceived. A perceptual matching task, shown to rapidly create associations between novel stimuli and the self concept (Sui et al., 2012), was used to incorporate a novel face into the conceptual self-representation. Recognition of the self-face was tested following self-association to investigate whether changes had occurred to the self-face representation.

9.2 Summary of Results

Experiment 1 investigated the role of the right temporoparietal area in self-recognition using tDCS. Participants completed a well-established self-other face discrimination task (e.g. Heinisch et al., 2011, 2012) in which videos morphed from the participant's face into a familiar face, or the familiar face into the participant's face. Participants responded when they perceived that the face in the video started to look more like the person it was morphing into. The task was completed over two blocks, and in between the blocks participants received either anodal, cathodal, or sham stimulation over the right temporoparietal area, localised using the EEG 10/20 system. RT performance on the video morphing task was converted to reflect the percentage of the self-face at the point in the videos that participants discriminated between the self-face and the other's face. Anodal tDCS over the right temporoparietal area resulted in an increase in the amount of self-face required to discriminate between self and other. Cathodal and sham stimulation had no effect on self-other discrimination. The finding supported previous research that had implicated the right TPJ in the process of self-other discrimination with rTMS (Heinisch et al., 2011, 2012; Uddin et al., 2006). Furthermore, the findings of Experiment 1 expanded upon previous research by providing evidence that the right temporoparietal area may contribute towards self-other discrimination by maintaining the boundary between the visual representations of self and other.

Experiment 2 aimed to expand upon the findings of Experiment 1 by investigating the role of the right temporoparietal area in mental body rotation. Participants performed a task in which they had to mentally rotate their own body to take the perspective of another person shown on screen. On half of the trials participants saw an image of a close friend's body, and on the other half of trials participants saw a photo of their own body. Before completing the mental body rotation task, participants received 20 minutes of either anodal tDCS to the right temporoparietal area, anodal tDCS to the left temporoparietal area, or sham tDCS. Participants who received anodal tDCS to the right temporoparietal area were significantly faster at taking the perspective of the body shown on screen (regardless of identity) than both other tDCS groups (left temporoparietal area and sham). Critically, there was no difference between tDCS groups on a similar control task in which participants did not have to perform mental body transformations. The findings provided evidence that the right temporoparietal area is causally involved in imagined transformations of one's body position and location.

Experiment 3 investigated the role of the intraparietal sulcus (IPS) in self-identification and self-updating. The IPS receives multimodal input and has recently been implicated in multisensory integration during the Enfacement Illusion (Apps et al., 2013). Experiment 3 aimed to provide causal evidence for the role of the IPS in multisensory integration for self-updating using tDCS. Participants took park in three experimental sessions in which they first received 20 minutes of tDCS (anodal IPS, anodal PFC, or sham), and then took part in a typical enfacement paradigm (self-recognition task > IMS > self-recognition task). Changes in the self-face representation following IMS, measured using the self-recognition task, were compared across the tDCS sessions. There was no specific effect of any of the tDCS conditions on changes in the self-face representation following IMS. The typical enfacement effect, an inclusion of the IMS face in the self-face representation, was observed following IMS in all tDCS conditions, regardless of synchronicity of the IMS session. The result may reflect increased familiarity with the IMS face due to practice effects of the video morphing self-recognition task, as participants took part in the task six times in total over the three experimental conditions. The results suggested that it may not be possible to facilitate self-updating by increasing cortical excitability in only one brain region involved in the process, without also increasing excitability in other areas of the network.

Experiment 4 investigated the role of the primary somatosensory cortex (S1) in the processes of self-identification and self-updating. Based on research showing that individuals with mirror touch synesthesia can experience enfacement without receiving touch to their own face – but by experiencing synesthetic touch while watching the enfacement face being touched, and research showing that MTS-like symptoms can be induced in neurotypical individuals through the application of anodal tDCS over S1, Experiment 4 aimed to induce symptoms of MTS with tDCS and investigate whether the induced synesthetic touch during a non-touch IMS session would be sufficient to cause a change in the self-face representation. Participants took part in two sessions: in one they received anodal tDCS over S1, and in the other they received sham tDCS. Each session started with a morphed photo self-recognition task, followed by 20 minutes of tDCS, a no-touch IMS session, and lastly a final self-recognition task. Performance on the pre-tDCS and post-tDCS self-recognition tasks was compared to investigate whether the self-face representation had been updated. The Interpersonal Reactivity Index was also used to measure empathic ability, as the experience of synesthetic touch appears to be linked with empathy. The results showed no specific effect of tDCS on performance on the self-recognition task, suggesting that the tDCS had failed to induce symptoms of MTS and lead to updating of the self-face representation during the no-touch IMS session. The results showed a similar change in self-recognition following the no-touch IMS session across both tDCS sessions, in the direction typically observed following the induction of a typical Enfacement Illusion. These results could suggest that vicarious, ‘mirroring’ activation of the somatosensory system in response to the observation of another person being touched are able to lead to self-updating under certain circumstances.

Experiment 5 investigated whether the self-face representation could be updated through the novel use of a self-association paradigm (Sui et al., 2012). Participants completed a self-recognition task before and after associating an unfamiliar face with themselves in a perceptual matching task. Prioritized perceptual processing of the self-associated face, reflected by faster RTs and higher accuracy, suggested the face had been successfully associated with the self and had become self-relevant. Performance on the self-recognition task before and after the perceptual matching task was compared to investigate whether self-association with the novel face had an effect on the self-face representation. No changes on the self-recognition task following self-association were observed, suggesting that association of the self with a new face is not able to update the stored mental representation of the self-face. Despite the fact that the association did not have an effect on the bodily, perceptual self-representation, the prioritized processing of the self-associated face suggested that it been incorporated into the conceptual self-representation. It was suggested that changes to the conceptual self-representation may not be able to elicit corresponding changes in the perceptual self-representation.

Experiment 6 aimed to explore the nature of the association created between the self and an unfamiliar face during the perceptual matching task. Based on the results of Experiment 5, it was suggested that the perceptual matching paradigm creates an association between the self-associated face and the conceptual self-representation, but not the perceptual self-representation. Experiment 6 aimed to investigate whether this dissociation was true. Participants completed the perceptual matching task, associating a previously unfamiliar face with themselves, as well as associating another unfamiliar face with a familiar famous person. They then completed a semantic priming task, in which prime stimuli were the self- and famous-associated faces, and target stimuli were the actual face (perceptual) and name (conceptual) of the participant and the famous person. The results of the priming task suggested that the self-associated face had not been associated with either the conceptual self-representation or the bodily self-representation. The results did suggest that the famous-associated face had been incorporated into the conceptual representation of the famous individual.

9.3 Interpretation

9.3.1 The role of the right temporoparietal area in bodily self-representation

The right temporoparietal junction (and encompassed right IPL) have been implicated in self-recognition by previous research with fMRI (Apps et al., 2013; Sugiura et al., 2005), and rTMS (Heinisch et al., 2011, 2012; Uddin et al., 2006). One aim of the current thesis was to further explore the role of this area in the process of self-recognition, described in the introductory chapter of this thesis as the process by which a self-face representation is maintained, such that it can be compared with visual stimuli. Firstly, the results of Experiment 1 provide causal evidence for the involvement of the right temporoparietal area in the process of self-recognition. Experiment 1 showed that increased excitability in the right temporoparietal area, induced with anodal tDCS, affects discrimination of the self-face from another familiar face. Additionally, when considered in relation to previous brain stimulation research, these results are able to provide further insight into the mechanism that underpins the process of self-other discrimination. Heinisch et al. (2011, 2012) and Uddin et al. (2006) both found that, after stimulating rTPJ and rIPL respectively, with low frequency rTMS to disrupt typical cortical functioning, participants accepted a face as their own that contained a larger amount of another person's face that before the rTMS. In contrast, Experiment 1 increased cortical excitability in the right temporoparietal area with tDCS and found that following stimulation, in a similar self-other face discrimination task, participants accepted less of another person's face in the self-other morph when recognizing their own face. Taken together these results suggest that the right temporoparietal area is involved in maintaining a boundary between visual representations of self and other, and that increasing coritical excitability in an area that underpins this mechanism reduces the overlap between self and other representations.

The proposal that this mechanism may modulate overlap between representations of the self and other is interesting when considered in relation to Banissy et al.'s (2009) neurocognitive model of MTS. Banissy et al. (2009) suggest that MTS arises due to a dysfunction of the mechanisms that distinguish between self and other, leading to the attribution of touch observed on others to the self. They argue that there is not one dedicated module for discriminating between the self and others, rather, discrimination of self from others relies on a number of processes involved in linking visual representations with internal body models. Banissy et al. (2009) speculate that the mechanisms that give rise to the synesthetic experience in MTS can be divided into three key processes. These processes are involved in identifying what has been touched (the 'what' mechanism), whether it is self or other that has been touched (the 'who' mechanism), and localising the observed touch onto the body (the 'where' mechanism). The authors suggest that one of the brain areas potentially involved in the 'who' mechanism may be the IPL (encompassed within the right TPJ), and that overactivity in this area and the right IFG may lead to the attribution of another's body parts into the self-body representation. The results of Experiment 1 in the present thesis showed that increasing cortical excitability in the right temporoparietal area led to a reduction in the amount of another person's face that was included in the self-face representation, supporting the idea that a dysfunction of this mechanism could lead to the attribution of another's physical features into the self-body representation.

Apps et al.'s (2013) neuroimaging study of the Enfacement Illusion suggested that the rTPJ was involved in the experience of Enfacement. Activity within the right TPJ was shown to vary parametrically with the reported subjective strength of the illusion, specifically, a stronger subjective experience was associated with a reduction in the magnitude of the BOLD response in rTPJ. This was interpreted as reflecting increased overlap between the self and the other, and thus a reduction in the extent to which the participant and the enfacement individual were being processing as two distinct individuals. Therefore, it appears that the involvement of the right temporoparietal area in discriminating between self and other is not only important for the process of *self-recognition*, but is also involved during *self-identification* and *self-updating*. Much like the speculated role of self-other discrimination processes in MTS, the right temporoparietal junction may contribute to self-identification and self-updating by increasing the overlap between the observed face (either a mirror-reflection of one's own face, or another's face as in the Enfacement Illusion) and the stored self-face representation.

The results of Experiment 2 further extend the understanding of the role of the right temporoparietal area in the representation of the physical self. In Experiment 2, participants performed a mental body rotation task in which they had to imagine themselves in the same spatial and anatomical position as a person shown on screen. Typically in this task, participants are slowler to adopt the other's perspective when the body position is more far removed from the participant's actual body position, as their own body representation must be inhibited. Experiment 2 showed that following anodal tDCS over the right temporoparietal area (relative to anodal over the left, and sham tDCS), participants were faster to adopt the perspective of the person on screen. This suggests that increased excitability in right temporoparietal area facilitated the inhibition of the participant's actual body representation, while facilitating the representation of the other's body.

9.3.2 The temporoparietal area in social cognition

It has been suggested that the rTPJ not only distinguishes between the self and others at a physical, bodily level, but also that the same mechanisms may be used to perform higher-level social cognitive processes in which distinctions between self and other representations must be maintained, such as mental perspective taking and empathy (Decety & Lamm, 2007). Decety and Lamm (2007) performed a meta-analysis of neuroimaging data spanning studies of agency, reorienting of attention, empathy, and theory of mind. They found substantial overlap in the activation within rTPJ during the performance of both the low-level (e.g. attention reorienting, agency processing) and high-level (e.g. theory of mind, empathy) tasks, suggesting that one mechanism supports different levels of processing. This domain-general account of social cognition proposes that higher levels of meta-cognition are supported by a low-level computational mechanism involved in comparing internal representations with external events. Spengler et al. (2009) directly tested this theory, providing neuroimaging evidence that mentalizing, agency processing, and imitative control activate the same regions of rTPJ in the same participants. These findings support a theory of embodied social cognition, in which higher-level social cognitive processes such as theory of mind recruit the same neural mechanisms as low-level body discrimination. Along these lines, Bird and Viding (2014) propose a model of empathy that relies a switch from focusing on the self, which they argue is the default state of the representational system, to focusing on the representation of the other's mental state. Bird and Viding (2014) also speculate that the location of this switching mechanism may be rTPJ.

Santiesteban et al. (2012, 2015) suggest that TPJ controls coactivated representations of the self and other, and supports the ability to switch between these representations, inhibiting or enhancing the representations of either individual depending on the task demands. This mechanism is required whenever a task requires an individual to enhance their own perspective while inhibiting another person's, or vice versa. For example, when completing a visual perspective taking task, representation of the other's perspective needs to be enhanced, while one's own conflicting perspective should be inhibited. On the other hand, in a control of imitation task in which one must perform movements that are incongruent with the movements of another person, one's own body representation should be enhanced while representation of the other's body (and actions) should be inhibited. Across two tDCS studies, Santiesteban et al. (2012, 2015) showed that both the left and right TPJ were causally involved in two tasks requiring control over self and other representations, and that anodal tDCS over these areas resulted in better performance in both tasks: one requiring self-enhancement and other-inhibition (imitation inhibition), and the other requiring other-enhancement and self-inhibition (perspective taking). Sowden et al. (2015) has further supported the involvement of rTPJ in social cognition by showing that anodal tDCS over rTPJ improved performance on a lie detection task when the other individual expressed an opinion that was incongruent with the participant's own opinion. The authors suggested that anodal tDCS over the rTPJ improved lie detection by inhibiting the participant's own views while enhancing those of the other.

This thesis has expanded upon the work of Santiesteban et al. (2012, 2015) and Sowden et al. (2015) by showing that tDCS over the right temporoparietal area also affects representation of the self and other at the physical, bodily level. Experiment 2 showed that 20 minutes of anodal tDCS over the right temporoparietal area affected discrimination between one's own face and the face of another. Furthermore, Experiment 2 showed that the same type of stimulation facilitated the mental rotation of one's body to take another's spatial perspective. Experiment 2 also suggested that the process of mental body rotation is lateralised to the right temporoparietal junction, as stimulation over the left did not enhance performance during the task.

9.3.3 The neural underpinnings of self-identification and self-updating

A further aim of this thesis was to use tDCS to explore the involvement of brain regions in the processes of self-identification and self-updating. Previously, the majority of research had focused on the process of self-recognition, neglecting the importance of self-identification and self-updating for the understanding of self-face recognition, and although research using bodily illusions had shed some light on these two processes, there was a lack of brain stimulation research. Experiments 3 and 4 aimed to provide some causal evidence for the roles of S1 and IPS in self-identification and self-updating. Firstly, it is important to note that neither of the two experiments found a specific effect of tDCS, and secondly, the results of both experiments suggest that the self-recognition tasks used to assess changes to the self-face representation following the Enfacement Illusion elicited practice effects. Or alternatively, that the increased familiarity with the IMS face, as a result of seeing the face during the IMS session, led to changes in the self-recognition tasks that mimicked those of the typical enfacement effect. It is therefore difficult to use the results of these experiments to inform the understanding of these two areas in self-identification and self-updating. However, it is worth considering the reasons which could explain the lack of stimulation specific effects.

Firstly, the results of Experiment 4 will be discussed. Experiment 4 aimed to induce symptoms of MTS by increasing cortical excitability in S1 and thus enhance the vicarious activation of the somatosensory system during the observation of touch, and investigate whether this vicarious activation was sufficient to elicit changes in the self-face representation. Individuals with MTS can experience enfacement while watching a video of another person being touched, without receiving any touch themselves, suggesting that vicarious activation of the somatosensory system during the observation of touch to another's face may be able to elicit a change in the self-face representation. The tDCS in Experiment 4 was not successful at inducing a conscious experience of synesthetic touch, or a change in the self-face representation. The results may reflect that the neural basis of MTS extends beyond mere over-activation of the somatosensory system in response to the observation of touch. Although the experience of synesthetic touch may in part reflect over-activation of a somatosensory mirror system, in which vicarious activation of the somatosensory cortex is heightened in individuals with MTS compared with neurotypical individuals, the dysfunction of other mechanisms that distinguish between the self and other alongside this enhanced mirroring of somatosensory experience appear to also be critically important to the experience of synesthetic touch (Banissy et al., 2009). Without the dysfunction of mechanisms that distinguish between self and other, even if vicarious somatosensory activation is increased with tDCS over S1 in neurotypical individuals, it may not be attributed to the self as it is in MTS.

Experiment 3 aimed to investigate the involvement of the IPS in multisensory integration during the Enfacement Illusion. It was hypothesized that increasingly cortical excitability in IPS may enhance the strength of the Enfacement Illusion by facilitating the integration of multisensory information. The results however showed no specific effect of the stimulation on the subjective or objective strength of the illusion. This may reflect the fact that within the process of self-updating, the IPS is one part of a large network that processes incoming multimodal signals. As the IPS receives multimodal input, from multiple areas, it may not benefit from increased cortical excitability while previous areas within the network still have baseline levels of cortical excitability. In other words, although cortical excitability may be enhanced in IPS, the areas of the network that send information to IPS will still have typical levels of cortical excitability, therefore, IPS is only able to process multimodal information at the rate that it receives it from other areas in the network.

9.3.4 Self-updating beyond multisensory integration?

A third aim of this thesis was to investigate whether the self-face representation could be updated by means other than multisensory integration. Experiment 5 used a perceptual matching task to form an association between participants and a novel face, and investigated, using a morphed images self-recognition task, whether this association was able to alter the self-face representation. The results showed that the association had no effect on the way that participants perceived their own face. Considering the developmental trajectory of self-face recognition, which develops upon a base of sensitivity to multisensory contingency from birth, it is not entirely surprising that a mere association formed between oneself and a previously unfamiliar face is not able to alter the self-face representation, which is built upon repeated mirror exposure throughout one's whole life.

The results are more interesting when considered in relation to research that has shown that changes to the self-body representation are able to elicit changes in the conceptual, social self. For example, Banakou et al. (2013) used virtual reality to create a sense of ownership over a child-like body in adult participants. Ownership over the body caused participants to overestimate the size of objects (compared to a baseline condition in which embodiment did not occur), as well as cause participants to classify child-like attributes with themselves faster than adult-like attributes, suggesting the self-concept had become associated with child-like features. Along similar lines, two experiments have found that changes in body ownership are able to elicit changes in implicit attitudes towards out-group members. Peck et al. (2013) conducted an experiment in which white participants experienced embodiment over a dark-skinned body in virtual reality, and Farmer et al. (2014) created the illusion of ownership over a dark-skinned rubber hand with white participants using the RHI. Following embodiment (over a whole body or a hand) both experiments found a reduction in implicit racial bias. The findings suggest that changes to the bodily self-representation are able to change interpersonal attitudes, and this may be due to the way the self is conceptualised. The group affiliation of the self may have been changed to match that of the racial-group of the embodied body (or body part), changing implicit attitudes towards that group.

Maister et al. (2014) suggest that changes in the self-body representation are able to lead to changes such as these through a process of self-association. Firstly, the self-body representation incorporates the new body part, leading to an increase in perceived similarity between the self and an out-group member. Secondly, the new perceived similarity between the self and the out-group leads to the association of the conceptual self-representation with the out-group, and the extension of positive self-attitudes to this group. This proposed model suggests that changes to the representation of the body can have a 'bottom-up' effect on other aspects of the self – namely how the self is conceptualized, leading to a change in social behaviour.

Currently, it is unclear whether there is a modulatory link between the conceptual and bodily self-representations in the opposite direction. A 'top-down' process by which changes to the conceptual self-representation lead to corresponding changes in the way one's body is perceived. Experiment 5 aimed to investigate whether changes to the conceptual self-representation could elicit changes in the physical self-representation by creating an association between the conceptual self and a novel face. A perceptual matching task (Sui et al., 2012) was used to create the association, which has been shown to quickly create a link between the self and a novel stimulus, making the stimulus self-relevant (Sui et al., 2012, 2013). Neuroimaging research shows that the self-associated stimulus activates areas of the brain associated with self-representation, providing evidence that the perceptual matching task establishes a link between the self-associated stimulus and the conceptual self-representation (Sui et al., 2013). Participants performed a self-recognition task before and after associating the novel face with themselves. Prioritised perceptual processing of the self-associated face suggested that it had been incorporated into the conceptual self-representation, however, no change in the self-face representation was observed following association. These results may suggest that modulatory links between the physical and conceptual self-representations only exist in a bottom-up direction, from physical to conceptual, and that changes to the conceptual self-representation are unable to elicit corresponding changes in the way one perceives their own body.

9.4 Limitations

9.4.1 Links between the bodily and conceptual self-representations

Chapter 7 explored whether changes to the conceptual self-representation could cause corresponding changes to the physical self-representation. This theory was drawn from research showing that changes in the way one's body is perceived can lead to changes in the way the self is conceptualized (Maister et al., 2014). It was hypothesized that links in the opposite direction may exist, however, Experiment 5 did not find evidence to support this. One reason may be that the changes observed in these experiments following changes to the bodily representation appear to affect the social self, that is, how the self is perceived in relation to others. For example, when white participants experienced ownership over a dark-skinned hand or a dark-skinned body, the change in body representation affected implicit attitudes towards people of that racial group (Farmer et al., 2014; Peck et al., 2013). The change in body representation leading to increased perceived similarity between the self and an outgroup might not cause a change in the conceptual representation of the self, but rather may only lead to a change in the way individuals from that outgroup are perceived by changing the conceptual representations of that outgroup. Maister et al. (2014) suggest that changes in social behaviour following experiences of body ownership occur due to associations being created between the conceptual representations of the self and the outgroup. This leads to positive associations of the self being extended to the out-group – but, importantly, it may not lead to any aspects of the outgroup representation being incorporated into the conceptual representation of the self. Therefore, changes to the bodily self-representation, increasing physical similarity between the self and another group, may affect perception and behaviour towards individuals of that group by changing the way they are conceptualised, without affecting the way the self is conceptualised. In summary, apparent links between the bodily and conceptual self-representations may actually reflect modulatory links between the physical representation of self and the perception of others, without affecting the conception of the self.

9.4.2 Issues in the measurement of self-recognition

The results of Experiments 3 and 4 highlight that the tasks commonly used to measure self-face recognition may suffer from practice effects. Both of these experiments used within-subjects designs, with multiple experimental sessions in which participants completed a self-recognition task two (Experiment 4) or four times (Experiment 3) per session. These Experiments did not find any specific effect of tDCS – which may be explained in part due to the lack of spatial focality of tDCS, as explained in more detail in the next section – but did find main effects of the timing of the administration of the self-recognition tasks. This lack of a specific effect of tDCS, and main effects of timing of the task even in the control (sham) sessions, would point to practice effects being present in the self-face recognition tasks. The nature of both of the tasks used - the video morphing, and the morphed static images – was very repetitive, and as the same photo of the IMS individual's face was used for all of the morphs, it is likely that participants became familiar with the IMS face very quickly. They may have therefore become better at discriminating between their own and the other's face as they became more practiced at the task, and thus the point at which they discriminated between their own and the other's face changed due to familiarity with the other's appearance, rather than a change in their own face-representation.

In contrast, there is no evidence for a practice effect in Experiment 1, despite the same self-recognition task being used in both Experiments 1 and 3. This may be due to the fact that Experiment 1 used a between-subjects design, and as such each participant only took part in one experimental session in which they completed the self-recognition twice, once before, and once after, receiving tDCS. For Experiments 3 and 4, it was important to use within-subjects designs, as both of these experiments used the Enfacement Illusion to attempt to change the mental self-face representation. The extent to which the enfacement paradigm is successful at eliciting the illusion varies between individuals, and as such it was important to use participants as their own controls by having them take part in all tDCS conditions. However, the repeated use of the self-recognition tasks seems to have resulted in practice effects which make it difficult to interpret the findings of these experiments. Or, alternatively, the results could be due to increased familiarity with the IMS face from exposure during the IMS session.

9.4.3 Lack of spatial focality of tDCS

TDCS applied using rectangular pad electrodes is considered to have relatively poor spatial focality. Firstly, a portion of the stimulation never reaches the cortex as it is dispersed by the scalp. Of the current that does pass through the scalp, it is first conducted by the cerebrospinal fluid before passing through into the brain. Once in the brain, the flow of the tDCS current is further influenced by the tissue morphology of the brain under the electrode site. Datta et al. (2009) used an MRI compatible tDCS device to model precisely the spread and magnitude of the current induced by tDCS in the brain. They found that tDCS induced by conventional 35cm^2 electrodes resulted in diffuse modulation of the cortical electric field, with the peak induced magnitude located away from the site of stimulation, at an intermediate lobe.

Spatial focality can be improved in a number of ways. Firstly, reducing the size of the electrodes used to apply the stimulation has been reported to provide better spatial focality (Nitsche et al., 2007). Nitsche et al. (2007) reduced the size of an anodal electrode used to stimulate the primary motor cortex to 3.5cm^2, relative to the conventional size of 35cm^2, and found that it reduced the dispersion of the current without diminishing the efficacy of the stimulation. Kwon et al. (2008) also used a reduced electrode size of 7.07cm^2 to successfully stimulate M1, observing the effects of the stimulation with fMRI. However, it is also important to consider safety guidelines on the use of tDCS. While neither of the above studies reported any adverse effects, suggesting that the combinations of electrode size and current strength may be safe for use in humans, both studies only applied stimulation for very short periods of time (between 4-84sec), so it is of yet unclear whether such small electrodes would be safe to use for extended stimulation periods (e.g. 20 minutes).

It has also been suggested that using a ring electrode configuration can result in more focal stimulation. Datta et al. (2009) compared the focality of conventional rectangular electrodes with a 5 point ring electrode configuration, and found that the ring electrode configuration resulted in a more focal modulation of the cortical electric field. They also observed that the peak induced electric field magnitude was located directly underneath the stimulation site when using the ring configuration, suggesting that the ring electrode configuration can be used to provide more accurately targeted stimulation to brain regions of interest. It is important to note that other research has suggested that the focality of the ring electrode configuration can be negatively affected by tissue anisotropy (Suh, Lee, Cho, Kim, & Kim, 2010), and so it is important to consider this factor in models of tDCS stimulation.

Lastly, accurate placement of electrodes on the scalp is critical in achieving modulation of the cortical electric field in the desired region. All of the experiments in the current thesis used the probabilistic approach of following the 10/20 EEG system for localisation of brain regions. Preferably, individual localisation in each participant using a structural MRI scan would be used, but this requires each participant to take part in an MRI scan, which was not feasible within the constraints of the research in this thesis. Sparing, Buelte, Meister, Pauš, and Fink (2008) compared placement of a TMS coil that was either guided by MRI data, or the 10/20 EEG system. Although neuro-guided TMS resulted in the most accurate stimulation, the probabilistic approach was shown to produce fairly consistent results, suggesting that it is an acceptable method of localisation when neuro-guided navigation is not feasible.

The Experiments in the present thesis attempted to follow, where possible, the localisation methods of previous studies that had been successful at stimulating the target regions with tDCS. Despite this, it is important to remember that however precise the positioning of the electrodes on the scalp, the current flow will always be influenced by the structure of the scalp and underlying brain tissue. Because of this it is difficult to be sure of the spread of the stimulation even when localisation on the scalp is accurate and consistent. It is therefore unlikely that the stimulation used in the experiments in this thesis only modulated cortical excitability in the targeted regions. It would be insightful for future research to use tDCS in combination with fMRI to gain an understanding of which regions have been stimulated, and combine this with measures of behaviour to provide a more accurate picture of the neural regions involved.

9.5 Future Directions

Future investigations should examine the relationship between the conceptual and the physical representations of the self. As discussed, in Experiment 5 a change in the conceptual self-representation did not cause a corresponding change in the perceptual self-representation. However, as discussed above, links between perceptual and conceptual aspects of self seem to play an important role in the perception of others. Therefore, it would be interesting to investigate whether changes in the way the self is conceptualized in relationship to an outgroup could lead to changes in the way the self is perceived physically in relation to that outgroup. It may be the case that perceived physical similarity between the self and others is not only determined by actual featural similarities, but is also mediated by perceived conceptual closeness, and that by manipulating this sense of closeness, one can change the physical perception of self. This could be explored experimentally by manipulating aspects of the conceptual self to include aspects of the outgroup, and testing to see whether the inclusion of conceptual aspects of the other in the representation of the self can lead to an increase in the perceived physical similarity between the self and members of that outgroup

Further research is still needed to investigate the neural underpinnings of self-identification and self-updating during multisensory integration. One possibility for further study would be to use rTMS to disrupt typical functioning within IPS during the Enfacement Illusion. Anodal tDCS over IPS may not be able to produce a measurable effect on the integration of observed and experienced tactile stimulation as the mechanisms underpinning integration may already be processing at a ceiling level. rTMS on the other hand should be able to demonstrate causality in this instance as it should disrupt the integration, resulting in a disruption to self-updating.

Future research should additionally investigate whether changes in self-other discrimination, induced by manipulations in cortical excitability within the temporoparietal area, have an effect on attitudes and behaviour towards others. The results of Experiment 1 show that the perceived level of physical overlap between the self and another person is determined in part by activity within the temporoparietal junction. This mechanism may also be involved in determining behaviour towards others by mediating this self-other overlap. As discussed previously, research with bodily illusions has shown that increasing perceived physical similarity with others can lead to more positive attitudes towards them (Maister et al., 2014), which could suggest that an increase in overlap between representations of the self and other, underpinned by a mechanism within the temporoparietal junction, may play a role in shaping attitudes and behaviour towards others.

9.6 Conclusions

This thesis investigated the neural and cognitive mechanisms underpinning self-face representation. TDCS was used to investigate the causal involvement of different brain regions in the processes of self-identification, self-recognition and self-updating, and a perceptual matching task was used to investigate potential mechanisms for self-updating. It was found that the right temporoparietal area plays an important role in self-recognition and distinguishing the self from others, but also, in taking the physical perspective of others. It was speculated that this mechanism may contribute not only to self-recognition, but also self-identification. It was also found that associating the self with a novel face is unable to change the self-face representation, suggesting that the bodily representations of self are grounded in multisensory experience, and that top-down processes do not serve to update bodily representations of self.

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