Distinguishing Self from Other in Vicarious Perception of Touch and Pain

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

Signed: Date:

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Abstract

Vicarious perception describes our ability to co-represent the experiences of others, by matching observed states onto representations of our own experience. For instance, seeing another person feel touch or pain elicits activity in regions associated with first-hand touch and pain sensation, including somatosensory cortices. Vicarious touch and pain perception is thought to facilitate complex social processes such as empathy, and also shows substantial inter-individual variability. For a minority of people, a physical sensation of touch (mirror-touch synaesthesia) or pain (conscious vicarious pain) is felt on their own body when observing someone experience the same sensation. Current theory suggests increased excitability in somatosensory cortices may underlie conscious vicarious experience. Recently, broader impairments in self-other distinction have also been implicated. This thesis first attempted to modulate vicarious tactile perception with transcranial current stimulation targeted at somatosensory cortices or the right temporo-parietal junction (linked to self-other control). A lack of modulation provided minimal support for either somatosensory excitability or self-other distinction accounts. Behaviourally, conscious vicarious pain responders and control participants did not significantly differ in self-other control abilities. Additional self-other distinction processes (beyond self-other control) were next considered. This revealed atypical bodily self-awareness in conscious vicarious pain responders. Lastly, perception of animacy was modulated by stimulus and perceiver variability, but did not significantly differ between mirror-touch synaesthetes and controls, providing implications for vicarious perception from inanimate stimuli. Collectively, this thesis highlights broader impairments involved in conscious vicarious perception, and the importance of the sense of bodily self-awareness for social perception and interaction in typical adults.

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Publications Arising from Thesis

Bowling, N. C. & Banissy, M. J. (2017). Modulating vicarious tactile perception with non-invasive brain stimulation. *European Journal of Neuroscience*, *46*(8), 2355-2364.

Bowling, N. C. & Banissy, M.J. (2017). Emotion expression modulates perception of animacy from faces. *Journal of Experimental Social Psychology, 71*, 83-95.

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Chapter 1

Introduction

This chapter provides a review of existing literature on two crucial processes for social interaction: vicarious perception and self-other distinction. Firstly, research is discussed regarding vicarious perception of touch and pain. Secondly, several processes involved in self-other distinction are discussed, with a specific consideration of how these processes may contribute to vicarious perception. A summary of current research on conscious vicarious perception, including mirror-touch synaesthesia and conscious vicarious pain, is also provided, with an emphasis on the possibility of atypical self-other distinction mechanisms in these extreme cases. The primary aims of this thesis will be to further examine self-other distinction processes and their potential contribution to vicarious experiences of touch and pain.

1.1 Vicarious perception of touch and pain in neurotypical adults

Vicarious perception refers to the ability to co-represent the experiences of other people by matching the observed state onto representations of our own first-hand experience. While vicarious perception has been extensively studied in the action domain, vicarious touch and pain has only gained attention in recent years (Gillmeister, Bowling, Rigato & Banissy, 2017; Lamm & Majdandžić, 2015). Vicarious tactile perception and nociception forms a particularly important field of study, since representing others' sensory experience is crucial to facilitate complex social processes such as affective understanding and empathy, and as such allows individuals to form social bonds (Bird & Viding, 2014). Accurately perceiving and representing others' sensory experiences is also thought to be important for developing and maintaining a stable sense of our own bodily self (Gallese & Sinigaglia, 2010; Adler, Schabinger, Michal, Beutel & Gillmeister, 2016).

Functional neuroimaging studies over the past decade have repeatedly shown that brain regions associated with experiencing touch on one’s own body are also activated by passively observing touch to another person, indicating a process of somatosensory mirroring. Overlapping regions of activity have been reported in both primary (SI) and secondary (SII) somatosensory cortex in several functional magnetic resonance imaging (fMRI) studies (e.g., Blakemore, Bristow, Bird, Frith & Ward, 2005; Ebisch et al., 2008; Holle, Banissy, & Ward, 2013; Keysers et al., 2004; Kuehn, Mueller, Turner & Schütz-Bosbach, 2014; Schaefer, Heinz & Rotte, 2012). Electroencephalography (EEG) studies also show modulation of somatosensory-evoked potential (SEP) components in response to a tactile stimulus, when concurrently observing touch to another person (e.g., Bufalari, Aprile, Avenanti, Di Russo & Aglioti, 2007; Deschrijver, Wiersema & Brass, 2016; Martínez-Jauand et al., 2012). Studies using methods of non-invasive brain stimulation provide further support for somatosensory representations of observed touch. Repetitive transcranial magnetic stimulation (rTMS) targeted at SI specifically impairs visual detection of touch to another person’s hand, compared with touch to an object (e.g., Bolognini, Rossetti, Maravita and Miniussi, 2011; Rossetti, Miniussi, Maravita & Bolognini, 2012). Further studies by Bologini and colleagues (Bolognini, Miniussi, Gallo & Vallar, 2013; Bolognini, Rossetti, Fusaro, Vallar & Miniussi, 2014) have also indicated that this region may be involved in the conscious vicarious perception of touch (i.e., mirror-touch synaesthesia, but see section 1.3 and Bowling & Banissy, In Press).

In the case of painful touch, it is important to consider the negative affective consequences of the sensation. The neural network involved in the first-hand processing of pain, known as the pain matrix, comprises regions associated with both the sensory (including SI, SII) and affective (including anterior cingulate cortex (ACC) and anterior insula (AI)) components of pain (Ingvar, 1999). Vicarious activity in areas representing the affective experience of pain, including the AI and ACC, has been found fairly consistently, across different experimental paradigms. For instance, vicarious affective response has been recorded from a cue that another person is receiving pain (e.g., Bird et al, 2010), and others' facial expressions of pain (e.g., Botvinick et al., 2005; Budell, Jackson & Rainville, 2010), as well as directly viewing the painful event (e.g., Lamm, Meltzoff & Decety, 2010). Rütgen, Seidel, Riečanský and Lamm (2015) suggest that this vicarious affective pain response involves neural mechanisms that are at least partially functionally equivalent to first-hand experience of pain. In this study placebo analgesia reduced amplitudes of P2 ERP components related not only to self-pain, but also to others' pain. This effect was supported by decreased self-reported empathy in the analgesia condition.

Studies using EEG and magnetoencephalography (MEG) provide some evidence for the involvement of somatosensory regions in vicarious pain representations. Similar to effects of observed touch, these studies have demonstrated increased amplitude of SEP components (Bufalari et al., 2007; Martínez-Jauand et al., 2012) when observing pain. In addition, increased somatosensory resonance, indexed by mu rhythm suppression (Cheng, Yang, Lin, Lee & Decety, 2008; Yang, Decety, Lee, Chen & Cheng, 2009), and synchronisation between sensory and motor cortices (Betti, Zappasodi, Rossini, Aglioti & Tecchio, 2009) has been found for observing other-pain compared with no pain. Viewing a painful stimulus to another person's body is also associated with corticospinal inhibition (examined using motor-evoked potentials (MEPs) induced by TMS) specific to the same muscle as the location of the observed painful stimulus (e.g., Avenanti, Bueti, Galati & Aglioti, 2005). While fMRI studies also provide some evidence for activation of somatosensory cortex when observing others in pain (e.g., Lamm et al., 2010; Lamm, Nusbaum, Meltzoff & Decety, 2007) a recent meta-analysis of fMRI data from 32 studies comparing activation for self- and other-pain found that this effect is not consistent (Lamm, Decety & Singer, 2011). In this analysis, common activation in regions associated with sensory processing of pain was found, but was limited to studies which had used visual images of painful events, rather than cues that another person was experiencing pain. With these studies in mind, there appears to be some evidence that regions associated with sensory processing do have a role to play in vicarious perception of pain.

Neuroanatomical evidence provides potential pathways by which visual input may be integrated with somatosensory information, and subsequently modulate activity in somatosensory cortex. In monkeys, Brodmann area 2 (a subdivision of SI) contains afferent and efferent connections with regions of the intraparietal sulcus, (particularly the ventral intraparietal area, VIP; Lewis & Van Essen, 2000) and with the inferior parietal lobule (specifically areas PF/PFG; Pandya & Seltzer, 1982). Both regions also receive input from visual cortex (Anderson, Asanuma, Essick & Siegel, 1990; Maunsell & Van Essen, 1983), providing candidate regions for where visual and somatosensory information are integrated in humans (Banati, Goerres, Tjoa, Aggleton & Grasby, 1999). Notably, single neurons in VIP have been shown to be activated by visual observation as well as the direct experience of touch (Ishida, Nakajima, Inase & Murata, 2010). Moreover, SII also contains indirect pathways with visual cortex, via reciprocal connections with VIP (Lewis & Van Essen, 2000) and IPL (Rozzi et al., 2006). As such, the cortical connections described above provide a pathway by which somatosensory cortices may be vicariously activated by the mere observation of touch or pain.

One region implicated in mediating somatosensory responses to observed stimuli is the temporo-parietal junction (TPJ). The TPJ refers to the area of the cortex covering the point at which the posterior temporal gyrus meets the parietal lobes. Within the literature there has not been complete consensus regarding the anatomical boundaries of the TPJ, since it does not map on to specific anatomical landmarks (Schurz, Tholen, Perner, Mars & Sallet, 2017), or indeed whether it should be considered as one unified region. Typically, the TPJ is considered to include regions of the angular gyrus (AG) and supramarginal gyrus (SMG), which correspond to areas PF/PFG of the IPL (Carter & Huettel, 2013). As discussed above, these neighbouring regions are thought to be involved in integrating multimodal (including visual and tactile) stimuli. Mars and colleagues (2012) propose a three-cluster structure to the TPJ, reporting that direct structural connections with somatosensory-related areas are found mostly in anterior regions of the TPJ. Connections were found with the postcentral gyrus (SI) as well as anterior insula (AI), which contains tactile receptive fields (Olausson et al., 2002) and further direct connections with primary and secondary somatosensory cortex (Mufson & Mesulam, 1982). Afferent connections with SI/SII provide a pathway by which mechanisms involved at the TPJ (discussed further in section 1.2) may mediate subsequent somatosensory activity. Consistent with this, lesions to the TPJ result in marked reductions in somatosensory-evoked potentials over (Yamaguchi & Knight, 1991), supporting a role in tactile processing.

Overlapping regions of activity in response to the experience or observation of touch and pain has given rise to speculation of somatosensory-related mirror-systems that respond to both own and others’ touch and pain sensations (Keysers, Kaas &

Gazzola, 2010), based on evidence of mirror neurons for action (di Pellegrino, Fadiga, Fogassi, Gallese & Rizzolatti, 1992) and touch (Ishida et al., 2010) in monkeys. While studies using fMRI methods can show overlapping activity in the same regions of the brain, they cannot provide evidence for specific mirror neurons, since each voxel can cover hundreds or thousands of neurons. At present only minimal direct evidence suggests that shared representations do reflect the activity of mirror neuron networks rather than separate networks within the same brain regions. Single cell recordings in awake participants have identified neurons that respond during the observation and execution of actions (Mukamel, Ekstrom, Kaplan, Iacoboni & Fried, 2010) as well as neurons in the ACC that respond to both the observation and experience of pain (Hutchison, Davis, Lozano, Tasker & Dostrovsky, 1999). In addition, Coll, Bird, Catmur and Press (2015) provide EEG evidence for a tactile-specific mirror system. In this study mu rhythm attenuation was observed over sensorimotor cortex following the observation and experience of touch, indicating vicarious activity during observation. Crucially, this attenuation was reduced when an observed or felt stimulus was repeated, either in the same or the other modality. This suggests that the same neural networks were employed for both types of stimulus, therefore indicating the involvement of tactile mirror systems. However, contrasting results from multivariate pattern analysis of fMRI data suggest that there are distinct neural signatures involved in perceiving own and others' pain (Krishnan et al., 2016). Further evidence is needed to provide convincing support for tactile mirror systems, and their potential involvement in vicarious perception.

1.1.1 Individual variability in vicarious perception of touch and pain

Several individual difference factors have been associated with variability in vicarious perception of touch and pain. In the case of pain, trait differences related to the perception of threat may be of relevance. Evidence of localised motor inhibition in response to observed pain indicates that vicarious perception may be important for predicting and preparing for potential harm to the self (e.g., Avenanti et al., 2005; Avenanti, Minio-Paluello, Bufalari & Aglioti, 2006; Avenanti, Minio-Paluello, Bufalari & Aglioti, 2009). Moreover, when observed pain is perceived as intentionally caused by another agent rather than accidental, stronger connectivity is observed between the amygdala and medial orbitofrontal cortex (Akitsuki & Decety, 2009). Connectivity between these regions has previously been associated with perceiving social threat (Coccaro, McCloskey, Fitzgerald & Phan, 2007). Ochsner and colleagues (2008) report an association between high trait anxiety and increased activity in rostral lateral prefrontal cortex in response to observed other-pain. The authors interpret this association as increased vigilance to potential threat in highly anxious individuals. In line with this assertion, scores on the pain vigilance and awareness questionnaire, a self-report measure of hypervigilance to pain (McCracken, 1997) have been found to modulate conscious vicarious pain perception (Vandenbroucke et al., 2013; Vandenbroucke, Bardi, Lamm & Goubert, 2016; see section 1.3). However, this association has not been consistently found in subsequent studies (Vandenbroucke, Crombez, Loeys & Goubert, 2014; Vandenbroucke, Crombez, Loeys & Goubert, 2015). Ward and Banissy (2017) also highlight that we cannot disentangle cause and effect regarding these factors, whether traits such as anxiety or hypervigilance to pain contribute to vicarious perception, or heightened vicarious perception leads to increased anxiety or vigilance to pain. Further work is therefore needed to establish the role of these traits in vicarious pain perception.

Alexithymia has also been associated with reduced vicarious response to seeing others in pain (Bird et al., 2010). Alexithymia refers to a difficulty identifying and describing emotions, as well as a tendency to reduce emotional experiences and focus attention externally (Bagby, Parker & Taylor, 1994). Bird and colleagues show a negative correlation between self-reported alexithymia and activity in the AI when a cue indicated that their partner would receive a painful electric shock, indicating a reduced vicarious affective response in alexithymics. Given that the AI has previously been linked with monitoring own internal bodily states (see section 1.2.2), this evidence has led to the suggestion that common neural networks underlie affective and bodily representations of the self and others.

Regarding tactile perception, Schaefer, Rotte, Heinze and Denke (2013) find an association between vicarious touch response and conscientiousness. Conscientiousness is a ‘Big Five’ trait referring to a disciplined, organised and achievement-orientated personality (McCrae & Costa, 1987). In this study higher self-reported conscientiousness was associated with reduced insula activation when viewing touch to a hand. The authors speculate that the relation with conscientiousness in this case may reflect the ability to inhibit the observed tactile stimulation in order to maintain a sense of self (see section 1.2.3).

1.1.2 The role of vicarious representations in empathy

The wealth of evidence regarding mechanisms of vicarious perception gained over the last decade has led to interest in the extent to which these contribute to the experience of empathy. To address this question it is important to define what we understand empathy to be. Most conceptions of empathy in recent research comprise an affective and a cognitive component. The affective component involves an emotional state which is isomorphic to and elicited by the emotional state of another person (de Vignemont and Singer, 2006). Importantly, this defines empathy as a process of feeling *as* the other, rather than feeling *for* the other, thus distinguishing the concept of empathy from related processes such as sympathy. The cognitive component pertains to the understanding of that other person's mental state, commonly referred to as perspective-taking, mentalizing, or theory of mind. This component separates empathy from emotion contagion, which usually refers to the pure affective mirroring of the other's state, without the self-other distinction necessary to acknowledge the other person as the source of that affective state (Bird & Viding, 2014; Lockwood, 2016).

Collected evidence indicating that passive observation of others' sensory experience can elicit neural activity similar to that involved in representing first-hand experience, particularly in regions involved in affective representation such as the AI and ACC, provides support for a simulation theory of empathy (Gallese & Goldman, 1998; Preston & de Waal, 2002). This line of argument follows the discovery of motor mirror neurons, which fire when either performing an action or viewing another individual perform the same action, and have been implicated in understanding others' goal-directed actions (di Pellegrino, Fadiga, Fogassi, Gallese & Rizzolatti, 1992). Simulation accounts suggest that similar mirroring mechanisms underlie the understanding of others' mental states, and elicit the isomorphic affective state defined by de Vignemont and Singer (2006). However, at present there is little direct evidence either that shared representations actually reflect mirror neuron activity, or that these contribute to empathy (see Lamm & Majdandžić, 2015).

Various studies into vicarious perception of touch and pain have identified links with self-reported empathy. Sensorimotor responses to observed pain (observable as attenuation of MEPs) are greater for individuals with higher trait cognitive empathy (Avenanti et al., 2009), as indicated on the perspective-taking and fantasy subscales of the Interpersonal Reactivity Index (IRI, Davis, 1980). Cheng and colleagues (2008) also demonstrate greater mu suppression (indicative of somatosensory resonance) in response to observed pain in individuals with higher perspective-taking scores. Extending this link the tactile domain, Martínez-Jauand and colleagues (2012) show that higher perspective-taking is also associated with greater amplification of SEPs when observing either touch or pain. Schaefer and colleagues (2012) also find a positive correlation between perspective-taking scores and vicarious activity in SI when viewing non-painful touch to another hand. In contrast with perspective-taking, the personal distress subscale of the IRI (reflecting the self-focused affective component of empathy) is associated with reduced vicarious sensorimotor response (Avenanti et al., 2009), but shows a positive correlation with activity at the right AI and the ACC (Vistoli, Achim, Lavoie & Jackson, 2016) when observing pain, providing further support for the involvement of these regions in affective representations of pain.

Recent theories of empathy incorporate vicarious representations as one set of mechanisms contributing to a highly complex process. For instance, Bird and Viding (2014) suggest that automatic mirroring may contribute to emotion contagion aspects of empathy. The authors also highlight a key role for self-other control in this model, positing that a self-other switch allows attention to be biased towards the affective state of the other individual, to inform understanding and empathic response. This may also be necessary to reduce excessive personal distress elicited by the situation in order to empathise effectively with another’s mental state. For instance, medical professionals appear to be able to down-regulate their vicarious response, as indicated by reduced vicarious activations in both sensory and affective regions of the pain matrix (Cheng et al., 2007), as well as reduced ERP responses to others’ pain (Decety, Yang & Cheng, 2010). De Guzman and colleagues (2016) showed that training the ability to control representations of self and other improved the ability to inhibit automatic imitation of others’ actions when required, but also increased vicarious perception of others’ pain and self-reported empathy. An alternative account of the observed link between vicarious perception and empathy could be provided by this self-other control switch, where a bias towards the other over the self may enhance both vicarious perception and empathy; rather than vicarious perception contributing to empathy directly. The role of self-other distinction in vicarious perception is discussed further in section 1.2.

1.2 Processes of self-other distinction

1.2.1 Perception of animacy

One vital perceptual process for social interaction is distinguishing between what is ‘like me’ and ‘not like me’ (see Meltzoff, 2007). This involves the accurate distinction of animate (i.e., living beings capable of independent actions, thoughts, and emotions) human faces and bodies from inanimate objects in our environment. Looser and Wheatley (2010) propose a two-stage ‘fast and slow’ process to animacy perception from faces. This involves an initial, rapid categorisation to allow allocation of resources to human face stimuli, observable as the N170 component. This initial stage is thought to be prone to errors, providing an account of the phenomenon of pareidolia, in which faces are perceived in face-like patterns or objects; such as plug sockets, cars or pieces of toast. The second stage, occurring at least 400ms from onset, involves a more conservative decision process (Wheatley, Weinberg, Looser, Moran & Hajcak, 2011). This highly accurate stage of processing may contribute to the "uncanny valley" theory (Mori, 1970), which describes the unpleasant, eerie feeling experienced with very lifelike inanimate faces, such as dolls or CGI animations. Looser, Guntupalli and Wheatley (2013) suggest that this process of animacy detection allows additional mental resources to be allocated to enhance the processing of animate agents.

In order to study perception of animacy, previous research has used face stimuli that are morphed between humans and dolls. These studies have identified the point along the continuum from doll to human at which we first perceive animacy, which consistently falls around 56-68% animate (Balas, 2013; Balas & Horski, 2012; Hackel, Looser & Van Bavel, 2014; Looser & Wheatley, 2010). This judgement of animacy can be modulated by the social identity of the stimulus face (e.g., Hackel et al., 2014; Swiderska, Krumhuber and Kappas, 2012), with out-group faces less likely to be perceived as animate than in-group faces, which may reflect a bias towards greater motivation for social interaction with the in-group than the out-group (Hackel et al., 2014). Stimulus gender (e.g., Balas, 2013) is another factor influencing perception of animacy, with female faces less likely to be perceived as animate than male. These findings have led to speculation that dehumanisation of women may influence animacy perception from faces (Balas, 2013), however, no there is currently no evidence to support this assertion over a purely perceptual account. Individual differences in the observer, as well as the stimulus, have been found to affect animacy detection, including the desire for social connection. Powers, Worsham, Freeman, Wheatley and Heatherton (2014) report that scores on the Need to Belong scale (Leary, Kelly, Cottrell & Schreindorfer, 2013) correlate with animacy perception thresholds, where animacy is perceived more readily by individuals with a greater desire for social acceptance. Additionally, inducing feelings of social disconnection was found to lower the threshold for perceiving animacy, compared with a socially connected induction. These findings may reflect an adaptive strategy for individuals who feel socially isolated, where perceiving animacy more readily increases the likelihood of the desired social interaction. Collectively, the evidence regarding stimulus and perceiver variability in the perception of animacy provides further support for the importance of this categorisation process in enabling effective social interaction.

The perception of animacy is thought to modulate vicarious perception of touch and pain. Previous research has demonstrated specificity of behavioural and neural responses for observed touch and pain to animate human bodies and to inanimate objects (Avenanti et al., 2005; Bolognini et al., 2013; Costantini, Galati, Romani & Aglioti, 2008), providing support for the notion that vicarious representations of other humans' sensory experiences may act as a mechanism for social cognition and empathy (see section 1.1.2). However, since these studies have typically used inanimate stimuli which do not visually resemble human body parts; it is unclear whether the different response patterns are related to stimulus differences in animacy, or in visual form. Recent work has provided some contribution to this question in other domains. For instance, motor priming from observation of others' actions is greater when that other is perceived as animate (Liepelt & Brass, 2010); and sensorimotor action observation networks show greater activity when observing an animate human form compared with inanimate (see Press, 2011 for a review). Animacy has also been found to modulate person perception and activity in mentalizing networks (Cross, Ramsey, Liepelt, Prinz & Hamilton, 2016), indicating a role in social cognition more broadly. While less research in direct relation to vicarious tactile perception has been conducted, Deschrijver, Wiersema and Brass (2015) show modulation of both early and late SEP components in response to a tactile stimulus on the finger while viewing the tapping finger of a wooden hand compared with a real human hand, indicating that vicarious somatosensory representations are associated with a process of distinguishing other animate agents with the capacity for physical sensation from inanimate objects. However, further research and replication is needed to establish the importance of animacy perception in modulating vicarious touch and pain.

1.2.2 Bodily self-awareness

In order to correctly distinguish between the self and other, it is necessary to maintain a stable and coherent sense of self. Interoception refers to the awareness of our own internal bodily states (Brewer, Cook & Bird, 2016), and makes an important contribution to bodily self-awareness. Interoception has frequently been linked to insular cortex, so much so that this region is often referred to as the 'interoceptive cortex' (Craig, 2003, 2009, Critchley, 2005). Much of recent research has focused on interoceptive accuracy (sometimes referred to as interoceptive sensitivity), the ability to correctly monitor internal states such as heartbeats (Garfinkel, Seth, Barrett, Suzuki and Critchley, 2015). Reduced interoceptive accuracy is associated with greater susceptibility to illusions of body ownership over external objects, including the rubber-hand illusion (Tsakiris, Tajadura-Jiménez & Costantini, 2011) and enfacement illusion (Tajadura-Jiménez & Tsakiris, 2014). An accurate awareness of internal bodily states therefore appears to contribute to self-other distinction in body ownership, maintaining a strong sense of one’s own body. Interoceptive accuracy is also associated with the ability to control representations of self and other in the motor domain. Ainley, Brass and Tsakiris (2014) report that individuals with higher interoceptive accuracy show greater interference effects on an imitation-inhibition task, which requires participants to enhance self-relevant while inhibiting other-relevant representations. Similar difficulty on this task is found for individuals with conscious vicarious perception of touch (Santiesteban, Bird, Tew, Cioffi & Banissy, 2015; see section 1.3). Interoception therefore appears to be an important factor in self-other distinction processes, potentially impacting on vicarious perception. Continued research is required to clarify the mechanisms underlying this contribution in different domains.

Depersonalisation occurs when there is a sense of detachment from the bodily self (American Psychiatric Association, 2013). As shown for individuals with low interoceptive accuracy, higher levels of depersonalisation are also associated with greater susceptibility to the rubber hand illusion (Kanayama, Sato & Ohira, 2009). This indicates a potential impairment in self-other distinction in individuals with depersonalisation, and so further highlights the importance of bodily self-awareness for self-other distinction processes. Adler and colleagues (2016) provide evidence for the role of bodily self-awareness in vicarious perception. In this study early SEP components distinguished images of the participant’s own face being touched (P45) from another face (N80), and later components (P200) were attenuated in the own-face condition compared with the other-face. This self-other distinction in vicarious somatosensory response was not present for individuals with high levels of depersonalisation. The sense of bodily self-awareness may then be important for accurate self-other distinction in the vicarious perception of touch.

1.2.3 Self-other control

A number of key social processes require the online control and manipulation of self-relevant and other-relevant representations. The temporo-parietal junction (TPJ) has been implicated in several such tasks, including, but not limited to, visual perspective taking (Aichhorn, Perner, Kronbichler, Staffen & Ladurner, 2006), theory of mind, or mentalizing (Saxe & Kanwisher, 2003; Völlm et al., 2006), control of imitation (Brass, Ruby & Spengler, 2009) and empathy (Völlm et al., 2006). Right hemisphere TPJ (rTPJ) specifically shows greater activation when focusing on representations of others than representations of the self (Ruby & Decety, 2004). Studies using transcranial direct-current stimulation (tDCS) provide evidence that increasing excitability of rTPJ enhances performance on tasks requiring self-other control (Santiesteban, Banissy, Catmur & Bird, 2012; Hogeveen et al., 2015). It therefore seems likely that rTPJ plays a role in directing attention to the self or the other where appropriate.

In addition to regions of the pain matrix associated with affective and sensory components of pain processing, fMRI studies of vicarious pain perception have identified activity in regions associated with representing mental states of the self and others, including the TPJ (see Lamm et al., 2011 for a meta-analysis). The TPJ appears to be most strongly activated when others' pain is represented by an abstract cue rather than an image of the painful event, indicating that this region may be involved with inferring the mental states of others. Jackson, Brunet, Meltzoff and Decety (2006) provide some further evidence regarding the role of the TPJ in vicarious perception. In this study participants were shown images of hands and feet in painful situations, and increased activity was detected at the TPJ when participants imagined that the pain was occurring to another person, compared with imagining themselves. Vistoli and colleagues (2016) report similar effects, adding that this difference was found only when stimuli were presented in a first-person rather than third-person perspective. Increased activity at TPJ may then reflect self-other control mechanisms required to enhance other-relevant representations, necessary to resolve the conflict between visual cues towards the self (i.e., first-person perspective) and the instruction cueing the participant to imagine another person. Most recently, Coll, Tremblay and Jackson (2017) report a reduction in the subjective perception of others' pain, in addition to a reduction in amplitude of late ERP components related to perceiving facial expressions of pain, following cathodal (inhibitory) tDCS over rTPJ. The functional relevance of the TPJ in these studies indicates the involvement of self-other control mechanisms in vicarious perception. De Guzman and colleagues (2016) have directly explored the role of self-other control (i.e., the ability to enhance or suppress representations of the self or other according to task demands) in modulating vicarious perception. This study found that training the ability to control self–other representations can enhance vicarious pain perception, as shown by a greater decrease in MEPs when viewing others in pain, and improved ability to control imitation. Taken together, the evidence provides support for the self-other control processes and the recruitment of the TPJ in vicarious perception of touch and pain.

However, recent models have suggested a more domain-general function of the TPJ. Cook (2014) proposes that previous findings indicating involvement of the TPJ in self-other control may in fact reflect control over task-relevant and irrelevant stimuli. In support of this, increased activity in the TPJ is also observed during non-social attentional reorienting tasks (Mitchell, 2008). Anatomical evidence is provided by Nicolle and colleagues (2012), who identify a ventral-dorsal organisation in temporo-parietal cortex according to task relevance, where ventral regions were associated more with task-relevant, and dorsal regions with task-irrelevant representations, irrespective of whether these corresponded to self- or other-focused decision making. The TPJ, which corresponds to the ventral portion of the TPC may therefore be involved in facilitating representations of task-relevant over irrelevant information, rather than representations of the self over others. Previous evidence regarding the involvement of the TPJ in self-other control can be reinterpreted in light of this model. For instance, Santiesteban and colleagues (2012) demonstrate enhancement of self-relevant representations on an imitation-inhibition task and other-relevant representations on a perspective-taking task following anodal stimulation of rTPJ with tDCS. While one interpretation could conclude an improvement in self-other control, it must be noted that in both cases the task-relevant representation was enhanced, and therefore increasing excitability of rTPJ may in fact lead to a domain-general facilitatory effect on task-relevant representations.

Carter and Huettel’s (2013) ‘nexus model’ provides some potential reconciliation of these two accounts, proposing that the convergence of multimodal representations (to include perception, memory, attention, and language as well as social processing) within spatially differentiable but overlapping regions of the TPJ establishes social context for behaviour. For instance, the TPJ has been identified as a core region within a ventral attention network, involved in stimulus-directed reorienting of attention (Corbetta & Shulman, 2002). Recent models suggest that the TPJ may also be involved in communicating between ventral and dorsal networks (engaged in goal-directed attention), allowing goal-directed attention to be interrupted to reorient towards a salient stimulus (Carter & Huettel, 2013; Corbetta, Patel and Shulman; 2008). This integration of modalities appears to be primarily relevant to social interactions. TPJ activity, for instance, has been shown to predict behaviour in an online poker game, when playing against opponents deemed to be competent (i.e. in situations which require complex representations of others' behaviour as well as one's own; Carter, Bowling, Reeck and Huettel, 2008). Altogether, this evidence can account for the involvement of the TPJ in non-social activities (i.e. attentional reorienting), but supports the overarching function of establishing social context based on these multimodal inputs. Considering the functional role of the TPJ in self-other control, Carter and Huettel's model therefore proposes that multiple inputs are integrated within the TPJ in order to enhance or suppress representations of the self or others according to task demands.

1.2.4 Self-other similarity

In further support of the importance of self-other distinction processes for vicarious perception, self-other similarity in the visual perspective of a stimulus has been found to modulate both vicarious touch and pain (Bach, Fenton-Adams & Tipper, 2014; Vandenbroucke et al., 2015). In these studies touch or pain observed to hands from a first-person perspective facilitated tactile detection of a stimulus on the participant's own hand, compared with the same stimulus viewed from a third-person perspective. Further, Canizales, Voisin, Michon, Roy and Jackson (2013) demonstrate greater modulation of somatosensory steady-state response when observing pain from a first-person compared with a third-person perspective. Mahayana and colleagues (2014) extend this evidence to show that vicarious perception of pain is modulated by whether the body part is seen close to the participant's own body (i.e., in peripersonal space) or further away. In this study a greater reduction of MEPs was found when viewing others' pain in near, peripersonal space than in far space. The behavioural and neural effects of visual perspective found across these studies suggests that vicarious perception can be reduced by enhancing self-other distinction between the observer and the person experiencing touch or pain.

Furthermore, manipulating contextual self-other similarity has been shown to influence vicarious perception of touch and pain. For instance, vicarious affective responses to pain, indicated in autonomic responses and subjective reports, are enhanced when the pain occurs to a hand which is imitating the participant's own movements (De Coster, Verschuere, Goubert, Tsakiris & Brass, 2013). Self-other similarity manipulations relevant to social group membership also affect both vicarious affective and sensorimotor responses to pain. Viewing a painful stimulus delivered to another person is associated with greater reduction in amplitude of motor-evoked potentials as well as greater activation of AI (Azevedo et al., 2013) when the person receiving pain is of the same race as the perceiver. A similar increase in AI activity can be found for observed pain of individuals who support the same football team, compared with a rival team (Hein, Silani, Preuschoff, Batson & Singer, 2010). Regarding vicarious touch, Serino and colleagues have demonstrated that viewing synchronous touch while being touched on one's own face improves tactile perception in the same location, compared with viewing asynchronous touch. This effect was strongest when participants viewed touch on their own face compared with another face (Serino, Pizzoferrato & Làdavas, 2008; Cardini, Tajadura-Jiménez, Serino & Tsakiris, 2010) and for the face of another person of the same race or political affiliation as the participant, compared with other racial or political groups (Serino, Giovagnoli & Làdavas, 2009). It appears then, that similarity between self and other enhances both affective and sensory vicarious representations.

1.2.5 Summary of self-other distinction processes in vicarious perception

Given the multiple sources of evidence discussed above suggesting that vicarious perception is enhanced when it is more difficult to distinguish between self and other, it has been suggested that previously reported vicarious somatosensory activity in response to touch and pain (see section 1.1) may reflect a misidentification with the viewed body that is not one's own. This may occur because typically used body parts in these experiments (e.g., hands, arms) are not as distinctive as the face, and so may appear very similar to the participant's own body. Body parts are also commonly presented in near-space, in a first-person position, while the participants' own body parts are hidden, which may further promote the other body part to be attributed to the self. In many EEG studies, simultaneous tactile stimulation will also be delivered, creating additional self-other similarity which may elicit a sense of ownership over the viewed body part (Schaefer et al., 2006; Tsakiris & Haggard, 2005). Collectively, these factors may lead to identification with the body part at early stages of somatosensory processing (Gillmeister et al., 2017).

1.3 Mirror-touch synaesthesia and conscious vicarious pain

1.3.1 Prevalence and characteristics

As discussed in section 1.1, while typical adults show vicarious somatosensory activation and physiological responses to others' experiences of touch and pain, the majority do not experience a conscious sensation on their own body from pure observation. For those with mirror-touch synaesthesia (MTS), an automatic and involuntary first-hand tactile sensation is experienced in response to observed touch

(Ward & Banissy, 2015). The prevalence of MTS is estimated at 1.6%; however, self-reported prevalence is much higher, at around 10.8% (Banissy et al., 2009). The estimate of 1.6% refers to participants that objectively differ to control participants on a visuotactile interference test designed to verify the authenticity of MTS (Banissy & Ward, 2007). In this task participants are required to report the location of a tactile stimulus on their own body while observing another person being touched. The tactile stimulus can either be spatially congruent or incongruent with the location of synaesthetic induced touch (i.e., the location where the individual reporting MTS claims to experience a sensation when observing touch). Compared with controls, MTS participants typically make more errors and show a greater congruency effect in their responses. This indicates that the observed touch generates a tactile sensation on the synaesthetes body that feels similar to first-hand tactile experience, leading to greater interference. Congruency effects on the visuotactile interference task are consistent with inter-individual differences within the MTS group. For instance, Banissy and Ward (2007; see also White & Aimola Davies, 2012) identify two contrasting spatial reference frames in MTS: anatomical (e.g., the synaesthete reports a sensation of touch on their own left cheek when observing another person being touched on the left cheek) and mirrored (e.g., the synaesthete reports touch on the right cheek when observing another person being touched on the left cheek, mapping to the same side of the body as if looking in a mirror). Individuals with a mirrored MTS show congruency effects under a mirrored frame of reference on the visuotactile interference task, while individuals with an anatomical MTS show congruency effects under an anatomical frame of reference.

In addition to vicarious touch, conscious vicarious perception of pain (also known as mirror-pain synaesthesia) has been reported from observing a painful stimulus to another person. A prevalence rate of 33-34% is reported for conscious vicarious pain in healthy individuals, although this figure is based on fairly liberal cut-offs (Giummarra et al., 2015; Osborn & Derbyshire, 2010). In a recent study, Grice-Jackson, Critchley, Banissy & Ward (2017) used a cluster analysis method to classify individuals conscious vicarious responders on the basis of self-reported responses to video stimuli. The study supports previous estimates, reporting a prevalence of around 31%. The authors also identify further sub-categories of conscious vicarious pain responders. These comprised a Sensory-Localised responder group who tended to use sensory descriptors to describe their experience, and report that it was localised to the same body part as the observed pain (estimated prevalence 19%) and an Affective-Generalised group who used more affective descriptors and reported a more generalised bodily sensation (estimated prevalence 12%).

Prevalence rates of MTS are based on individuals that show conscious vicarious tactile sensations in response to other human bodies being touched. Some synaesthetes also report conscious sensations in response to inanimate objects or dummy body parts (Banissy & Ward, 2007; Banissy et al., 2009). However, these vicarious experiences are typically described as less intense than touch to an animate human (Holle, Banissy, Wright, Bowling and Ward, 2011; Holle et al., 2013). Despite reporting some synaesthetic experience in response to dummies being touched, individuals with MTS show significantly less activity in primary somatosensory cortex when viewing dummies compared with humans, indicating some specificity of vicarious representations for human bodies. Collectively, this behavioural and neural evidence indicates that conscious vicarious touch may be modulated by self-other similarity with the stimulus, where touch involving subjects more similar to the self elicit greater vicarious response (see section 1.3.3). However, further work is needed to establish the sources of inter-individual variability in conscious vicarious responses to inanimate stimuli. If perceived dissimilarity between the self and the dummy does indeed underlie the reduced vicarious response found in prior work, then inter-individual differences in conscious vicarious experience may arise from variability in self-other distinction (see section 1.2), influencing the extent to which dummy bodies are perceived as similar to the self.

Of relevance to the connection between vicarious perception and empathy, Banissy and Ward (2007) demonstrate that individuals with MTS obtain significantly higher scores on the emotional reactivity subscale (pertaining to the affective experience of empathising with others) of the Empathy Quotient (EQ; Baron-Cohen et al., 2004) than non-synaesthetes. This increase in emotional reactivity is also found for individuals with an acquired form of MTS, who experience vicarious touch in a phantom limb (Goller, Richards, Novak & Ward, 2013). While recent work has failed to replicate this finding in developmental MTS (Baron-Cohen, Robson, Lai & Allison, 2016), there were key methodological differences in this study, including a less stringent method of participant selection. Individuals with MTS were recruited solely from self-report rather than objective behavioural differences, as used by Banissy and Ward (on the visuotactile interference task described above). Banissy and Ward demonstrate that many individuals who report experiencing MTS do not differ from controls on this verification measure. A self-report selection process alone may therefore not have been sensitive enough to detect between-group differences, highlighting the need for standard methods of verification that can be administered across different labs. Qualitative evidence from participants with MTS also indicates experiences of excessive emotion contagion (Martin, Cleghorn & Ward, 2017). For individuals who report conscious vicarious pain, empathic concern (a subscale of the IRI referring to the other-oriented affective component of empathy; Davis, 1980) is also increased (Vandenbroucke et al., 2013, 2014). These findings provide support for theories of empathy which involve a process of simulating others' experiences, (Bird & Viding, 2014; Gallese & Goldman, 1998). As such, mirror-touch synaesthesia and conscious vicarious pain can provide insight into social cognition and interaction more in the wider population.

1.3.2 Threshold Theory of Mirror-Touch Synaesthesia

Functional MRI studies have shown that, compared with controls, individuals with MTS display greater activation of both primary (SI) and secondary (SII) somatosensory cortex during the observation of touch (Blakemore et al., 2005) and that this can match a pattern that would be expected given their self-reported frame of reference (Holle et al., 2013). Individuals with MTS therefore show greater activation in the same regions involved in vicarious tactile perception in typical adults (see section 1.1). In addition, MTS participants show greater grey matter density in SII than controls (Holle et al., 2013). Threshold Theory arises from these observations, arguing that hyperactivity of tactile mirror systems underlies conscious vicarious experience in MTS (see Ward and Banissy, 2015), in which vicarious activity is raised above a threshold for conscious perception. In this respect, conscious vicarious perception is considered to be an extreme case of normal vicarious processing. In support of Threshold Theory, congruency effects on the visuotactile interference task described above (typically displayed by individuals with MTS) have been induced in controls by increasing excitability in somatosensory cortex using anodal tDCS (Bolognini et al., 2013). Similar evidence of increased activity in somatosensory cortices has been found for conscious vicarious pain responders when observing pain, reflected in both fMRI BOLD signal

(Osborn & Derbyshire, 2010) and in mu rhythm suppression (Grice-Jackson et al., 2017). In addition, these individuals show increased activity in insular cortex, associated with affective responses to pain (Osborn & Derbyshire, 2010). Increased grey-matter density is also found in both insula and somatosensory cortex in conscious vicarious pain responders compared with controls (Grice-Jackson et al., 2017). Due to these similarities in vicarious somatosensory activity, Threshold Theory has also been applied to account for conscious vicarious pain experiences.

1.3.3 Self-Other Theory

While previous evidence points to hyperactive tactile mirroring in MTS and conscious vicarious pain, the cause of this increased activity remains unclear. Furthermore, a somatosensory hyperactivity account cannot explain additional differences in brain structure and behaviour outside of the domains of touch and pain that have been associated with these conditions. For example, both MTS and conscious vicarious pain have been linked to reduced grey matter density in rTPJ (Grice-Jackson et al., 2017; Holle et al., 2013) as well as altered bodily awareness and ability to control representations of self and other even in the absence of inducing experiences (e.g., Cioffi, Banissy & Moore, 2016; Santiesteban et al. 2015b; Derbyshire, Osborn & Brown, 2013; Aimola Davies & White, 2013). The more recent Self–Other Theory (Banissy & Ward, 2013; Ward and Banissy, 2015) was originally proposed to account for some of these factors with regards to MTS, but can also be applied to conscious vicarious pain. Self–Other Theory suggests that conscious vicarious experiences are related to atypical abilities in distinguishing the self from others. This ability to distinguish self and other could act as a gating mechanism by which somatosensory activity is moderated, explaining the hyperactivity associated with conscious vicarious touch and pain. As such, MTS and conscious vicarious pain may reflect more than just a heightened example of typical vicarious perception.

One mechanism by which self-other distinction is thought to be impaired is through an extension of bodily self-awareness, with MTS being linked to a more expansive plasticity of the bodily self (Banissy & Ward, 2013; Banissy et al., 2009). Individuals with MTS as well as those with conscious vicarious pain experience the rubber hand illusion (Botvinick & Cohen, 1998), and individuals with MTS the enfacement illusion (Tsakiris, 2008), without the synchronous tactile stimulation necessary to induce a sense of ownership over the other body for typical adults (Aimola Davies & White, 2013; Osborn & Derbyshire, 2010; Maister et al., 2013). In addition to body-ownership, MTS is associated with a greater sense of vicarious agency. In a study by Cioffi et al., (2016), participants saw hand actions performed by an experimenter in a mirror placed in front of them while listening to action instructions that either matched or mismatched the actions performed. Although the actions in the mirror were performed by the experimenter, they appeared to the participant in a congruent location with where they would be if the participant performed the actions themselves. The procedure therefore induces blurred boundaries between the self and other. Compared with controls, participants with MTS reported a greater sense of agency over the experimenter's actions in the match condition. Individuals with MTS also showed a stronger sense of ownership of the experimenter's hand compared to controls, in both the match and mismatch conditions. This crucial finding suggests that merely seeing another body making an action in a congruent location with where one expects to see one's own body was sufficient for the synaesthetes to represent the other body as their own. Collectively, the evidence regarding sense of ownership and agency over another body indicates a greater susceptibility to self–other merging in MTS and conscious vicarious pain, which may contribute to the atypical vicarious experiences of this group.

Another important aspect of self-other distinction for vicarious perception is the ability to control the degree to which we prioritise representations of the self or representations of other people. For instance, in order to experience appropriate levels of vicarious response it is necessary to enhance representations of others and inhibit representations of one's own affective or sensory state. However, to prevent excessive personal distress from another's negative state, it can be adaptive to inhibit representations of the other's state and enhance representations of the self (Cheng et al., 2007; Decety et al., 2010). Impairments in self-other control therefore provide another candidate mechanism which may contribute to atypical vicarious perception according to Self-Other Theory. In line with this suggestion, individuals with MTS show a difficulty with appropriate self–other control in situations that require inhibiting representations of others and enhancing representations of the self. In a study by Santiesteban and colleagues (2015b) individuals with MTS performed less accurately than controls on an imitation-inhibition task (see section 1.2) requiring the inhibition of other-relevant representations and enhancement of the self, while their performance on visual perspective-taking and theory of mind tasks which require enhancing representations of others while inhibiting the self were comparable with controls. Derbyshire and colleagues (2013) provide additional evidence regarding self-other control ability in conscious vicarious pain responders. On a dot-perspective task, participants with conscious vicarious pain showed greater difficulty than controls in enhancing representations of the self while inhibiting the other, similar to the pattern observed in MTS.

An alternative interpretation of these results is suggested by Heyes and Catmur (2015), who propose that vicarious touch and pain experiences may reflect domain-general inhibitory control mechanisms rather than those specific to self and other representations (Task Control Theory). Indeed, the dot-perspective task used by Derbyshire and colleagues (2013) has been criticised for not being a pure measure of self-other processing. Santiesteban, Catmur, Hopkins, Bird and Heyes (2014) demonstrate that replacing the human avatar in this task with an arrow leads to similar interference effects. Further, it is possible that prior evidence of atypical self-awareness, such as increased susceptibility to the rubber hand illusion (Aimola Davies & White, 2013; Derbyshire et al., 2013), could also be explained in terms of domain-general mechanisms of associative learning. Indeed, a lack of domain-general control conditions in previous research prevents interpretation in terms of domain-general or purely social mechanisms. However, the results presented by Santiesteban and colleagues (2015) somewhat conflict with Task-Control Theory, since individuals with MTS performed comparably with controls on a perspective-taking task requiring participants to enhance representations others and inhibit representations of the self. If MTS were associated with a domain-general impairment in task control, then we should predict that they would also perform more poorly than controls in this domain (see Ward & Banissy, 2017 for a similar discussion). Further research is necessary to fully explore the mechanisms underlying group differences on tasks of self-other control.

Collectively, evidence of atypical self-other distinction makes an important contribution to understanding vicarious perception, as it indicates that individuals who experience conscious vicarious touch and pain have a difficulty inhibiting representations of others even in the absence of the vicarious touch or pain stimulus. These broader differences in cognitive ability cannot be accounted for by Threshold

Theory in isolation. Considering current evidence, an interaction between mechanisms involved in somatosensory mirroring (proposed in Threshold Theory) and self–other distinction (proposed in Self–Other Theory) may provide the most comprehensive account of conscious vicarious perception.

1.4 Aims of thesis

The primary focus of this thesis was to examine self-other distinction processes and their contribution to vicarious perception of touch and pain. Primary aims were:

1. To examine the extent to which vicarious tactile perception can be modulated by increasing excitability in primary somatosensory cortex or the right temporo-parietal junction with transcranial current stimulation (Chapter 3)

2. To clarify the contribution of self-other control and domain-general inhibitory control mechanisms to vicarious perception by comparing the performance of conscious vicarious pain responders and controls on an imitation inhibition and a domain-general task (Chapter 4).

3. To assess the involvement of self-other distinction processes with regard to bodily self-awareness in vicarious pain perception, comparing trait levels of depersonalisation and interoceptive sensibility in conscious vicarious pain responders and controls (Chapter 5).

4. To identify individual and stimulus factors contributing to the distinction between animate and inanimate human faces, with a view to developing future studies to examine the role of animacy in modulating vicarious perception (Chapter 6).

Chapter 2

Methodological Introduction to Transcranial Current Stimulation

This chapter contains an overview of the methodological principles of different forms of transcranial current stimulation (tCS), including direct current (tDCS), alternating current (tACS) and random noise (tRNS). Each method is discussed in terms of its effect on neural activity and potential to modulate cognitive function. Practical issues such as spatial resolution and the effect of varying intensity and duration of stimulation are discussed, along with individual variability factors and ethical and safety issues. The following chapter (Chapter 3) will present two studies which attempted to modulate vicarious tactile perception using tDCS and tRNS, and so a particular emphasis is placed on these methods in the present chapter.

2.1 Transcranial direct current stimulation (tDCS)

Among different methods of transcranial current stimulation, the most widely used is tDCS. This technique was first used over 200 years ago, but has gained significant attention in the last decade, with research moving from animal models to human participants (Nitsche et al., 2008). This particular method of stimulation passes a constant, low-level electrical current, usually between 1-2 milliamps (mA), through external saline-soaked sponge electrodes placed on the scalp (Nitsche & Paulus, 2000). Using tDCS, electrical current flows from the anodal electrode to the cathodal electrode, and this is thought to increase cortical excitability at the region under the anode, and decrease excitability in the region under the cathode (Paulus, Nitsche & Antal, 2016). A comparison of anodal and cathodal tDCS waveforms with other methods of tCS is shown in Figure 2.1. One electrode is typically placed over a region of interest, and the other (sometimes referred to as the ‘reference’ electrode) is placed either over the vertex, the contralateral hemisphere, or can be placed on the body, such as the contralateral shoulder (Moliadze, Antal & Paulus, 2010). TDCS therefore provides a versatile technique to modulate cortical function in the desired brain area, in a chosen direction.

This method of stimulation appears to have potential to modulate a range of perceptual and cognitive functions, including language, working memory and vicarious perception (Bolognini et al., 2013; Coll, Tremblay & Jackson, 2017) to name a few (see Parkin, Ekhtiari & Walsh, 2015). For this reason, tDCS has become a method of great interest and attention in recent years.

2.1.1 Mechanisms of action

Rather than directly inducing an action potential, tDCS is thought to polarise the resting membrane potential of neurons in the cortical region of interest, affecting the spontaneous firing rate of the neuron. While anodal stimulation depolarises the membrane potential, increasing the spontaneous firing rate, cathodal stimulation hyperpolarises, decreasing the firing rate (Woods, Bryant, Sacchetti, Gervits and Hamilton, 2016). Neurotransmitter concentrations in regions under the electrode may also be affected by tDCS, with anodal stimulation thought to have an inhibitory effect on GABA concentration (e.g., Nitsche et al. 2004) while cathodal tDCS may inhibit glutamate levels (e.g., Stagg et al., 2009). However, while tDCS has become a popular method of neuromodulation in the last decade, the mechanisms which underlie its action are still not thoroughly understood (Bestmann, de Berker & Bonaiuto, 2015).

Recent research has indicated that tDCS may be effective for clinical application (Brunoni et al., 2012) or to enhance cognitive function in neurotypical adults (Paulus et al., 2016). In these cases, effects of stimulation must be long-lasting, beyond the termination of stimulation, for there to be a benefit to the individual. In addition to online effects during stimulation, sufficient periods of tDCS have been shown to have offline aftereffects. For instance, tDCS targeted at primary motor cortex is reported to increase excitability in this area for up to 90 minutes after stimulation (Nitsche & Paulus, 2001). Repeated sessions of tDCS may also have long-term cognitive effects which last up to several weeks when paired with behavioural training (Vestito, Rosellini, Mantero, and Bandini, 2014). These offline aftereffects are likely to reflect mechanisms of synaptic plasticity, such as long term potentiation and long term depression (Fritsch, et al. 2010).

2.2 Transcranial alternating current stimulation (tACS)

An alternative method of transcranial current stimulation, tACS, delivers a sinusoidal electrical current of up to 2mA which alternates between two external electrodes placed over the region of interest (see Figure 2.1c). The aim when using tACS is to entrain neural oscillations within physiologically relevant frequency bands: delta (0–3Hz), theta (4–7 Hz), alpha (8–12 Hz), beta (13–30Hz), or gamma (30–200 Hz) (Antal and Paulus, 2013). This technique is therefore useful to study the role of particular oscillations in a given cognitive function.

Several sources have demonstrated the effectiveness of tACS in entraining particular frequencies of neural oscillations (Helfrich et al., 2014; Vosskuhl, Huster & Hermann, 2015; Zaehle, Rach & Herrmann, 2010). For instance, Zaehle and colleagues (2010) demonstrate that tACS delivered at each participant's predetermined individual alpha frequency (recorded using EEG) is effective in increasing subsequent alpha power. Measurable cognitive and perceptual effects of tACS have also been demonstrated, including visual perception (Kanai, Chaieb, Antal, Walsh & Paulus, 2008; Kanai, Paulus & Walsh, 2010), tactile perception (Feurra, Paulus, Walsh & Kanai, 2011) and memory (Polanía, Paulus & Nitsche, 2012).

2.3 Transcranial random noise stimulation (tRNS)

A specific form of alternating current stimulation which has begun to be used more recently is tRNS. This technique passes a current between the two electrodes which varies randomly between 0.1-640Hz (see Figure 2.1d). High frequency tRNS restricts oscillations to higher frequencies in this range, between 100-640 Hz, and is more commonly used in neuroscientific research. High frequency tRNS has been found to enhance cortical excitability at both electrode sites (Terney, Chaieb, Moliadze, Antal, and Paulus, 2008), in contrast with tDCS, which increases excitability under one electrode, and decreases at the other (Paulus et al., 2016). This method therefore has the advantage of targeting stimulation bilaterally.

While fewer studies have been conducted into the potential to modulate cognitive function using high-frequency tRNS compared with tDCS, effects have been reported in several domains, include numerical cognition (Cappelletti et al., 2013), facial identity perception (Romanska, Rezlescu, Susilo, Duchaine, and Banissy, 2015) and perceptual learning (Fertonani, Pirulli & Miniussi, 2011). In this case tRNS was found to be more effective than tDCS for modulating performance.

2.3.1 Mechanisms of action

Compared with tDCS, very few studies regarding the mechanism of action of tRNS have thus far been carried out. One account that has been proposed is that tRNS modulates cortical excitability through stochastic resonance (Miniussi, Harris & Ruzzoli, 2013). Stochastic resonance is the effect of boosting a weak signal above a threshold for detection by adding noise (McDonnell & Abbott, 2009). In this case, a sub-threshold neural signal may be amplified by adding random noise using tRNS. Continuous depolarization and repolarization of neuronal membrane potential may also contribute to an increase in cortical excitability (e.g., Chaieb, Antal, and Paulus, 2015; Chaieb et al., 2011). Like other methods of tCS, stimulation aftereffects have been found using high-frequency tRNS. Terney and colleagues (2008) report that 10 minutes of stimulation at 1mA over the motor cortex lead to increased excitability lasting up to 1.5 hours.

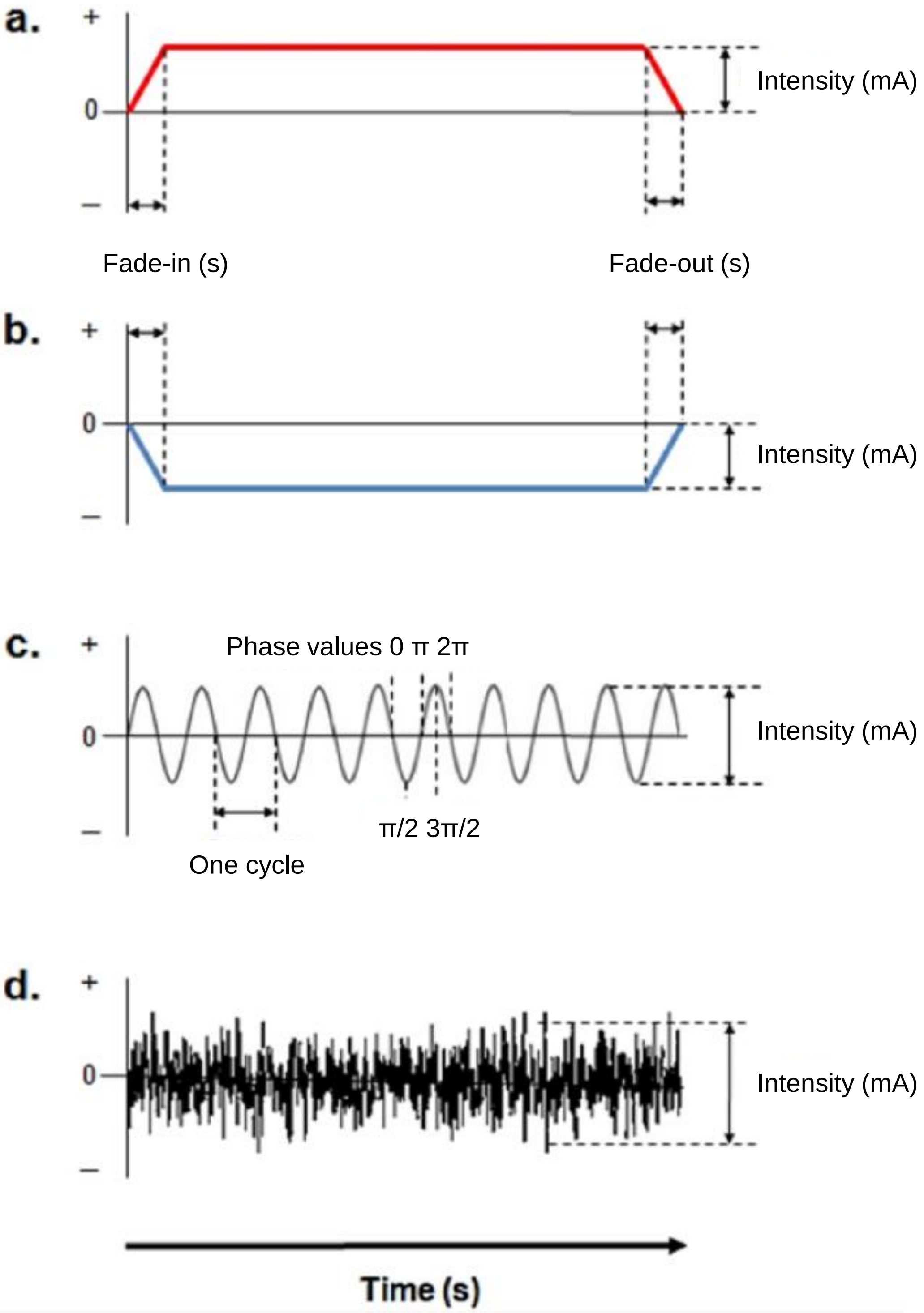

Figure 2.1: Waveforms of different methods of transcranial current stimulation, including a) anodal tDCS, b) cathodal tDCS, c) tACS and d) tRNS. Adapted from Fertonani and Miniussi (2017).

2.4 Spatial resolution

Importantly, effects of stimulation are not limited to the target site under the electrodes, but spread through surrounding tissue and regions between the two electrodes (Miranda, Mekonnen, Salvador & Ruffini, 2013; Opitz, Paulus, Will, Antunes, & Thielscher, 2015). Despite this spread of current flow, however, numerous studies have been able to demonstrate the efficacy of tCS in modulating excitability at specific target sites. For instance, increased excitability of primary motor cortex can be demonstrated in MEPs following both tDCS (Nitsche & Paulus, 2000; Nitsche & Paulus, 2001) and high-frequency tRNS (Terney et al., 2008) over this region. The spatial resolution of tDCS can also be improved with the use of different electrode montages. Using a smaller stimulation electrode and a larger reference electrode focuses the electrical current over a smaller area to direct the stimulation towards to target region (Nitsche et al., 2007). High definition tDCS uses multiple small electrodes in place of the large electrodes typically used, and is thought to improve the spatial resolution of the technique (Dmochowski, Datta, Bikson, Su & Parra, 2011; Minhas et al., 2010). Head models can also predict the direction of current flow, and enable the researcher to choose appropriate electrode montages (e.g., BONSAI and SPHERES; Rahman, Lafon & Bikson, 2015; Truong et al., 2014). Further research is required to improve the focal specificity of tDCS, as well as tRNS and tACS.

In order to target a region of interest, it is vital to use a reliable method of localisation to place electrodes which can account for individual differences in the anatomy of the head. Woods et al., (2016) demonstrate that electrode movement of as little as 1cm can significantly alter tDCS current flow within the brain. The most common method of localisation is the International 10-20 system (Herwig et al., 2003).

Electrodes can also be placed using neuronavigation systems, which rely on structural brain scans; or with physiological methods, for example using TMS to generate MEPs (Woods et al., 2016).

2.5 Stimulation protocol

When deciding on a tCS protocol, both the intensity and duration of stimulation delivered are important considerations. In a previous study, increasing the intensity of tDCS from 1mA to 2mA reversed stimulation effects in the motor domain (Batsikadze, Moliadze, Paulus, Kuo & Nitsche, 2013). Increasing the duration of tDCS stimulation from 4 seconds to 3 minutes leads to aftereffects in motor cortex (Nitsche and Paulus, 2000). However, increasing duration to 26 minutes may result in inhibition of aftereffects (Batsikadze et al., 2013). The influence of changing the duration and intensity of stimulation is also inconsistent across domains. Pirulli, Fertonani and Miniussi (2014) show that increasing the duration of tDCS over visual cortex from 9 to 22 minutes did not significantly alter stimulation effects. Stimulating for longer periods or at higher intensity therefore does not necessarily increase desired effects, and protocols should be based closely on prior work in the relevant domain.

Another factor to consider is whether stimulation should be delivered online (i.e., during the experimental testing session) or offline (i.e., prior to testing). TCS is associated with some mild tingling and itching sensations (e.g., Poreisz, Boros, Antal & Paulus, 2007; Paneri et al., 2016), and so it is important to consider the impact this distraction may have on behavioural performance during online stimulation. Despite this, it has been found that online tDCS can be more effective for enhancing cognitive performance than offline stimulation (Martin, Liu, Alonzo, Green & Loo, 2014). However, the relative advantages of online and offline stimulation are likely to vary for different cognitive domains, and according to the method of tCS used. Further research is necessary to identify ideal stimulation parameters for different areas of research.

A further consideration in tCS experimental design is the addition of appropriate control conditions. This is most commonly achieved using sham stimulation. Sham stimulation involves the same procedure as active conditions, but the electrical current is typically delivered for only 15-30 seconds. This allows the same initial sensations (e.g., mild scratching, tingling) to be experienced without inducing aftereffects. Evidence has shown that this procedure reliably blinds participants receiving tDCS (Gandiga, Hummel & Cohen, 2006; Nitsche et al., 2008; Poreisz et al., 2007) or tRNS (Ambrus, Paulus & Antal, 2010; Fertonani, Ferrari & Miniussi, 2015).

2.6 Individual variability in tCS effects

Recent research has raised the importance of individual variability in responsiveness to tCS (see Krause & Cohen Kadosh, 2014). Several studies have reported variable effects of tDCS in several domains, according to baseline ability (e.g., Hsu, Tseng, Liang, Cheng & Juan, 2014; Tseng et al., 2012), traits (e.g., Sarkar, Dowker & Kadosh, 2014), neuropsychological diagnosis (Boggio et al., 2006) neurophysiological state (e.g., Fresnoza, Paulus, Nitsche & Kuo, 2014; Labruna et al., 2016), gender (e.g., Chaieb, Antal & Paulus, 2008; Kuo, Paulus & Nitsche, 2006), age (e.g., Moliadze et al., 2015; Ross, McCoy, Wolk, Coslett & Olson, 2011), and cranial anatomy (e.g., Datta, Truong, Minhas, Parra & Bikson, 2012; Opitz et al., 2015). To give an example, Sarkar and colleagues (2014) show that tDCS targeted at dorsolateral prefrontal cortex improved performance on a numerical task for individuals with high mathematics anxiety, but actually impaired performance for those with low anxiety. Some sources of variation can be controlled with careful experimental design, for example the age and gender of participants. Other factors, such as trait differences or baseline task ability, are more difficult to control but can be monitored to assess potential moderating effects (as for Sarkar et al., 2014). Future research should involve careful consideration of these additional sources of variance to avoid additional noise in the data, and to identify further potential sources of individual variability.

2.7 Ethical and safety considerations

In tCS research to date there has been no report of long-term side effects or seizures (Woods et al., 2016). Although rare, some cases of seizures have been reported following transcranial magnetic stimulation (TMS), and tCS is considered to elevate the risk of seizure in those that are predisposed to them (for example, individuals with a history of epilepsy). To ensure that tCS is delivered safely, it is therefore essential to carry out careful screening of potential participants (Bikson et al., 2009). Contraindications to tCS and TMS include having any metal object in the body, such as a heart pacemaker, cochlear implant or aneurysm clip. Any individual with a personal or family history of epilepsy or any other medical, psychiatric or neurological disorders should also be excluded. Certain prescription medications, including antidepressants, also preclude participation in tCS (see Rossi, Hallett, Rossini & Pascual-Leone, 2009). Individuals who may be pregnant or have received any other brain stimulation (either tCS or TMS) within the previous 24 hours are excluded from participating. Participants are also instructed to avoid any recreational drugs (including alcohol) for 24 hours prior to the stimulation.

In terms of safe limits for stimulation parameters, Nitsche and colleagues (2003) recommend a maximum current density of 0.02857 mA/cm^2 for tDCS; since stimulation above this level may be painful. In a recent review Bikson and colleagues (2016) suggest that this limit may now be too conservative, given that no irreversible injury has been sustained using intensities of up to 4mA, durations of 40 minutes, and a stimulation charge of up to 7.2 coulombs; in evidence from over 1000 participants. Since tCS remains a relatively new field, it is advisable to keep stimulation parameters well within these known limits. This is especially true for alternating current techniques (e.g., tRNS, tACS), for which no specific guidance currently exists.

Although tCS is not associated with serious complications, some adverse short-term effects are common, including itchiness, tingling or mild burning (e.g., Poreisz et al., 2007; Paneri et al., 2016). These sensations are more common for tDCS than tACS or tRNS (Fertonani et al., 2015). Minor discomfort such as this can be minimised by carefully cleaning the area of the scalp, and applying extra saline or gel to the electrode site to reduce electrical impedance (although care must be taken not to oversaturate sponges with saline, as leakage can cause the electrical current to spread beyond the area of the electrode). A gradual fade in and fade out of the stimulation (over 15-30 seconds) should also minimise discomfort, and prevent the participant from experiencing flashes of light, which can occur if the stimulation is terminated abruptly (Nitsche et al., 2003). Minimising any sensations associated with stimulation has the additional advantage of impairing the participant’s ability to detect sham conditions in the experiment. Participants should also be fully informed regarding possible discomfort and all potential risks and benefits involved before they decide to participate in tCS research. The experiments described in Chapter 3 of this thesis follow the precautions and guidance described here. The experimenter was trained in operating tCS as well as emergency first aid, to ensure ethical and safe practice.

Chapter 3

Modulating Vicarious Tactile Perception with Transcranial Current Stimulation

Recent work has attempted to induce conscious vicarious touch in those that do not normally experience these sensations, using transcranial direct current stimulation (tDCS). Anodal tDCS applied to primary somatosensory cortex (SI) was found to induce behavioural performance akin to mirror-touch synaesthesia on a visuotactile interference task. In this chapter, two experiments were conducted that sought to replicate and extend these findings by examining: a) the effects of tDCS and high frequency transcranial random noise stimulation (tRNS) targeted at SI and temporo-parietal junction (TPJ) on vicarious tactile perception, b) the extent to which any stimulation effects were specific to viewing touch to humans versus inanimate agents, and c) the influence of visual perspective (viewing touch from one's own versus another's perspective) on vicarious perception. In Experiment One, tRNS targeted at SI did not modulate vicarious tactile perception. In Experiment Two, tDCS targeted at SI, but not TPJ, resulted in some modulation of vicarious tactile perception, but there were important caveats to this effect. Implications regarding mechanisms of vicarious perception are discussed. Collectively, the findings do not provide convincing evidence for the potential to modulate vicarious tactile perception with transcranial electrical current stimulation.

3.1 Introduction

Passively observing another person being touched appears to recruit overlapping brain regions as are involved in first-hand experiences of touch, including activity in primary (SI) and secondary (SII) somatosensory cortex (Keysers et al., 2010; see section 1.1 for further discussion). While vicarious tactile perception is common, there are important individual variability factors associated with this (Gillmeister et al., 2017). One source of variation is a distinction between those who experience conscious as opposed to unconscious vicarious tactile responses. In particular, for a small minority of individuals (< 2%; Banissy, Cohen Kadosh, Maus, Walsh & Ward, 2009), with mirror-touch synaesthesia (MTS), seeing another person being touched elicits a conscious sensation of touch on their own body, as if they were being touched themselves (see Ward & Banissy, 2015 for a review).

One account explaining why some people experience conscious vicarious touch, but others do not (known as Threshold Theory; see Ward & Banissy, 2015), assumes that the conscious sensation of touch arises from hyperactivity in somatosensory cortex when viewing touch to others. This activity is thought to boost vicarious responses above a threshold for conscious perception. In line with this, individuals with MTS demonstrate greater activation compared to controls in SI and SII during the observation of touch (Blakemore et al., 2005; Holle et al., 2013). Further, there is some evidence suggesting that increasing cortical excitability in the somatosensory cortex of individuals that do not experience MTS can induce behavioural correlates of the experience, when viewing touch to others (Bolognini et al., 2013). In that study, participants were tested on an adapted version of a visuotactile interference task that had previously been shown to distinguish individuals with MTS from control participants

(Banissy and Ward, 2007). This task requires participants to state the location of a tactile stimulus on their own body while simultaneously observing another person being touched. The felt touch can either be congruent (in the same spatial location) or incongruent (on the opposite side of the body) to the observed touch. For individuals with MTS there are increased congruency effects, with incongruent trials producing longer reaction times and a greater number of errors consistent with their conscious vicarious touch (Banissy & Ward, 2007). Bolognini and colleagues report that greater congruency effects can be induced in non-synaesthetes on this task by increasing SI excitability using transcranial direct current stimulation (tDCS; see section 2.1). More specifically, participants showed increased congruency effects in their reaction times after tDCS over SI on the ipsilateral side to the tactile stimulus (and thus the contralateral side to the observed touch), when another hand was seen being touched, compared with an inanimate object (a lightbulb). Further, participants with higher self-reported perspective taking (a subscale of the Interpersonal Reactivity Index measure of empathy; Davis, 1980) showed a greater effect of stimulation, indicating that individual difference factors might mediate the effects of tDCS on task performance. The results suggest that increased excitability of SI underlies vicarious tactile experience, supporting a Threshold Theory account.

While the study from Bolognini and colleagues (2013) points to cortical excitability in the somatosensory system playing a pivotal role in vicarious tactile perception, there are a number of important questions that need to be clarified. For example, since the only control task used in the experiment involved touch to a lightbulb, it remains unclear whether the effects are specific to human touch or whether a human form physically and spatially congruent with the participant’s own body is sufficient (e.g., dummy body parts). Previous behavioural research has also found that viewing touch to hands in a first- versus third-person perspective can influence task performance (Vandenbroucke et al., 2015), but whether visual perspective influences performance change following brain stimulation has not been studied. Additional work is therefore needed to a) examine the replicability of findings indicating that increasing excitability within the somatosensory system can induce MTS in non-synaesthete controls and b) consider how variations in stimulus presentation (e.g., animacy, perspective of viewed stimuli) contribute to previously reported effects.

Further, in addition to tDCS, other forms of electrical current stimulation have recently been used to modulate perceptual and cognitive task performance, for example with transcranial alternating current stimulation (Kanai et al., 2008; Marshall, Helgadóttir, Mölle & Born, 2006; Benwell, Learmonth, Miniussi, Harvey & Thut, 2015; Janik et al., 2015) and with high-frequency transcranial random noise stimulation (tRNS; Cappelletti et al., 2013; Fertonani et al., 2011; Snowball et al., 2013; Romanska et al., 2015). Of relevance to the current study is high frequency tRNS. As with tDCS, this method involves passing a weak electrical current to the brain via electrodes placed on the scalp, but tRNS differs in delivery and inducing neural change. While tDCS involves passing a homogenous current leading to a unilateral increase or decrease in brain excitability, tRNS involves passing an alternating current at a range of frequencies (from 100-640 Hz in high frequency tRNS) that results in a bilateral increase in cortical excitability (e.g., Terney et al., 2008). Comparisons of the two techniques suggest that high frequency tRNS may exert greater effects on changing cortical excitability (Vanneste, Fregni & De Ridder, 2013), although different mechanisms of action may contribute to cortical excitability effects of tRNS and tDCS (Miniussi, Harris & Ruzzoli, 2013; Paulus, Nitsche & Antal, 2016). As yet, no study has examined if high frequency tRNS might be useful to modulate vicarious perception, but given that in some circumstances bilateral somatosensory cortex activity is likely to contribute to perceiving touch to other people, then this technique may offer a useful approach to examine the effect of increasing bilateral cortical excitability in the somatosensory cortices on tactile perception. In light of this, in addition to re-examining prior effects suggesting that tDCS targeted at SI on the contralateral side to observed touch can induce MTS in non-synaesthetes, Experiment One also examined whether high frequency tRNS targeted at SI bilaterally would have similar effects.

With the above in mind, the present experiments aimed to identify the contribution of body congruency and perception of animacy in modulating vicarious tactile perception following transcranial electrical stimulation. To study this, visuotactile interference tasks were administered in which touch is viewed to an object, to inanimate dummy hands, and to human hands in either a first-person or third-person perspective, relative to the observer. Experiment One examined the impact of tRNS targeted at bilateral primary somatosensory cortices (SI), and Experiment Two the effects of tDCS targeted at right somatosensory cortex (rSI) and the right temporo-parietal junction (rTPJ). Based on prior research, increasing cortical excitability in SI was expected to increase vicarious tactile perception when viewing another person being touched.

3.2 Experiment One

Experiment One sought to extend prior findings regarding the effects of tDCS in vicarious tactile perception (Bolognini et al., 2013) by determining whether vicarious responses can also be enhanced following high frequency tRNS targeted at SI. Like tDCS, tRNS has been shown to directly increase cortical excitability, but the mechanisms of action may differ (Miniussi et al., 2013; Paulus et al., 2016; Terney et al., 2008). Since tRNS can be used to stimulate the cortical region of interest bilaterally, the present experiment examined the effect of high frequency tRNS targeted at SI on vicarious tactile perception of touch applied to both left and right hands. This method therefore removes the need to compare trials where touch is ipsilateral or contralateral to the stimulation site that was a prerequisite in the study by Bolognini and colleagues due to the use of tDCS.

A further difference between this experiment and prior work (Bolognini et al., 2013; Vandenbroucke et al., 2016) was the inclusion of two novel tasks and increase in trial numbers on the vicarious touch tasks. More specifically, the effect of first- (egocentric) versus third-person (allocentric) perspective in vicarious tactile perception was assessed. For this, images of human hands were observed inverted so that they appear an allocentric position. An inanimate object control task with the same visual form as a hand (i.e., a dummy hand) was also created, in order to isolate the effects of animacy and human-like appearance in eliciting vicarious tactile response. In all tasks 180 trials were presented, contrasting to 144 in prior studies. Since the use of tRNS removes the need to compare ipsilateral and contralateral trials, this increased the number of trials in each experimental condition to 60 compared with 24 in the previous method.

3.2.1 Materials and methods

Participants

24 healthy participants took part in both sessions of Experiment One (22F, 2M; 24 right-handed; age 18-58 years, *M* = 21.7, *SD* = 8.2). All participants were paid £20 to take part, had normal or corrected-to-normal vision and met the required safety precautions to take part in electrical brain stimulation outlined by Bikson, Datta and Elwassif (2009). Ethical approval was granted by the Department of Psychology at Goldsmiths, University of London.

High-frequency transcranial random noise stimulation (tRNS) protocol

The experiment had a within-subjects design, with all participants completing the tasks under active SI tRNS and sham conditions. Bilateral stimulation was delivered with two 5x5cm saline-soaked sponge electrodes and a constant-current stimulator (NeuroComm, DC-Stimulator Plus). To target SI the electrodes were placed 2cm posterior to C3/C4, according to the 10-20 electroencephalography system (Herwig, Satrapi & Schönfeldt-Lecuona, 2003). High-frequency tRNS was delivered offline, immediately prior to the tasks. Since effects of offline tRNS have been shown to last up to one hour following 10 minutes of stimulation (Terney et al., 2008), this allowed a longer time window to complete the additional tasks discussed below. The current was ramped up for 15 seconds to 1.5mA (based on the intensity used in prior work – Bolognini et al., 2013) and was followed by ten minutes of stimulation, before ramping down again for 15 seconds. The sham protocol was identical to active stimulation, with the exception that the current was held constant for only 15 seconds before ramping down (although the electrodes were left in place for 10 minutes). This allowed the same initial mild scratching sensation to be experienced in the same location as during active stimulation (Ambrus, Paulus & Antal, 2010; Fertonani et al., 2015). Participants received bilateral SI and sham high frequency tRNS across two separate sessions, conducted 3-7 days apart, with the order of the sessions counterbalanced between participants.

Procedure

There were two sessions to the experiment, one for sham and one for SI stimulation. Stimulation was delivered offline, immediately prior to the visuotactile tasks. The order of four tasks (‘self’, ‘other’, ‘dummy’ and ‘sponge’) was counterbalanced between participants. It took no more than 40 minutes to complete all four tasks. During the tasks participants were instructed to place their hands flat on the desk in front of them, in the same manner as the visual stimuli shown in the ‘self’ task (Figure 3.1a), and to keep their eyes focused on the screen. Participants completed items from the QMTS (Bolognini et al., 2013) at the end of both sham and active sessions, and the IRI (Davis, 1980) at the end of the sham session.

Visuotactile Interference Tasks

In each experimental session participants completed four visuotactile interference tasks (adapted from Banissy & Ward, 2007), the order of which was counterbalanced between participants in ABCD-BADC-DCAB-CDBA order. For each, participants were required to state the location of a tactile sensation on their own hand, whilst simultaneously observing another agent (hand or object depending on task) being touched. Observed touch occurred either to another human hand in an egocentric body location (‘self’ task), an allocentric location (‘other’ task), to a dummy hand (‘dummy’ task), or to a sponge (‘sponge’ task). Visual stimuli are shown in Figure 3.1a. The tactile stimulus was delivered using two miniature solenoid tappers attached to the dorsum of the participant’s left and right hands with medical tape. A Dual Channel Solenoid Controller (MSTC3-2; M & E Solve) was used to control the tappers.

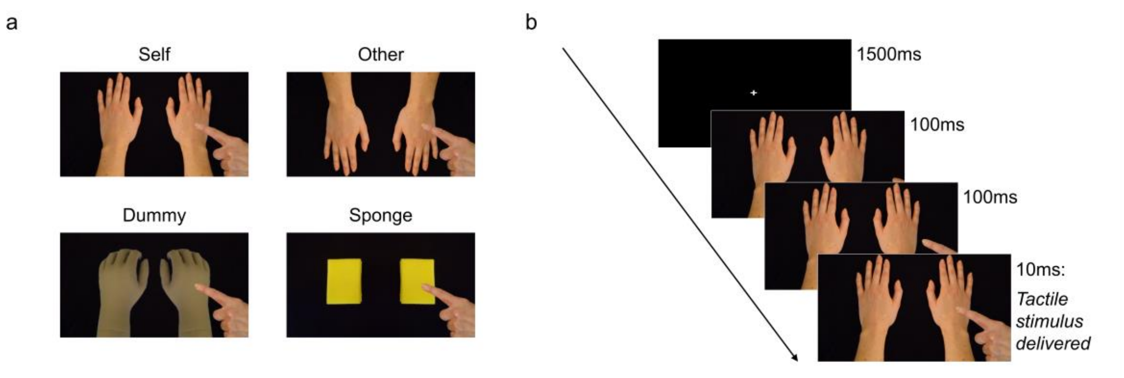

Figure 3.1: a) Visual stimuli depicting the agent in the ‘self’, ‘other’, ‘dummy’ and ‘sponge’ tasks, and b) Example trial structure from the ‘self’ task.

Tasks were presented in E-Prime 1.0 (Psychology Software Tools Inc., Pittsburgh, PA), using a 19” Hannspree monitor placed approximately 50cm in front of the participant. On each trial, participants viewed three consecutive images displaying hands being approached and touched by an index finger (Figure 3.1b). Observed touch was shown on the left, right or both sides. Each trial was preceded by a 1500ms fixation cross. A tactile stimulus was delivered via the solenoid tappers attached to the hands 10ms after the onset of observed touch. The observed touch then remained on the screen until the participant gave a response. The tactile stimulus was either delivered on the left, right or both sides, or there was no touch at all. On 60 trials the felt touch was spatially congruent with the observed touch or flash, on 60 trials it was incongruent, and on 60 trials there was no touch. Participants gave verbal responses using a voice key by stating “left”, “right”, “both” or “none”, according to which location they felt the tactile stimulus. All participants were asked to respond as quickly and accurately as possible. The order of trials was pseudorandomised over three blocks. White noise was played through headphones during each trial to mask the noise of the solenoid tappers.

Self-report measures

Self-reported mirror-touch synaesthesia

At the beginning of the first session of the experiment, participants were asked “Do you experience touch sensations on your own body when you see them on another person’s body?” (from Banissy et al., 2009), and could respond on a 5-point Likert scale from ‘Strongly Disagree’ to ‘Strongly Agree’. Responses were coded from -2 to +2, where a positive score indicates self-reported experience of synaesthesia. This was completed in order to screen participants for potential mirror-touch synaesthesia.

Questionnaire of Mirror-Touch Synaesthesia

Each participant’s experience during the interference tasks was assessed using items 1, 4 and 5 from the Questionnaire of Mirror-Touch Synaesthesia (QMTS) used by Bolognini and colleagues (2013). This was administered at the end of each session. Participants were required to state the extent to which they agreed with six statements using a 5-point scale ranging from ‘Strongly Disagree’ to ‘Strongly Agree’. Items comprised: 1) “I felt that I was touched when I saw the human hand/dummy hand being touched”, 2) “Seeing the human hand/dummy hand being touched made it difficult to localise the actual touch” and 3) “The observed touch to the human hand/dummy hand appeared to be very intense”. Again, scores for each item were coded from -2 to +2 during data analysis.

Interpersonal Reactivity Index

The 28-item Interpersonal Reactivity Index (IRI; Davis, 1980) was used to assess self-report trait empathy. This questionnaire asks participants to indicate the extent to which they agree with each of 28 statements, such as “I often have tender, concerned feelings for people less fortunate than me”, using a 5-point scale ranging from “Does not describe me well” to “Describes me very well”. Total scores range from 0-112, with a higher score indicating higher trait empathy. Scores can also be clustered into 4 subscales, reflecting ‘”Fantasy”, “Perspective Taking”, “Empathic Concern”, and “Personal Distress” Davis (1980) reports an acceptable internal consistency for each of the subscales ($\alpha = .70 - .78$).

3.2.2 Results

Prior to analyses data was trimmed for each participant to exclude any reaction time (RT) that fell two standard deviations above or below the mean for each task and stimulation condition. This resulted in 5.0% of data removal. Two participants were identified as significant outliers based on Grubb’s test calculations on RTs, and were excluded prior to analysis. This resulted in the following demographic characteristics of the sample: 20 female, 2 male; age 18-58 years, *M* = 22.0, *SD* = 8.5. This did not differ significantly from the sample recruited by Bolognini and colleagues (2013) in terms of age ($t[52] = 0.84$, $p = 0.41$), but did differ in the proportion of males and females ($\chi^2_1 = 6.97$, [$n = 54$], $p = 0.01$), with fewer males participating in this experiment compared with the previous sample.

It was also necessary to calculate individual spatial reference frames for all participants, in order to categorise trials as either congruent or incongruent. There are two potential reference frames that can be adopted during the allocentric task: 1) anatomically congruent (where viewing touch to a left hand is matched to participants' left hand) or 2) specular congruence (where viewing touch to a left hand is matched to a participants' right hand). Congruency was defined for each participant depending on whichever mapping gave the largest congruency score in the sham condition of the 'other' task, and this was used in analyses throughout a given participant (i.e., if the RT was longer for a specular mapping in the sham task then the participant was classified as a specular mapper, and vice versa). This analysis revealed 20 specular and 2 anatomical mappers.

Individual differences in trait empathy and sham task performance

To identify whether reaction times on the vicarious tactile perception tasks were related to individual differences in empathy, Pearsons's correlation analyses were carried out between scores on the IRI subscales and RTs on each of the four tasks in the sham condition. A statistically significant correlation was found between scores on the 'perspective taking' subscale and RTs on congruent trials of the 'self' task, in sham stimulation conditions ($r[20] = -0.43$, $p = 0.05$). The negative correlation indicates that higher perspective taking ability facilitated tactile detection on the ‘self’ task when observed touched was spatially congruent with touch felt on the hand.

Effects of high-frequency tRNS on task performance

To examine the effects of high frequency tRNS on task performance a 4 x 2 x 2 repeated-measures ANOVA was carried out to identify the effects of Task (‘self’/‘dummy’/‘other’/‘sponge’), tRNS Stimulation condition (sham/SI), and Congruency (congruent/incongruent) on reaction times. There was a significant main effect of Congruency ($F[1,21] = 56.24$, $p < 0.01$, $\eta_p^2 = 0.73$), with longer reaction times on incongruent trials than congruent trials. However, there was no significant main effect of Task ($F[3,63] = 1.48$, $p = 0.23$, $\eta_p^2 = 0.07$), or Stimulation condition ($F[1,21] = 0.03$, $p = 0.86$, $\eta_p^2 < 0.01$) or interactions between any of the three factors (*p*s > 0.12). In this regard, high frequency tRNS targeted over SI did not differentially modulate vicarious tactile perception relative to sham stimulation (Figure 3.2).

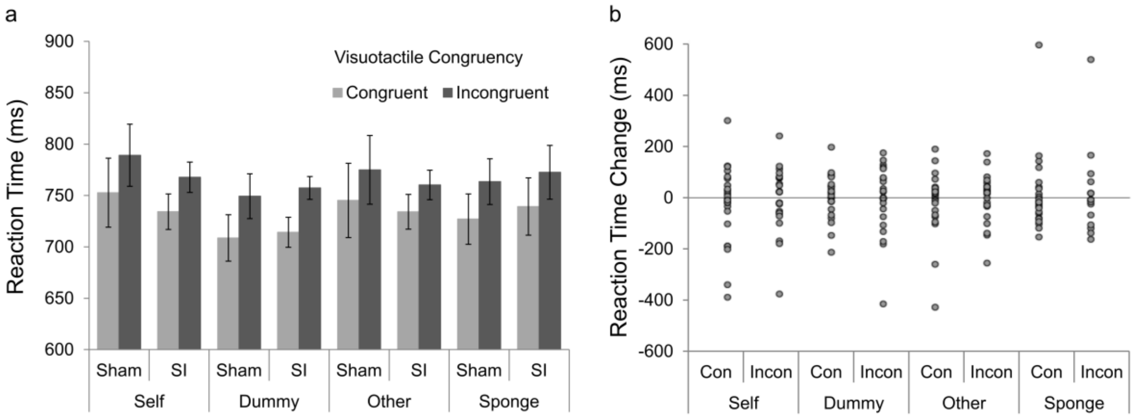

Figure 3.2: a) Mean reaction times for congruent and incongruent trials on each of the four visuotactile interference tasks following sham or tRNS targeted at SI. Significant congruency effects were found on all tasks. b) Individual stimulation effects (reaction time in tRNS condition – reaction time in sham condition) for congruent and incongruent trials on each task. Con, Congruent; Incon, Incongruent. Error bars represent +/- 1 S.E.M.

To further assess any effects of stimulation, scores on the QMTS self-report measure of potential MTS experience on each task were also assessed. To do this, a 4 (Task) x 2 (Stimulation) ANOVA was conducted on overall scores. This identified a significant main effect of Task (*F*[3,60] = 9.86, $p < 0.01$, $\eta_p^2 = 0.33$), but no significant main effect of Stimulation condition (*F*[1,20] = 0.34, $p = 0.57$, $\eta_p^2 = 0.02$), or interaction between Stimulation and Task (*F*[3,60] = 0.53, $p = 0.66$, $\eta_p^2 = 0.03$). Bonferroni-corrected post-hoc t-tests demonstrated that the main effect of task was due to significantly lower scores (indicating reduced vicarious sensation) for the ‘dummy’ task compared with the ‘self’ (*t*[20] = 3.46, $p < 0.01$, Cohen’s $d = 0.90$) or ‘other’ task (*t*[20] = 3.19, $p < 0.01$, Cohen’s $d = 0.80$), and for the ‘sponge’ task compared with the ‘self’ (*t*[20] = 3.43, *p* < 0.01, Cohen's *d* = 1.01) and 'other' tasks (*t*[20] = 3.05, *p* < 0.01, Cohen's *d* = 0.88). No significant difference in scores was found between the 'dummy' and 'sponge' tasks (*t*[20] = 1.09, *p* = 0.29, Cohen's *d* = 0.27), or the 'self' and 'other' tasks (*t*[20] = 1.96, *p* = 0.06, Cohen's *d* = 0.48). Means are displayed in Table 3.1. The pattern of results indicates a greater tendency towards conscious vicarious tactile perception on the tasks in which touch was viewed to another human hand, compared with an inanimate object, but that this was not modulated by high frequency tRNS targeted at SI.

Table 3.1: Mean scores and standard deviations for QMTS items, following each tRNS stimulation session in Experiment 1. Possible scores range from -6 to +6, with higher scores indicating greater self-reported vicarious tactile perception

	Active SI tRNS		Sham tRNS	
Visuotactile Interference Task	*M*	*SD*	*M*	*SD*
Self	-2.05	2.85	-1.59	3.32
Other	-2.23	2.71	-2.14	3.14
Dummy	-3.10	2.21	-3.05	2.28
Sponge	-3.27	1.88	-3.23	1.90

N = 22

<u>*Individual differences in trait empathy and effects of tRNS on task performance*</u>

While tRNS stimulation targeted at SI did not significantly alter task performance at the group level, based on the results above and prior research (Bolognini et al., 2013) there was reason to predict that the effects of tRNS on task performance may interact with individual differences in trait empathy (specifically the perspective taking subscale of the IRI). To examine this prediction, a series of correlations between scores on perspective taking subscale of the IRI and stimulation effect scores (the difference between congruency effects in the active tRNS and sham condition) on the 'self', 'other', 'dummy' and 'sponge' tasks were conducted. This revealed no significant relationships (*p*s < . 40).

3.2.3 Discussion

Collectively the findings from Experiment One indicate that active compared to sham high frequency tRNS targeted at SI does not modulate vicarious tactile perception on tasks assessing visuotactile interference effects when observing touch to humans (from an allocentric and egocentric perspective) and objects. This result conflicts with prior findings suggesting that increasing excitability in SI can lead to greater vicarious tactile perception and induce behavioural performance consistent with that found in mirror-touch synaesthetes (Bolognini et al., 2013). In this context, it is also of note that no significant differences were found between active SI and sham tRNS conditions on self-reported mirror-touch synaesthesia experiences across the tasks or relationship between levels of perspective taking and performance change following stimulation (as was found in Bolognini et al., 2013).

One reason why there may have been differences between the present high frequency tRNS results and those using tDCS to increase excitability in SI in prior work could relate to the mechanism of action of the different types of stimulation. Moreover, prior work suggests that high frequency tRNS and tDCS may influence brain excitability via different mechanisms (Miniussi et al., 2013; Paulus et al., 2016; Terney et al., 2008). As a consequence a second experiment was conducted, with a new group of participants, more closely following the same brain stimulation procedure (i.e., using matched tDCS parameters) as that used in prior work in attempt to determine if it was possible to replicate the prior pattern of data.

Experiment Two further extends prior work by considering extra questions related to vicarious tactile perception. In particular, in addition to SI, the study was designed to examine whether tDCS targeted at rTPJ may influence vicarious perception. The rationale for examining the effect of stimulating the rTPJ was to assess whether modulating a brain region linked to self-other control may also modulate vicarious tactile perception. Although excitability within the somatosensory system is likely to contribute to how we perceive tactile events to others, the ability to correctly distinguish and manipulate self-relevant or other-relevant representations is another mechanism which is thought to be involved. Appropriate levels of vicarious perception require enhancing representations of other people and inhibiting the representation of one’s own affective state; however in order to prevent excessive personal distress from another’s negative affective state, it can be adaptive to inhibit the representation of the other’s affective state and enhance the representations of the self (Cheng et al., 2007; Decety et al., 2010). In this regard, the interplay between mechanisms of vicarious perception and mechanisms of self-other representation has been highlighted as a crucial interaction in understanding other people’s experiences (Bird & Viding, 2014; Lamm, Bukowski & Silani, 2016; Ward & Banissy, 2015). Indeed, recent work suggests that training the ability to control self-other representations can result in modulation of vicarious pain perception (de Guzman, Bird, Banissy & Catmur, 2016). Crucially, tDCS targeted at the rTPJ has been shown to increase the ability to control self-other representations (Santiesteban et al., 2012), and modulate cognitive components of empathy for pain (Coll, Tremblay & Jackson, 2017). To date, a single study has attempted to examine whether stimulating rTPJ can influence vicarious tactile perception. Vandenbroucke and colleagues (2016) repeated the visuotactile interference task used by Banissy and Ward (2007) and Bolognini and colleagues (2013), this time aiming to modulate performance following tDCS targeted at rTPJ. Since increasing cortical excitability in rTPJ has been shown to improve self-other control, the authors predicted that accuracy and reaction times would improve on the task following stimulation. However, this modulation was not found, in response to either viewed touch or pain (conflicting with Coll et al., 2017). One possible reason for this was that touch was always viewed to another human hand in a first-person perspective, which could conceivably be viewed as belonging to the self. This possibility was considered in Experiment Two by assessing whether any effect of stimulation targeted at rTPJ was specific to viewing touch to human versus inanimate agents by including a dummy hand control task – a question that has not been addressed in prior work.

3.3. Experiment Two

The present study aimed to replicate the procedure of Bolognini and colleagues (2013), assessing performance on two visuotactile interference tasks during active or sham right-hemisphere tDCS targeted at primary somatosensory cortex. Based on the results of Experiment One, observed touch to a dummy hand was selected as a control task for touch to a human hand. Additionally, to probe the potential role of self-other control in vicarious tactile perception, a third stimulation condition was added, in which stimulation was delivered to right temporo-parietal junction (rTPJ).

3.3.1 Materials and methods

Participants

24 participants (16F, 8M; 23 right-handed; age 20-29 years, *M* = 23.2, *SD* = 2.6) who did not take part in Experiment One were recruited from Goldsmiths College. All volunteers were paid £20 on completion of the study. All participants had normal or corrected-to-normal vision and met the required safety precautions to take part in electrical brain stimulation (Bikson et al., 2009). Ethical approval was granted by the Department of Psychology at Goldsmiths, University of London.

Transcranial direct current stimulation (tDCS) protocol

The experiment had a within-subjects design, with all participants completing the tasks under active right SI (rSI), active right TPJ (rTPJ) stimulation, and sham conditions. In contrast to Experiment One, stimulation was delivered unilaterally using tDCS. To target rSI the anodal electrode was placed 2cm posterior to C4, and for rTPJ, the anode was placed over CP6 (Herwig et al., 2003). A supraorbital reference on the contralateral hemisphere was used for both sites. For 50% of participants, the rSI site was used during sham, and for 50% the rTPJ site was used. Active stimulation was delivered online for 20 minutes during completion of the tasks. As before, the current was ramped up for 15 seconds to 1.5mA, based on prior work (Bolognini et al., 2013), and then held constant for 20 minutes. Stimulation was terminated if participants completed both tasks in less than 20 minutes. In the sham session stimulation was delivered for only 15 seconds (Gandiga, Hummel & Cohen, 2006; Nitsche et al., 2008; Poreisz et al., 2007). All aspects of the stimulation protocol were selected to match that used by Bolognini and colleagues (2013), aside from the placement of electrodes for rTPJ stimulation, which was guided by consensus in previous tDCS research (e.g., Santiesteban et al., 2012, Santiesteban, Banissy, Catmur & Bird, 2015; Vandenbroucke et al., 2016). Participants received rSI, rTPJ and sham stimulation across three separate sessions, scheduled approximately one week apart to avoid practice effects. The order of the three sessions was counterbalanced between participants in an ABC-BCA-CAB design.

Procedure

The experiment comprised three sessions: rSI, rTPJ and sham stimulation. In this procedure tDCS was delivered online whilst the two visuotactile interference tasks ('self' and 'dummy') were completed. Online tDCS was used to replicate prior work. It took no more than 20 minutes to complete both tasks. As in Experiment One, participants completed the QMTS (Bolognini et al., 2013) at the end of every session, and the IRI (Davis, 1980) at the end of the sham session.

Visuotactile Interference Tasks

Participants completed the 'self' and 'dummy' tasks as in Experiment One (Figure 3.1), with the order of tasks counterbalanced between participants.

3.3.2 Results

Prior to analysis, data was trimmed for each participant to exclude any reaction time (RT) that fell two standard deviations above or below the mean for each task and stimulation condition. This resulted in 4.6% of data removal. One participant was also excluded prior to the analysis, as they were identified as a significant outlier based on Grubb's test calculations on RTs. This resulted in the following demographic characteristics of the sample: 15 female, 8 male; age 20-29 years, $M = 23.3$, $SD = 2.7$. This did not differ significantly from the sample recruited by Bolognini and colleagues (2013) in terms of age ($t[53] = 0.63$, $p = 0.53$) or gender ($\chi^2_1 = 0.38$, [$n = 55$], $p = 0.54$).

Individual variability in trait empathy and task performance in sham condition

Scores on the IRI (Davis, 1980), were first correlated against RTs in each of the stimulation, task and congruency conditions. Unlike Experiment One, no significant correlations were found.

Effects of tDCS on task performance

To examine whether active or sham tDCS to rSI or rTPJ resulted in differential effects on performance a 3 x 2 x 2 x 2 repeated-measures ANOVA was carried out to assess the effects of tDCS Stimulation condition (rSI/rTPJ/sham), Task ('self'/'dummy'), Congruency (congruent/incongruent) and Location of the tactile stimulus (left/right) on RTs.

The analysis revealed a significant main effect of Congruency ($F[1,22] = 45.93$, $p < 0.01$, $\eta_p^2 = 0.68$) and Location ($F[1,22] = 41.29$, $p < 0.01$, $\eta_p^2 = 0.65$) on RTs, with participants taking longer to respond when the tactile stimulus was incongruent with the visual stimulus, and when the tactile stimulus was presented on the right hand rather than the left. Main effects of Stimulation ($F[2,44] = 0.47$, $p = 0.63$, $\eta_p^2 = 0.02$) and Task ($F[1,22] = 0.30$, $p = 0.59$, $\eta_p^2 = 0.01$) were not significant. The interaction between Stimulation and Task was significant ($F[2,44] = 3.37$, $p = 0.04$, $\eta_p^2 = 0.13$). Post-hoc t-tests demonstrate a trend towards significance following rSI stimulation on the ‘self’ task ($t[22] = 2.05$, $p = 0.05$, Cohen’s $d = 0.43$), but not the ‘dummy’ task ($t[22] = 0.01$, $p = 0.99$, Cohen’s $d < 0.01$), and no significant effects of rTPJ stimulation on either the ‘self’ ($t[22] = 1.54$, $p = 0.14$, Cohen’s $d = 0.32$) or ‘dummy’ task ($t[22] = 0.46$, $p = 0.65$, Cohen’s $d = 0.10$). Together, this indicates that participants were slower to respond on the ‘self’ task following rSI stimulation. Crucially, the interaction between Stimulation and Congruency did not reach significance ($F[2,44] = 2.51$, $p = 0.09$, $\eta_p^2 = 0.10$). In this regard, the evidence did not suggest a significantly different pattern of results between the size of congruency effects across the stimulation conditions.

Despite the lack of interaction with regards to reaction time differences, there was rationale to consider a slightly less conservative approach to analysis given prior predictions regarding SI effects based on the previous study (e.g., Bolognini et al, 2013). With this in mind, in order to further identify whether the results presented by Bolognini and colleagues had been replicated, a series of independent t-tests were carried out to assess whether RTs in each task, congruency, side and stimulation condition (rSI or rTPJ) significantly differed from sham. This revealed a significant increase in RT on incongruent trials of the ‘self’ task during rSI stimulation relative to sham, when touch was felt on the right and observed on the left (contralateral) side to the stimulation ($t[22] = 2.31$, $p = 0.02$, Cohen's $d = 0.51$), although note that this would not survive correction for multiple comparison (Figure 3.3). Stimulation effects were not significant when observed touch was ipsilateral to stimulation, although there was a trend in this direction ($t[22] = 1.97$, $p = 0.06$, Cohen's $d = 0.41$). A similar trend was found on congruent trials of the 'self' task, when viewed/observed touch was on the left (contralateral) side to both rSI ($t[22] = 2.05$, $p = 0.05$, Cohen's $d = 0.43$) and rTPJ ($t[22] = 2.02$, $p = 0.06$, Cohen's $d = 0.42$) stimulation, relative to sham. No further comparisons reached significance (ps > 0.12). In this regard, although some evidence is provided which points towards data that is consistent with prior work suggesting that increasing cortical excitability in SI can modulate the degree of vicarious tactile perception, the present data struggle to provide strong evidence (e.g., differential effects across stimulation sites as supported by a top level ANOVA) to support this claim. There was also not sufficient evidence to suggest that rTPJ stimulation influences vicarious tactile perception.

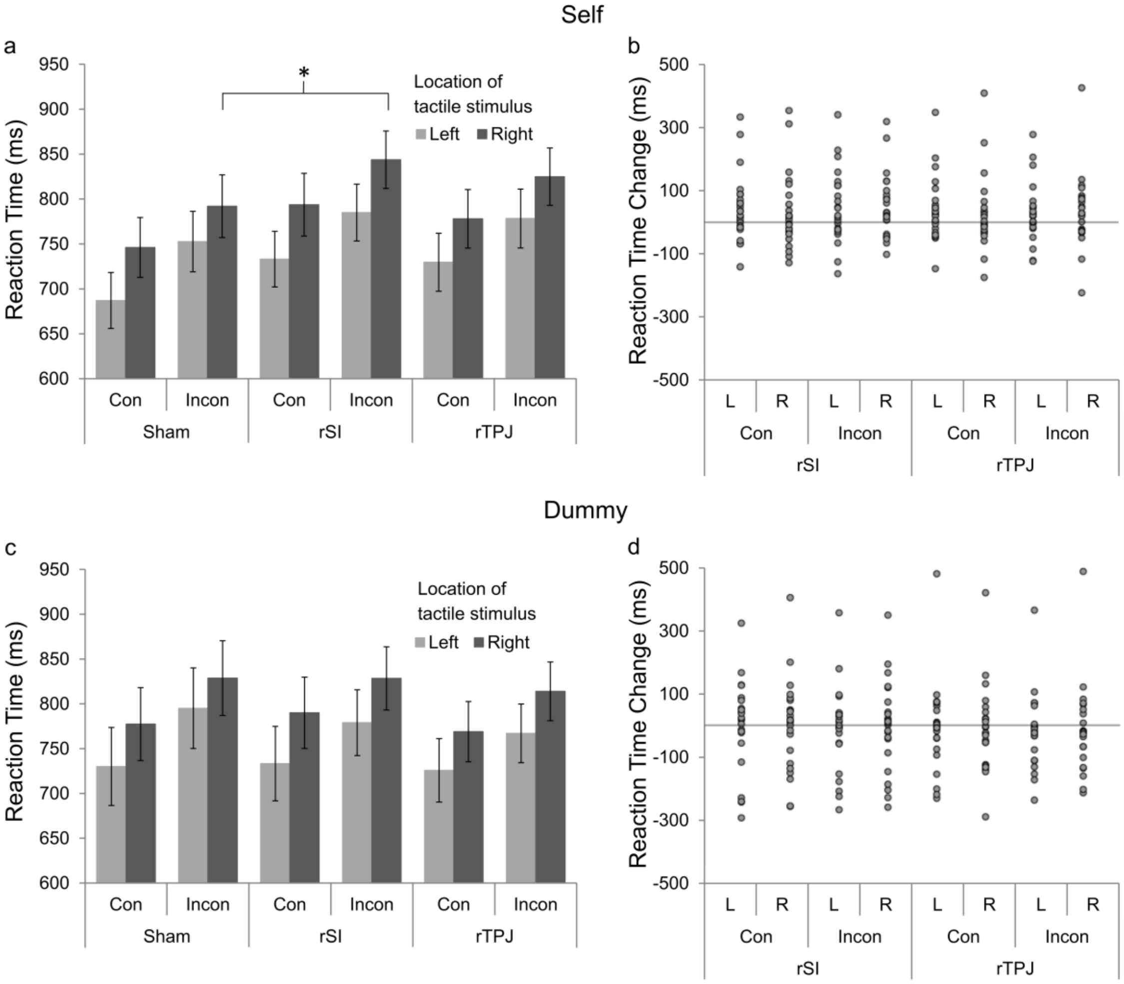

*Figure 3.3: a) Mean reaction times for each trial type on the 'self' task during sham conditions and tDCS targeted at rSI and rTPJ. A significant increase in RT was observed following SI stimulation, for incongruent trials where observed touch was contralateral to the stimulation site (*p < .05). b) Individual stimulation effects (reaction time in tDCS condition – reaction time in sham condition) for each trial type on the 'self' task. c) Mean reaction times for each trial and stimulation type on the 'dummy' task. No significant effects of stimulation were observed on this task. d) Individual stimulation effects for each trial type on the 'dummy' task. Con, Congruent; Incon, Incongruent. L, Left; R, Right. Error bars represent +/- 1 S.E.M.*

As with Experiment One, the effect of stimulation on the QMTS self-report measure of potential MTS experiences on each task was assessed. A further 2 (Task) x 3 (Stimulation) ANOVA identified a main effect of Task on the QMTS, with higher ratings of conscious vicarious experience on the 'self' task than the 'dummy' task ($F[1,21] = 13.57$, $p < 0.01$, $\eta_p^2 = 0.39$). However, there was no significant main effect ($F[1,21] = 0.63$, $p = 0.54$, $\eta_p^2 = 0.03$) or interaction ($F[2,42] = 0.65$, $p = 0.53$, $\eta_p^2 = 0.03$) with Stimulation condition, indicating that conscious vicarious experience during the tasks did not change substantially between sessions (means are displayed in Table 3.2). This is consistent with the lack of effect of tDCS on congruency reaction times reported above and the lack of effect of active high frequency tRNS in Experiment One.

Table 3.2: Mean scores and standard deviations for QMTS items, following each tDCS stimulation session in Experiment 2. Possible scores range from -6 to +6, with higher scores indicating greater self-reported vicarious tactile perception.

	Active rSI tDCS		Active rTPJ tDCS		Sham tDCS	
Visuotactile Interference Task	*M*	*SD*	*M*	*SD*	*M*	*SD*
Self	-1.57	2.45	-1.23	3.01	-1.74	2.40
Dummy	-2.78	2.15	-3.00	2.25	-3.17	2.08

N = 23

<u>*Individual Differences in Trait Empathy and Effects of tDCS on Task Performance*</u>

As with Experiment One, it was considered that the effect of tDCS on task performance may interact with individual differences in trait empathy (specifically the perspective taking subscale of the IRI). To examine this prediction, a series of correlations were conducted between scores on perspective taking subscale of the IRI and stimulation effect scores (the difference between congruency effects in the active tDCS and sham conditions) on the ‘self’ and ‘dummy’ tasks. This revealed no significant association between perspective taking and stimulation effects (*p*s > .26).

3.3.3. Discussion

Taken collectively, while the results from Experiment Two provide some evidence in support of the claim that increasing unilateral cortical excitability in rSI with anodal tDCS was able to increase vicarious tactile perception in typical adults, this was only apparent when using liberal statistical thresholds. Indeed, the overall pattern of the current data struggles to lend strong support to the possibility that increasing unilateral cortical excitability in rSI modulates vicarious tactile perception in a site or task specific manner. Instead, there is not clear evidence that increasing cortical excitability in rSI with tDCS leads to differential changes in vicarious tactile perception from sham stimulation or stimulation to rTPJ.

3.4. General discussion

The present studies aimed to build on past evidence suggesting that vicarious responses to touch may be enhanced by increasing excitability of SI. In Experiment One there was no evidence for modulation of vicarious response by raising bilateral cortical excitability with high frequency tRNS targeted at SI. Experiment Two attempted to more directly replicate previous work using tDCS targeted at SI to modulate vicarious tactile perception, but did not find convincing evidence for the potential to modulate vicarious response with unilateral tDCS targeted at right SI in a task and site specific manner. In addition, no evidence was found to suggest that tDCS targeted at rTPJ could modulate vicarious tactile perception.

The present findings conflict with a prior tDCS study, which suggests that tDCS targeted at SI can modulate vicarious tactile perception (Bolognini et al., 2013). In this previous study the authors claim to induce behavioural performance consistent with individuals that experience mirror-touch synaesthesia following anodal tDCS to somatosensory related regions. Although a similar task and identical stimulation parameters were used, this pattern of data could not be clearly replicated. Some evidence was found to support this account in Experiment Two, using tDCS targeted at right SI, but this relied on uncorrected statistical analyses and was not significantly different to the pattern of data following sham or rTPJ stimulation.

Although stimulation parameters were the same between studies (at least in Experiment Two), subtle differences in procedure and individual variability in responsiveness of tDCS may explain this discrepancy. With regards to procedural differences it is of note that an additional brain stimulation condition and trials were included compared to Bolognini and colleagues. Different stimuli and tasks were also used (from Banissy & Ward, 2007) and a different control task involving dummy hand stimuli as opposed to light bulb stimuli that were used previously. While it seems unlikely that this should decrease the likelihood of finding an effect, it is possible that these subtle variations may have contributed to the different pattern of data between the studies. Another possible reason for the discrepancy between the studies may be individual variability in responsiveness of tDCS. As discussed in section 2.6 of this thesis, several studies now point to the importance of individual variation in tDCS responsiveness, with differential effects being reported in other domains (i.e., not vicarious perception studies) according to baseline ability (e.g., Hsu et al., 2014; Tseng et al., 2012), traits (e.g., Sarkar et al., 2014), baseline level of neurophysiological state (e.g., Fresnoza et al., 2014; Labruna et al., 2016), gender (e.g., Chaieb et al., 2008; Kuo, Paulus & Nitsche, 2006), age (e.g., Moliadze et al., 2015; Ross et al., 2011), and anatomy (e.g., Datta et al., 2012; Opitz et al., 2015). While the age and gender of participants in Experiment Two is consistent with Bolognini and colleagues, it is possible that other individual difference factors that may distinguish the present sample from the participants used in the prior study. Some potentially relevant individual differences were found in the current study (e.g., trait empathy), but these did not modulate stimulation effects in a systematic fashion. Future work should more closely examine how individual variability may influence changes in vicarious tactile perception following tDCS targeted at somatosensory related areas.

The lack of significant increase in vicarious tactile perception following high frequency tRNS or tDCS targeted at somatosensory regions also contradicts predictions based on a Threshold Theory account of mirror-touch synaesthesia, which suggests that increased baseline excitability in somatosensory regions may boost vicarious responses to observed touch over a threshold for conscious perception (see Ward & Banissy, 2015 for review). In both experiments no strong evidence for modulation in conscious vicarious perception was found, either behaviourally or in self-reported experience, when excitability was increased in SI. Past research has identified structural brain differences associated with MTS that extend outside of the somatosensory system (Holle et al., 2013), suggesting a potentially contrasting neural profile between individuals with and without MTS. For this reason it may be wrong to assume that this unique perceptual experience can be induced in controls.

In line with the results of previous research (Vandenbroucke et al., 2016) enhancing excitability of rTPJ with tDCS also did not significantly modulate vicarious tactile perception. This region has previously been linked with self-other control mechanisms, and stimulation of rTPJ with tDCS has been shown to improve the ability to accurately switch between representations of self and others, according to task demand (Santiesteban et al., 2012; Santiesteban et al., 2015a). Individuals with MTS have been shown to have deficits in the ability to control self-other representations when there is a need to inhibit others and enhance the self (Santiesteban et al., 2015b). Further, training typical adults to become better able to control self-other representations can lead to modulation of vicarious pain perception, although the neural locus of how self-other control training contributes to this effect has not been investigated (de Guzman et al., 2016). With this in mind, it is perhaps surprising that tDCS targeted at rTPJ did not improve the ability to inhibit vicarious responses to observed touch to another person, when responding to felt touch on the participant’s own hands.

The degree to which self-other control is pivotal to the particular tasks used is an important consideration. Participants were instructed to respond with the location where they felt touch on their own hands, but were not explicitly told to inhibit the touch they saw on the screen (i.e., there were no explicit self-other control demands). Further, it is possible that when viewing hands from an egocentric perspective, the hands are represented as part of the self rather than other (see section 1.2). In this case, there are fewer requirements to control self-other representations. In future it would be interesting to consider whether these mechanisms can be engaged to a greater extent by manipulating task instructions and design. Behavioural differences in self-other control associated with conscious vicarious perception are explored further in the next chapter.

Recent models of TPJ function have argued that this region is not solely involved in social processing, suggesting that anodal stimulation of rTPJ might facilitate task-relevant representations in a domain-general way (Carter & Huettel, 2013; Cook, 2014; see section 1.2). These models imply that modulation of task performance would be expected in the current experiment despite the possibility of low self-other control demands discussed above. Following this assumption, increasing excitability of the rTPJ might be expected to reduce reaction times for reporting the location of the tactile stimulus due to enhancement of this task-relevant representation over the task-irrelevant observed touch, rather than through improvements in specifically self-other control ability. Nevertheless, this pattern of results was not found. Carter and Huettel, among others, have argued that the TPJ should not be considered a unified region, due to the multiple functions thought to occur within distinct sub-regions. The use of 5x5 cm electrodes over rTPJ may therefore not have been sufficiently focal to target the most relevant sub-regions. Carter & Huettel suggest, for example, that the area of the TPJ within the angular gyrus is a likely candidate for where multimodal information is integrated to construct social context, and so provides a sub-region of interest to target. Future work could explore this possibility using more focal stimulation methods, such as neuronavigation-guided TMS.

It should be noted that the tDCS parameters in the present study differed from those used in previous experiments modulating activity of rTPJ with tDCS. For instance, prior work examining self-other representation using tDCS targeted at rTPJ has stimulated offline at 1mA using 5x7 cm electrodes (e.g., Santiesteban et al., 2012; Santiesteban et al., 2015a; Sowden et al., 2015) or 5x7 cm and 10x10 cm electrodes (e.g., Liepelt et al., 2016). Similarly, Coll and colleagues (2017) used 2mA tDCS with 5x7cm electrodes to assess vicarious pain perception. Our decision to use a protocol involving online stimulation at 1.5mA using 5x5cm electrodes was selected to match that in the rSI stimulation condition (which was selected to replicate prior work - Bolognini et al., 2013). The differences between our rTPJ stimulation montage and those used in other studies may have affected the degree of modulation of rTPJ compared with past research. This could account for the lack of influence of rTPJ stimulation on vicarious perception in Experiment 2.

It is also important to consider how the present findings relate to the broader literature regarding the role of sensorimotor contributions to social perception. For instance, recent evidence has indicated that a range of social perception abilities are linked with sensorimotor cortex activity (e.g., Adolphs et al., 2000; Banissy et al., 2010; Jacquet & Avenanti, 2015; Keysers et al., 2010; Paracampo et al., 2016; Pitcher et al., 2008; Pourtois et al., 2004; Valchev et al., 2017). Several of these have used non-invasive brain stimulation to show changes in social perception skills following sensorimotor cortex stimulation relative to appropriate control conditions (e.g., baseline, control brain stimulation conditions). There have, however, been few published replication attempts for these studies. The present study, together with the evidence of large inter-individual differences in the effects of non-invasive brain stimulation (e.g., Fertonani & Miniussi, 2017; Hsu et al., 2016; Ridding & Ziemann, 2010), calls for more systematic investigations and replications in this area.

While stimulation effects were not observed, there were some behavioural effects of note. For example, the degree of vicarious touch perception was associated with self-reported perspective taking when viewing spatially congruent touch to another human hand (versus a dummy hand or object). Previous research has shown a positive correlation between perspective taking scores and activation in SI (Schaefer et al., 2012), as well as amplitudes of somatosensory-evoked potentials (Martínez-Jauand et al., 2012) when observing touch. The present results are in line with these findings. Despite this association between perspective taking and vicarious tactile perception, this factor was not found to interact with the effects of tDCS or high frequency tRNS on task performance in the present studies.

In summary, across two studies no clear evidence was found to support the suggestion that increasing cortical excitability in somatosensory regions of typical younger adult participants leads to differential changes in vicarious tactile perception from sham stimulation or stimulation to the rTPJ. These findings conflict with prior results and threshold based accounts of individual differences in vicarious perception.

Chapter 4

Inhibitory Control in Vicarious Pain Responders

Prior research has identified considerable variation in the vicarious perception of pain, with some individuals experiencing a conscious sensation on their own body when viewing another person in pain. Self-Other Theory could provide a potential explanation of conscious vicarious pain, suggesting that impairments in inhibiting representations of others and enhancing representations of the self may underlie atypical vicarious perception. Alternatively, Task Control Theory suggests that impairments in domain-general inhibitory control processes, rather than those specific to self and other can account for the perceptual and behavioural differences observed in MTS and conscious vicarious pain. In Chapter 3, enhancing excitability at the right temporo-parietal junction, a region previously associated with self-other control, did not modulate vicarious tactile perception. The present experiment aimed to follow-up claims of atypical self-other control in conscious vicarious perception with a behavioural task. It also aimed to clarify whether impairment in domain-general inhibitory control ability can provide a better account of how vicarious pain is experienced as a conscious percept. In this sample, no significant differences in either self-other control or domain–general inhibitory control were observed between Sensory-Localised or Affective-Generalised conscious vicarious pain responders and controls. Participants also completed a visuotactile interference task, similar to that in Chapter 3, involving images of pain. Again, conscious vicarious pain responders did not differ from controls in their performance on this task, but hypervigilance to pain was associated with greater congruency effects in control participants.

4.1 Introduction

Vicarious perception of pain varies considerably from person to person, with some individuals reporting a conscious sensation of pain on their own body when seeing another person in pain. Conscious vicarious pain which evokes a physical response localised to the same body part as the observed pain (i.e., Sensory-Localised) is estimated at around 19% prevalence (Grice-Jackson et al., 2017). Other individuals report a more affective vicarious pain response, which is generalised over the body (Affective-Generalised, estimated prevalence 12%); but for the majority of people observing pain does not elicit conscious vicarious experiences (estimated prevalence 69%). Based on a procedure designed to verify mirror touch synaesthesia (MTS), a related form of conscious vicarious perception (Banissy & Ward, 2007), Vandenbroucke and colleagues (2013) developed a task to assess conscious vicarious pain experience. In this task participants were required to detect the location of a tactile stimulus on their right or left hand while concurrently viewing images of hands being pricked by a needle. This observed pain could either be spatially congruent (i.e., on the same hand) or incongruent (i.e., on the opposite hand) with the tactile stimulus. On incongruent trials, conscious vicarious pain responders were more likely than control participants to erroneously state that they felt the tactile stimulus in the same location that the visual stimulus was presented. This type of error indicates that viewing pain elicited a vicarious physical sensation on the participant’s own body which interfered with accurate detection of the tactile stimulus. Results from a previously used tactile version of this task indicate that greater visual interference is associated with higher self-reported empathy, specifically the perspective-taking subscale of the IRI (see Chapter 3; Davis, 1980) and the emotional reactivity subscale of the Empathy Quotient

(Banissy & Ward, 2007; Baron-Cohen & Wheelwright, 2004). Hypervigilance to pain has also been suggested as a potential moderator of performance on the pain version of this task (Fitzgibbon et al., 2010; Vandenbroucke et al., 2013).

Theories regarding the causes of MTS have been applied to account for individual variability in vicarious pain. In particular, the Self-Other Theory of mirror-touch synaesthesia (MTS) proposes that impairment in controlling representations of the self and others underlies conscious vicarious perception (Ward & Banissy, 2015; see section 1.3 for a discussion). In line with this account, conscious vicarious pain responders (both Sensory-Localised and Affective-Generalised) show reduced grey matter density at the right temporo-parietal junction (rTPJ) in comparison with controls (Grice-Jackson et al., 2017). Several studies indicate that the rTPJ is involved in the ability to represent and control representations of the self and others. For instance, anodal transcranial direct current stimulation (tDCS) over rTPJ improves performance on tasks of imitation-inhibition, which requires enhancing representations of the self and suppressing those of the other, and perspective-taking, which requires suppressing representations of the self and enhancing those of the other, but not on a non-imitative inhibitory control task, requiring inhibition of an irrelevant cue, but not the specific control of representations of self and other (Hogeveen et al., 2015; Santiesteban et al., 2012).

An important contribution to the Self-Other Theory relative to MTS is provided by Santiesteban and colleagues (2015b). In this study, participants with MTS performed comparably with control participants on measures of perspective-taking and theory of mind. However, controls outperformed MTS on an imitation-inhibition task (matching that used by Santiesteban et al., 2012 and Hogeveen et al., 2015). The task requires participants to perform finger movements which are either congruent or incongruent with the movements of a hand viewed on the screen. Enhancing representations of the self and inhibiting representations of the other are therefore required when actions are incongruent. In this condition participants with MTS made more errors and had slower reaction times than controls without MTS, indicating a specific difficulty with inhibiting other-relevant representations.

Self-other control ability has also been linked to vicarious perception of pain. Training the ability to control representations of the self and other can enhance vicarious pain perception, leading to a greater decrease in MEPs when viewing others in pain (de Guzman et al., 2016). Derbyshire and colleagues (2013) provide evidence for impaired self-other control ability in conscious vicarious pain responders. The authors demonstrate this using the dot-perspective task, which presents participants with an image of an avatar placed in a room with three walls. On each trial, between 0-3 dots appear on the walls, either facing the avatar or away from the avatar. This meant that the number of dots the participant could see either matched the number the avatar could see (congruent trials) or was different (incongruent trials). Participants were cued to either confirm the number of dots that they could see themselves (self-perspective) or the number the avatar could see (other-perspective). When adopting a self-perspective, vicarious pain responders showed a significant increase in reaction times on incongruent trials compared with congruent trials, while controls did not. When adopting an other-perspective, both groups showed a significant effect of congruency, although this difference was larger for controls than for vicarious pain responders. Impairment in inhibiting representations of others’ mental states when focusing on the self therefore appears to be shared by individuals with MTS and vicarious pain responders.

However, the study by Derbyshire and colleagues (2013) has been criticised for reflecting domain-general cognitive processes rather than self-other control.

Santiesteban and colleagues (2014) conducted a version of this task in which the avatar was replaced with an arrow (i.e., a non-social agent) on 50% of blocks. Participants were again required to confirm the number of dots they could see, the number that the avatar could see, or the number that the arrow was pointing at. Comparable effects were found on both tasks, where reaction times were slower when the perspective of either the avatar or the arrow did not match the perspective of the participant. Differences in behavioural performance in and vicarious pain responders compared with controls reported by Derbyshire and colleagues may then reflect a deficit in domain-general inhibitory control rather than specific to self-other control.

Heyes and Catmur (2015) extend this evidence to propose that vicarious touch and pain experiences may be better understood in terms of domain-general inhibitory control mechanisms (Task Control Theory). The authors highlight that prior evidence of atypical self-awareness in MTS and vicarious pain responders, including susceptibility to the rubber hand illusion (Aimola Davies & White, 2013; Derbyshire et al., 2013), could also be accounted for in terms of domain-general mechanisms of associative learning. The results presented by Santiesteban and colleagues (2015b) conflict with this theory, since no significant differences were found between individuals with MTS and controls on a perspective-taking task which required participants to enhance representations of the other and inhibit representations of the self. If MTS were associated with domain-general impairment in task control then we should also predict poorer performance on this task. However, whether this specificity also exists for vicarious pain responders is yet to be seen. In light of this, the present study aimed to identify whether those that experience conscious vicarious pain show similar performance to MTS on tasks which require self-other control, and the extent to which this reflects impairments in domain-general or purely social cognitive processes.

The present experiment compared the performance of conscious vicarious pain responders with non-responder controls on a visuotactile interference task, and across three tasks of inhibitory control: imitation-inhibition, perspective-taking, and a domain-general stop-signal task. All three tasks involve the need to switch between task-relevant and task-irrelevant information, but vary in the focus of this switching (i.e., between representations of self and other, or in non-social information). Contrasting performance across these measures can therefore inform us about domain-general or domain-specific differences in inhibitory control in vicarious pain responders. Self-report measures of empathy and hypervigiliance to pain were also administered. Based on prior research with mirror-touch synaesthetes, it was predicted that vicarious pain responders would exhibit greater difficulty enhancing the self and inhibiting the other on the imitation-inhibition task, but comparable performance on the perspective-taking and stop-signal tasks compared with controls. It was also predicted that vicarious pain responders would show greater interference from the visual pain stimulus on the visuotactile interference task than controls, and that self-reported empathy and hypervigilance to pain would moderate interference effects on this task.

4.2 Materials and methods

4.2.1 Participants

37 healthy participants took part in the experiment for course credit or £10 payment. All participants were assigned to one of three pain responder groups on the basis of a cluster analysis of their responses on an online vicarious pain questionnaire (see section 5.2). This comprised 10 Sensory-Localised pain responders (8F, 2M; age

18-21 years, *M* = 19.3, *SD* = 0.8), 3 Affective-Generalised pain responders (3F, 0M; age 20-34 years, *M* = 26.7, *SD* = 7.0), and 24 non-responder controls (21F, 3M; age 18-45 years, *M* = 21.9, *SD* = 6.1). There were no significant differences in age (*F*[2,34] = 2.35, *p* = .110) between the pain responder groups. Gender differences between groups were also not significant, according to Fisher's exact test (*p* = .756). Normal or corrected-to-normal vision was a requirement to participate. The project was approved by the Goldsmiths Psychology department ethics committee.

4.2.2 Procedure

In the experimental session, participants first answered self-report measures assessing pain vigilance and empathy. Participants then completed four experimental tasks. The order of the first three tasks was counterbalanced, and included an imitation-inhibition task, a perspective-taking task, and a stop-signal task as a measure of domain-general inhibitory control. Following these tasks participants completed a pain version of a visuotactile interference task. This task was administered at the end of the session in case the sight of pain should cause distress, or synaesthetic sensations in the Sensory-Localised responder group, which might affect performance on subsequent tasks.

Stop-Signal Task

The commonly used Stop-signal task (e.g., Logan & Cowan, 1984) was administered as a measure of domain-general (i.e., non-social) inhibitory control. Participants first complete one block containing 64 Go-trials, in which either a letter X or O appears on the screen. Participants are instructed to "press the Z key when you see

X and the M key when you see O”, and to respond as quickly as possible. The following three test blocks contain 144 Go-trials, and 48 Stop-trials, presented in random order. On Stop-trials, a red box occasionally appears around the letter, indicating that the participant must inhibit their response (i.e., refrain from the key press). The signal appears after a short stop-signal delay (SSD), which is staircased according to the participant’s performance, such that a correct inhibition of response leads to a 50ms increase in SSD, and failure to inhibit leads to a 50ms decrease. This ensured inhibition accuracy was maintained at around 50% across participants. If participants do not respond to Go-trials within two standard deviations of their median response time on the initial Go-trial block, they are prompted to “Go Faster!”.

Imitation-Inhibition Task

The imitation-inhibition task (Brass, Bekkering, Wohlschläger & Prinz, 2000) required participants to move either their index or middle finger upwards as cued by a number (1 for index, 2 for middle) which appeared on the computer screen in front of them. Simultaneously, participants viewed a hand making finger movements on the screen that were either congruent (i.e., index finger moves when participant is instructed to move index finger) or incongruent (i.e., middle finger moves when participant is instructed to move index finger). The participant must then inhibit the imitation of the observed finger movement on incongruent trials. The task consists of 60 congruent and 60 incongruent trials, which were randomised across two blocks.

Perspective-Taking Task

Perspective-Taking ability was assessed using the ‘Director’ task (Keysar, Barr, Balin & Brauner, 2000). Each trial of this task depicts a shelf containing several items, with a figure (the director) standing behind the shelf facing the participant. The participant is instructed to move items on the shelf using the mouse, following directions from the perspective of the director. For instance, if the instruction is to move an item “left”, the correct response is to drag the item to the director’s left, meaning the participant’s right. In addition some items are apparently visible only to the participant, and not to the director, due to a panel at the back of the shelf. Participants must be aware that the director will not instruct them to move any item which he cannot see. For example, if they are instructed by the director to move the vase, the correct response is to move the vase which is visible to the director, not one which is blocked by a panel. On 36 experimental trials the perspective of the director is incongruent with the perspective of the participant, and on 72 control trials the participant and director’s perspectives are congruent. All trials were randomised across three blocks.

Visuotactile Interference Task

For this task participants were required to state the location of a tactile sensation on their own hand, while simultaneously observing another hand on the computer screen being pricked by a needle. The method was adapted from a version containing a non-painful touch stimulus by Banissy and Ward (2007), in light of recent work by Vandenbroucke et al., (2014). For each trial, participants viewed a 1500ms fixation cross, followed by three consecutive images showing the hands approached and penetrated by the needle. This observed painful event occurred either on the left, right or both hands, which were presented in an egocentric perspective. The tactile stimulus was delivered to the participant's hands 10ms after the onset of the needle prick. This image then remained on the screen until the participant gave a response. The tactile stimulus was delivered either to the participant's left, right or both hands, or there was no stimulus at all. On 60 trials the felt sensation was spatially congruent with the observed pain, on 60 trials it was incongruent, and on 60 trials there was no tactile stimulus. The order of trials was counterbalanced across three blocks. Participants gave verbal responses using a voice key, by stating "left", "right", "both" or "none", according to the location they felt the sensation, and were asked to respond as quickly and accurately as possible. The stimulus was delivered using 2 miniature solenoid tappers attached to the dorsum of the participant's left and right hands with medical tape. A Dual Channel Solenoid Controller (MSTC3-2; M & E Solve) was used to control the tappers. During the task white noise was played through headphones during each trial to mask the sound of the tappers.

4.2.3 Self-report measures

Pain Vigilance and Awareness Questionnaire

The Pain Vigilance and Awareness Questionnaire (PVAQ; McCracken, 1997) was administered as a measure of hypervigilance to pain. The 16-item questionnaire requires participants to consider their experience of pain over the past two weeks and to indicate how frequently each item, such as "I pay close attention to pain", is true of them, on a six-point scale from "never" to "always". Total scores can range from 0 to 80, with a higher score indicating greater pain vigilance. The author reports good internal consistency ($\alpha = .86$) and validity for the scale as an indicator of attention to pain.

Empathy Quotient

The 40-item version of the Empathy Quotient (EQ-40; Baron-Cohen & Wheelwright, 2004) was used to assess self-report trait empathy. This questionnaire asks participants to indicate the extent to which they agree with each of 40 statements, such as “I find it easy to put myself in somebody else's shoes”, using a four-point scale from strongly agree to strongly disagree. Total scores range from 0 to 80, with a higher score indicating higher trait empathy. Scores can also be clustered into three subscales, reflecting ‘cognitive empathy’, ‘emotional reactivity’ and ‘social skills’ (Lawrence, Shaw, Baker, Baron-Cohen & David, 2004). The cognitive empathy subscale refers to the appreciation of others’ affective states, for instance “I can tell if someone is masking their true emotion”. Emotional reactivity reflects the emotional response to others’ states, for instance “Seeing people cry doesn’t really upset me”, while the social skills subscale refers to intuitive social understanding, such as “I often find it hard to understand whether something is rude or polite”. Lawrence et al. report good test-retest reliability ($r = .84$) and validity for the scale.

4.3 Results

4.3.1 Data analysis

Performance on the stop-signal task was analysed in terms of inhibition accuracy and stop-signal reaction time (SSRT). Accuracy scores represent the percentage of correct responses (i.e., response or inhibition), calculated individually for Go-trials and Stop-trials. Since SSRT cannot be directly recorded, a quantile method was used to estimate SSRT for each participant (see Figure 4.1). In this method, Go-trial reaction times (RTs) are sorted in ascending order, and SSRT is taken as the RT corresponding to the proportion of failed Stop-trials, minus the mean SSD (see methods). To give an example, if a participant failed to inhibit the button press on 30% of Stop-trials, the RT which is slower than 30% of Go-trial RTs would be selected. Under this model, the 30% of RTs faster than this would be those that were too fast to inhibit the stop-signal (represented by the shaded area in Figure 4.1). Mean SSD is then subtracted to give the time from when the stop-signal was first presented (see Congdon et al., 2012 for a full discussion of this method).

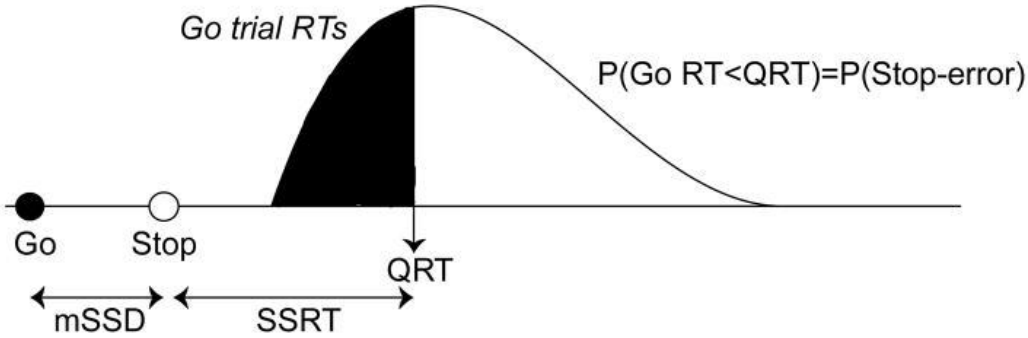

Figure 4.1: Illustration of SSRT calculation on the stop-signal task (from Thakkar et al., 2014)

One participant with Go-trial accuracy of less than 60% was excluded prior to further analysis on the stop-signal task, based on exclusion criteria recommended by Congdon and colleagues (2012).

The ability to control representations of self and other on the imitation-inhibition and perspective-taking tasks was assessed with reaction times and percentage accuracy on congruent and incongruent trials. Increased reaction times and poorer accuracy on incongruent trials was taken as an indication of greater difficulty inhibiting task-irrelevant representations (i.e., those relevant to the self on the perspective-taking task and those relevant to the other on the imitation-inhibition task), as per Santiesteban and colleagues (2015b).

Performance on the visuotactile interference task was also assessed using reaction times and the number of errors on congruent and incongruent trials. In addition, mirror-pain errors were categorised as those on which the participant responded with the location of the visual stimulus rather than the tactile stimulus, or responded “Both”, on incongruent trials. For example, a response of either “Right” or “Both” when the stimulus is delivered on the left hand, but observed on the right, would be categorised as a mirror-pain error. Associations between self-reported empathy and hypervigilance to pain and interference on this task were examined using Pearson’s correlations. For this, congruency effects in reaction time (Incongruent RT – Congruent RT) and accuracy (Congruent Accuracy – Incongruent Accuracy) were also calculated. In both cases, a greater congruency effect indicates greater interference from the visual stimulus (as per Banissy & Ward, 2007; see Chapter 3).

4.3.2 Self-report measures

Self-report measures were compared between pain responder groups with a series of univariate ANOVA tests. This revealed no significant differences in emotional reactivity (*F*[2,34] = 0.32, *p* = .732, η_p^2 = .02), cognitive empathy (*F*[2,34] = 0.36, *p* = .701, η_p^2 = .02), social skills (*F*[2,34] = 0.30, *p* = .740, η_p^2 = .02) or overall EQ scores (*F*[2,34] = 0.11, *p* = .898, η_p^2 = .01). There were also no significant differences on the PVAQ (*F*[2,33] = 0.12, *p* = .884, η_p^2 = .01). Mean questionnaire scores are displayed in Table 4.1.

Table 4.1: Means and standard deviations of self-reported empathy and vigilance to pain for each of the three pain responder groups. No significant between-group differences were observed.

	Controls		Sensory-Localised		Affective-Generalised	
Self-Report Measure	*M*	*SD*	*M*	*SD*	*M*	*SD*
Empathy Quotient	48.7	13.0	48.7	9.9	52.3	22.1
Emotional Reactivity	14.7	5.6	15.8	2.4	16.7	8.4
Cognitive Empathy	14.0	4.7	14.6	4.3	16.3	5.5
Social Skills	6.3	2.2	5.6	3.2	5.7	2.1
Pain Vigilance and Awareness Questionnaire	44.4	11.7	46.2	8.7	43.3	14.8

Note: Controls N = 24, Sensory-Localised N = 10, Affective-Generalised N = 3.

Inter-correlations between the self-report scales showed that high pain vigilance was significantly associated with higher emotional reactivity (*r* (34) = .47, *p* = .004), while associations with cognitive empathy (r (34) = .22, p = .207) and social skills (r (34) = .25, p = .141) were not significant.

4.3.3 Visuotactile Interference Task

A 3 x 2 (Pain responder group x Congruency) mixed ANOVA was used to analyse reaction times on the visuotactile interference task. As shown in Figure 4.2a, there was a main effect of Congruency ($F[1,34] = 14.25$, $p = .001$, $\eta_p^2 = .30$), where participants were slower to respond on incongruent trials than congruent trials. The main effect of Pain responder group was not significant ($F[2,34] = 0.99$, $p = .382$, $\eta_p^2 = .06$), and there was no significant interaction between variables ($F[2,34] = 1.31$, $p = .284$, $\eta_p^2 = .07$).

Due to a negative skew present in accuracy scores on the visuotactile interference task, a non-parametric Kruskal-Wallis H test was used to compare accuracy on the visuotactile interference task across pain responder groups. No significant effect of responder group was found for accuracy on congruent (H [2] = 1.71, p = .424) or incongruent (H [2] = 1.04, p = .595) trials (see Figure 4.2b). A further analysis compared the number of mirror-pain errors made in each responder group. Again, no significant between-group difference was found (H [2] = 3.10, p = .212). Results are shown in Figure 4.2c.

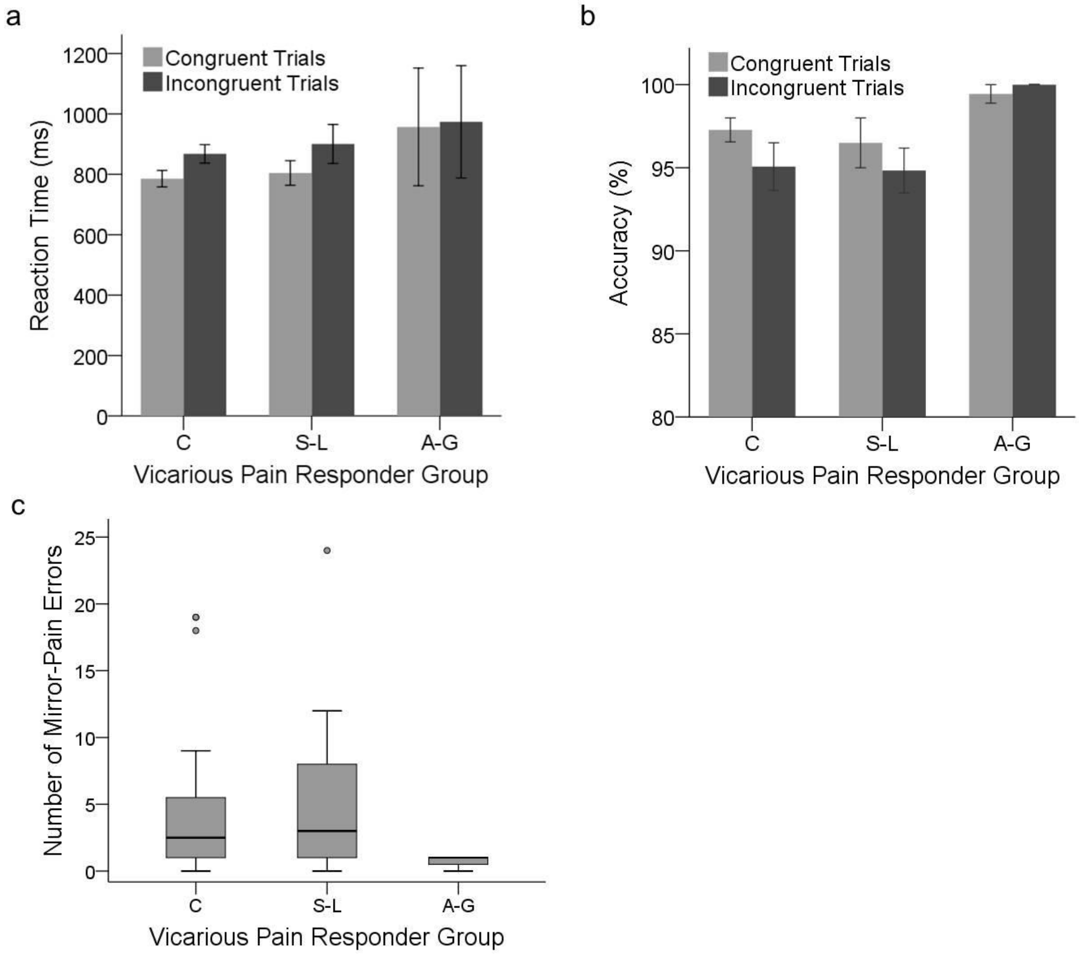

Figure 4.2: Reaction times (a), accuracy (b), and number of mirror-pain errors (c) on the visuotactile interference task. A significant congruency effect was found in reaction times on the task, but there was no significant effect of responder group. No significant effects of congruency or responder group were found in accuracy or the number of mirror-pain errors. C, Control; S-L, Sensory-Localised; A-G, Affective-Generalised. Error bars represent +/- 1 S.E.M.

Self-reported empathy on the EQ did not correlate significantly with congruency effects in RT (*r* [35] = .19, *p* = .252) or accuracy (*r* [35] = .20, *p* = .239), nor with the number of mirror-pain errors made (*r* [35] = .15, *p* = .380) across all participants combined. Correlations with each of the EQ subscales (Cognitive Empathy, Emotional

Reactivity and Social Skills) were also not significant (*p*s > .18). Hypervigilance to pain showed no significant association with congruency effects in RT (*r* [34] = .15, *p* = .385), accuracy (*r* [34] = -.07, *p* = .713) or mirror-pain errors (*r* [34] = .07, *p* = .675).

Table 4.2: Pearson's correlations between self-report measures and performance on the visuotactile interference task. For control participants there was a positive correlation between self-reported pain vigilance and congruency effects in reaction times, indicating an association between hypervigilance to pain and increased vicarious response.

	CE RT		CE Accuracy		MP Errors	
Self-Report Measure	C	S-L	C	S-L	C	S-L
Empathy Quotient	.08	.55	.28	-.02	.20	-.23
Emotional Reactivity	.02	.51	.18	-.19	.10	-.28
Cognitive Empathy	.17	.35	.19	-.05	.12	-.35
Social Skills	.06	.22	.26	.14	.31	-.16
Pain Vigilance and Awareness Questionnaire	$.53^{*}$	-.25	.01	-.37	.09	.04

*Note: Control N = 24, Sensory-Localised N = 10. C, Control; S-L, Sensory-Localised; CE RT, Congruency Effect in Reaction Times; CE Accuracy, Congruency Effect in Accuracy; MP Errors, Mirror-Pain Errors. * p* < .05

Since prior work found an association between hypervigilance to pain and vicarious perception only in conscious vicarious pain responders, correlations were examined in Sensory-Localised pain responders and control participant groups individually (the Affective-Generalised group were not analysed due to the low sample size). In this analysis no significant correlations involving empathy were found. There was a positive correlation between vigilance to pain and congruency effects in reaction times, in the control participants but not Sensory-Localised pain responders, **where there was a non-significant negative trend *(see Table 4.2)*. Fisher's r-to-z transformation revealed a marginally-significant difference between the correlations for Sensory-Localised and control participants ($z = 1.94$, $p = .052$).** All other correlations with pain vigilance were not significant.

4.3.4 Stop-Signal Task

First, inhibition accuracy on Go-trials and Stop-trials was analysed with a 3x2 (Pain responder group x Trial Type) mixed ANOVA. The main effect of Trial Type was significant ($F[1,33] = 120.24$, $p < .001$, $\eta_p^2 = .79$), where participants were more accurate on Go-trials than Stop-trials. However, the main effect of Pain responder group ($F[2,33] = 0.90$, $p = .418$, $\eta_p^2 = .05$) and interaction between the two independent variables ($F[2,33] = 1.73$, $p = .193$, $\eta_p^2 = .10$) were not significant (see Figure 4.3a).

Between-group differences in SSRT for each of the pain responder clusters were then analysed using one-way independent ANOVA. Again, the effect of responder group was not significant ($F[2,33] = 0.01$, $p = .990$, $\eta_p^2 < .01$). Results are shown in Figure 4.3b. Collectively, the results indicate that domain-general inhibitory control is comparable between all subtypes of vicarious pain responders.

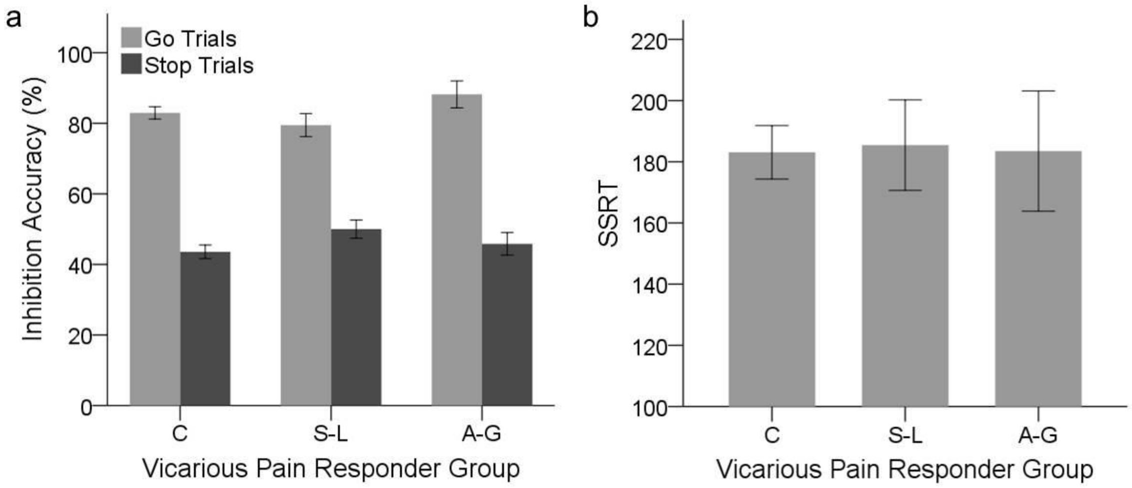

Figure 4.3: Inhibition accuracy for Go Trials and Stop Trials (a) and SSRT (b) on the stop-signal task in each of the vicarious pain responder groups. Accuracy was higher on Go trials than Stop trials. No significant between-group differences were found in inhibition accuracy or SSRT. C, Control; S-L, Sensory-Localised; A-G, Affective-Generalised. Error bars represent +/- 1 S.E.M.

4.3.5 Imitation-Inhibition

A 3x2 (Pain responder group x Congruency) mixed ANOVA was carried out on accuracy scores on the imitation-inhibition task, to address the prediction that pain responders would show reduced accuracy inhibiting imitation when finger movements were incongruent. The main effect of Congruency was significant ($F[1,34] = 11.48$, $p = .002$, $\eta_p^2 = .25$), confirming that participants were less accurate when observed movements were incongruent with instructed movements. However, the main effect of Pain responder group ($F[2,34] = 1.01$, $p = .376$, $\eta_p^2 = .06$) and crucially the interaction between Pain responder group and Congruency ($F[2,34] = 2.04$, $p = .145$, $\eta_p^2 = .11$)

were not significant, indicating that vicarious pain responders did not differ from non-responders in accuracy on this task (see Figure 4.4a).

A second 3x2 (Pain responder group x Congruency) ANOVA was conducted on reaction times on the task. Again, a main effect of Congruency indicated that participants were slower to respond on incongruent than congruent trials ($F[1,34] = 33.18$, $p < .001$, $\eta_p^2 = .49$), but the main effect of Pain responder group ($F[2,34] = 0.70$, $p = .505$, $\eta_p^2 = .04$) and the interaction between Pain responder group and Congruency ($F[2,34] = 0.34$, $p = .715$, $\eta_p^2 = .02$) were not significant(see Figure 4.4b).

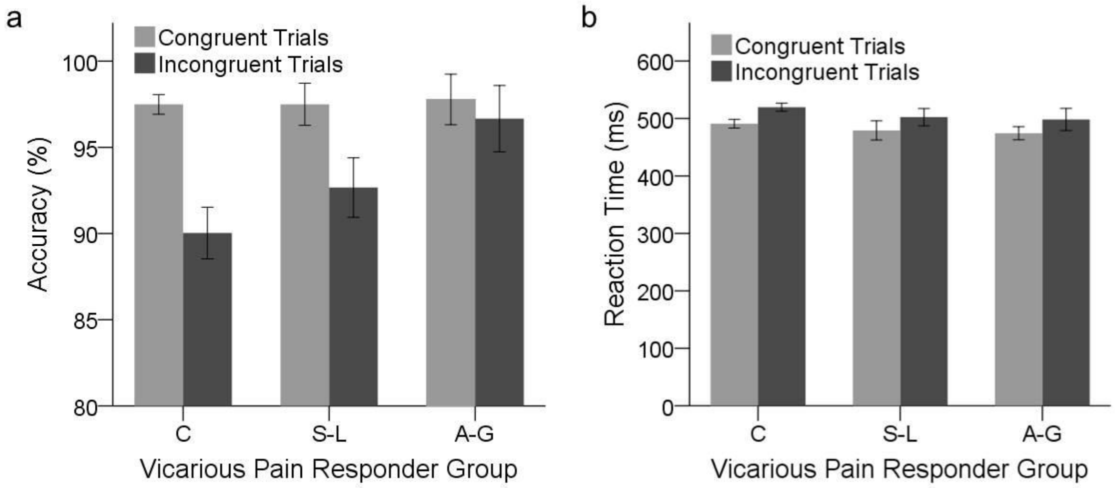

Figure 4.4: Accuracy (a) and reaction times (b) on congruent and incongruent trials of the imitation-inhibition task in each vicarious pain responder group. Higher accuracy and faster reaction times were observed on congruent trials than incongruent trials overall. No significant differences in either accuracy or reaction time were found between the pain responder groups. C, Control; S-L, Sensory-Localised; A-G, Affective-Generalised. Error bars represent +/- 1 S.E.M.

4.3.6 Perspective-Taking

A 3x2 (Pain responder group x Congruency) mixed ANOVA was carried out on accuracy scores on the director task. In this case, the main effect of Congruency was not significant ($F[1,28] = 0.84$, $p = .368$, $\eta_p^2 = .03$). Neither was the main effect of Pain responder group ($F[2,28] = 0.05$, $p = .954$, $\eta_p^2 < .01$) or the interaction between variables ($F[2,28] = 0.40$, $p = .677$, $\eta_p^2 = .03$). Results are displayed in Figure 4.5a.

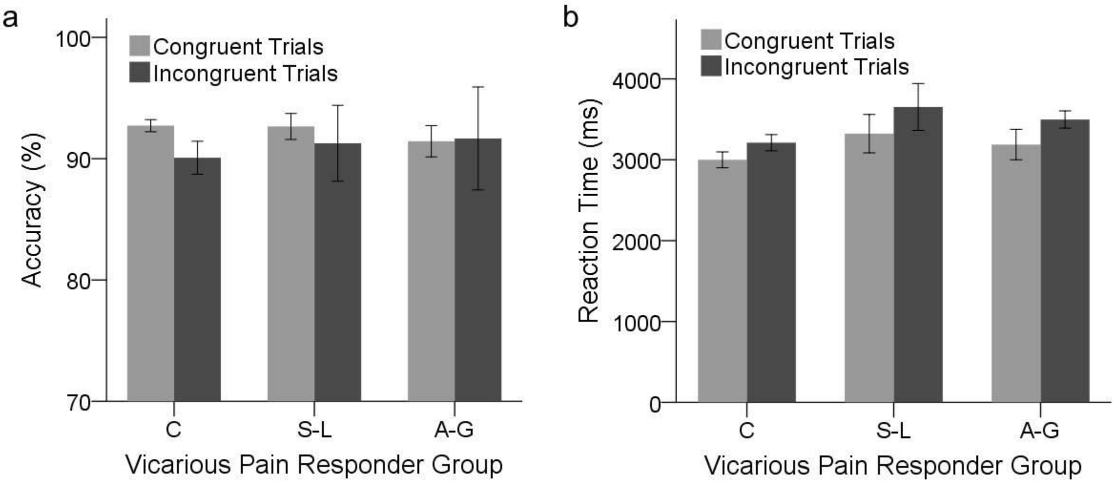

Figure 4.5: Accuracy (a) and reaction times (b) on congruent and incongruent trials of the perspective-taking task in each vicarious pain responder group. Overall, faster reaction times were observed on congruent trials than incongruent trials, but the effect of congruency on accuracy was not significant. No significant between-group differences in either accuracy or reaction time were observed. C, Control; S-L, Sensory-Localised; A-G, Affective-Generalised. Error bars represent +/- 1 S.E.M.

A further 3x2 (Pain responder group x Congruency) ANOVA compared reaction times on the task. This revealed a significant main effect of Congruency ($F[1,28] =$

30.65, $p < .001$, $\eta_p^2 = .52$), where participants were slower to respond where the perspective of the director was incongruent with the their own, than when it was congruent (see Figure 4.5b). Again, however, the effect of Pain responder group was not significant ($F[2,28] = 1.66$, $p = .209$, $\eta_p^2 = .11$), and neither was the interaction between Congruency and Pain responder group ($F[2,28] = 1.39$, $p = .265$, $\eta_p^2 = .09$).

4.4 Discussion

The present study compared inhibitory control ability in Sensory-Localised and Affective-Generalised vicarious pain responders with controls who do not experience conscious vicarious pain. No significant differences between pain responder groups were found on tasks requiring the control of self-relevant and other-relevant representations, or on a non-social inhibitory control task. On a visuotactile interference task, conscious vicarious pain responders did not significantly differ from controls in their ability to detect a tactile stimulus on their own hand while viewing a painful stimulus delivered to another hand. No moderating effects of empathy were found on this task, but greater congruency effects were observed for control participants with higher self-reported vigilance to pain.

The present results found no evidence for atypical self-other control abilities in either Sensory-Localised or Affective-Generalised vicarious pain responders. These results contrast with past research which has indicated that vicarious pain responders (Derbyshire et al., 2013) are impaired in inhibiting other-relevant representations. The dot-perspective task used in this prior work has been criticised for reflecting domain-general processes rather than specifically self-other control mechanisms (Santiesteban et al., 2014), which could account for the discrepancy with the current results. However, since conscious vicarious pain responders also did not significantly differ from controls on a domain-general inhibitory control task in the present study, this explanation is not supported. Further, individuals with MTS have previously shown impairments in self-other control ability using the same tasks as the present study (Santiesteban et al., 2015b), indicating that they are sensitive to the predicted differences in conscious vicarious pain responders. One potential implication of evidence for impaired self-other control in MTS but not in this conscious vicarious pain sample is that it may be over-simplistic to assume that these two conditions share underlying mechanisms. While the Self-Other Theory of MTS (see Ward & Banissy, 2015) has also been applied to vicarious pain experience, differences in prevalence of the two conditions (Sensory-Localised vicarious pain is thought to be over ten times more common than MTS, see section 1.3) suggest that additional factors may be important. The question of whether conscious vicarious pain is associated with impairments in self-other control mechanisms or domain-general inhibitory control processes is therefore worthy of further investigation.

The results from the visuotactile interference task contrast with the results of studies from Vandenbroucke and colleagues (2013, 2014). Across two experiments, using a procedure similar in design to the method used here, the authors report a greater number of mirror-pain errors (referred to as vicarious pain errors) in vicarious pain responders compared with controls. No such difference was found here. There is one key methodological difference which could account for this discrepancy. While in the present study the tactile stimulus on the dorsum of the hand was a tap delivered using a miniature solenoid tapper, Vandenbroucke and colleagues used electrocutaneous stimulation to elicit a “pricking” sensation (2013), and in their second study vibrotactile stimulation to elicit “tingling” (2014). It is possible that these stimuli may have generated a greater number of mirror-pain errors in the vicarious pain responders than found in the present study if they more closely matched the vicarious sensation elicited by the visual stimulus. It has been shown that conscious vicarious pain responders most commonly label their vicarious experience as “tingling”, when asked to choose descriptors from the McGill Pain Questionnaire (Osborn & Derbyshire, 2010), suggesting the vibrotactile stimulus may be most appropriate. Additionally, while the tactile stimulus in the present experiment was kept constant across participants, the intensity of the stimuli used in both experiments by Vandenbroucke and colleagues was individually determined using a thresholding process. The minimum intensity required to elicit a conscious sensation was selected. It may then be that the intensity of the present tactile stimulus was too high, such that any conscious vicarious sensation elicited by the images was not sufficiently intense to interfere with the tactile stimulus. Future work using this paradigm should pay close attention to the intensity and the subjective quality of tactile stimulus used.

Performance on the visuotactile interference task was not related to individual variability in empathy, but was related to hypervigilance to pain cues, in control participants but not Sensory-Localised pain responders. Fitzgibbon and colleagues (2010) propose that hypervigilance to pain may underlie conscious vicarious pain experience in individuals with prior history of traumatic pain, such as amputees. The results provide some support for this suggestion, since increased vigilance to pain was associated with greater interference from the visual pain stimulus. However, this effect was only found for control participants, suggesting that while vigilance to pain increased interference on the task, it is not sufficient to elicit conscious vicarious perception. Prior work has also identified an association between pain vigilance and performance on the visuotactile interference task in conscious vicarious pain responders, however in this case higher vigilance to pain was associated with reduced vicarious perception (Vandenbroucke et al., 2013). A similar negative trend was found in the current Sensory-Localised pain responder group. However, this negative correlation was not significant, and comparison of the correlations between pain vigilance and task performance in each responder group (Sensory-Localised responders and controls) found a marginal but not significant difference between the two. Collectively then, while the results of the current study and previous evidence from Vandenbroucke and colleagues point towards the opposite relation between hypervigilance and vicarious pain in conscious vicarious pain responders and in controls, this hypothesis does not receive strong statistical support in the current experiment. It should be noted that the present sample of Sensory-Localised pain responders was only ten, reducing the ability to detect significant differences between groups (see section 7.6 for further discussion of statistical power). The relation between pain vigilance and visuotactile stroop task interference therefore warrants further study on larger samples of Sensory-Localised pain responders to clarify this apparent distinction in the relation between pain vigilance and vicarious perception.

The lack of observable between-group differences on either the visuotactile interference task or the inhibitory control tasks in the present study could be attributable to the lack of an objective measure of conscious vicarious pain experiences. This could mean that individuals were misclassified in terms of their vicarious pain perception. Banissy and colleagues (2009) report an inflated self-report rate for MTS (around 10.8%) compared with the number of individuals that meet criteria for MTS on their objective behavioural measure (around 1.6%), indicating that self-report alone may not be sensitive enough to classify individuals. Vandenbroucke and colleagues (2013) do find between-group differences on a visuotactile interference task following a more basic self-report measure of vicarious pain, however, this group effect was driven by just two conscious vicarious pain responders, who made 66% of all mirror-pain errors, suggesting that individuals without conscious perception may have been categorised into this group. However, prior work using the online assessment of vicarious pain used here has been effective in categorising individuals into groups which show quantitative differences in brain structure and function (Grice-Jackson et al, 2017). Future work should aim to combine detailed self-report measures, such as that used in the present experiment, with sensitive behavioural measures, as has been effective in confirming experience of MTS (Banissy et al., 2009). This method should allow accurate categorisation of individuals and increase the sensitivity to detect between-group differences in broader cognitive abilities. Since previous studies on conscious vicarious pain have used different methods to assess vicarious pain perception, researchers should also focus on consistency in their approach to categorisation in future replication attempts.

In summary, the present study found no significant difference between two subtypes of vicarious pain responders and control participants, across two social and one domain-general measure of inhibitory control. There was also no significant difference observed in performance on a visuotactile interference task involving observed pain. Greater interference on this task, indicative of heightened vicarious pain perception, was associated with hypervigilance to pain. However, this relation was only present for control participants and not conscious vicarious pain responders, and no significant differences in trait hypervigilance to pain were found between responders and controls. The results therefore provide little support for the role of pain vigilance in eliciting conscious vicarious perception, proposed by Fitzgibbon and colleagues (2010).

The findings highlight the need for sensitive self-report and behavioural measures of conscious vicarious pain perception.

Chapter 5

Atypical Bodily Self-Awareness in Vicarious Pain Responders

Chapters 3 and 4 of this thesis have provided little additional support for the role of self-other control mechanisms in vicarious perception of touch and pain, using neuroscientific and behavioural approaches. The current chapter therefore aims to explore alternative self-other distinction processes proposed under Self-Other Theory, in particular those relevant to maintaining a coherent sense of the bodily self. Past research has indicated increased susceptibility to illusions of body ownership and agency in individuals who experience conscious vicarious touch and pain, indicating atypical bodily self-awareness. Trait differences in bodily self-awareness have also been linked to impairments in self-other distinction. However, little work has been done to assess trait differences in bodily self-awareness associated with conscious vicarious perception. The present experiment compared trait depersonalisation, associated with a detachment from the bodily self, interoception, associated with a focus on internal bodily signals, and alexithymia, associated with a focus on external stimuli and a difficulty identifying and labelling own emotions, in conscious vicarious pain responders and control participants. The results demonstrated increased self-reported depersonalisation as well as interoceptive sensibility in conscious vicarious pain responders than controls, but no significant differences in alexithymia. The results provide evidence for broader differences associated with self-other distinction in conscious vicarious pain, providing support for a Self-Other account.

5.1 Introduction

The passive observation of touch or pain experienced by another individual appears to elicit vicarious activity in somatosensory cortices similar to when these sensations are experienced first-hand (see Keysers et al., 2010; Lamm et al., 2011 for reviews). This evidence has led to the assertion that we are able to understand and empathise with the sensory experiences of others by representing them ourselves, and as such this vicarious activation is a requirement for effective social interaction. Vicarious perception can therefore provide a useful model for studying complex social processes such as empathy (Bird & Viding, 2014). Previous research has identified individual variability in vicarious responses to others' sensory experiences. For some individuals, a conscious percept is elicited on their own body purely from the observation of sensation experienced by another individual. Subtypes of this condition include mirror-touch synaesthesia (MTS) and conscious vicarious pain. A prevalence rate of 33-34% is reported for conscious vicarious pain in healthy individuals, although this figure is based on liberal cut-offs (Giummarra et al., 2015; Osborn & Derbyshire, 2010). Grice-Jackson and colleagues (2017) provide confirmation for this prevalence rate using a cluster analysis method, estimating the number of responders at around 31%. The authors also provide further sub-categories to vicarious pain perception, identifying a Sensory-Localised responder group who tended to use sensory descriptors to describe their experience, and report that it was localised to a particular body part (estimated prevalence 19%) and an Affective-Generalised group who used more affective descriptors and reported a more generalised bodily sensation (estimated prevalence 12%).

While strong support for individual variability in vicarious pain has been reported, so far the mechanisms that underlie it are not as well understood. Explanations for the experience have adopted some of those used to explain a related experience, mirror-touch synaesthesia. In particular, Threshold Theory (Blakemore et al., 2005; Ward & Banissy, 2015) proposes that conscious vicarious perception is caused by hyperactivity in somatosensory cortex, which boosts vicarious activation in response to observed sensation above a threshold for conscious perception. While there is evidence for somatosensory hyperactivity in vicarious pain responders (Grice-Jackson et al., 2017; Holle et al., 2013; Osborn & Derbyshire, 2010); further evidence suggests a broader pattern of underlying mechanisms, including those relevant to maintaining a coherent sense of the body. For instance, vicarious pain responders are more susceptible to illusions of body ownership, including the rubber-hand illusion (Derbyshire et al., Osborn & Brown, 2013) in which a sensation of ownership over the rubber hand is elicited without the synchronous tactile stimulation necessary for most participants. These results indicate an extended plasticity of bodily self-awareness associated with conscious vicarious pain. Self-Other Theory (see Ward & Banissy, 2105) provides an account for these broader differences observed in vicarious pain responders, proposing that impairments in the ability to effectively distinguish and switch between self- and other-relevant representations underlies conscious vicarious experience. In support of this, vicarious pain responders show reduced grey matter density in the right temporo-parietal junction (rTPJ) compared with controls (Grice-Jackson et al., 2017). This region has repeatedly been linked with the ability to represent and control representations of the self and other (e.g., Blanke & Arzy, 2005; Hogeveen et al., 2015; Ruby & Decety, 2004; Santiesteban et al., 2012; Tsakiris, Costantini & Haggard, 2008).

While the evidence discussed above points towards atypical representations of the bodily self in individuals who experience conscious vicarious pain, there has thus far been little investigation into the extent to which traits and abilities related to bodily self-awareness differ between these individuals and those who do not experience conscious vicarious sensations. The current study sought to address this gap in the literature by examining trait differences in three constructs previously linked to the sense of bodily self-awareness: depersonalisation, interoception and alexithymia. Below is explained why each of these factors may be of theoretical interest for bodily self-awareness and conscious vicarious pain.

Depersonalisation is a clinical trait characterised by a feeling of detachment from one's own bodily self (American Psychiatric Association, 2013). In a recent study by Adler and colleagues (2016) individuals with low self-reported depersonalisation showed differences to vicarious tactile perception compared to individuals with high self-reported depersonalisation. More specifically, low self-reported depersonalisation was linked with attenuation of the P200 somatosensory-evoked potential component in response to observed touch seen on the participant's own versus another person's face. This distinction between the self and other was not reflected in the P200 component of the high depersonalisation group, indicating that depersonalisation may be associated with reduced self-other distinction, which, as proposed by Ward and Banissy (2015) may play a key role in vicarious tactile perception. Individuals with higher levels of depersonalisation are also more susceptible to the rubber hand illusion (Kanayama et al., 2009), suggesting that this construct might be interesting to examine in conscious vicarious pain responders, given prior work highlighting altered body ownership in the rubber hand illusion for this group (Derbyshire et al., 2013).

Interoception refers to the awareness and perception of one’s own internal bodily states (Brewer et al., 2016). Recent work has proposed three distinct components to interoception, namely interoceptive accuracy (the ability to accurately detect internal sensations, e.g., heartbeats), interoceptive sensibility (self-perception of this trait, e.g., reporting a focus on internal sensations), and interoceptive awareness (the metacognitive awareness of one’s own interoceptive accuracy, e.g., knowing that you can accurately detect your own heartbeat) (Garfinkel, Seth, Barrett, Suzuki and Critchley, 2015). Complementing earlier work on depersonalisation, which is associated with a reduction in bodily self-awareness, individuals with lower interoceptive accuracy are also more susceptible to illusions of body ownership, including the rubber hand (Tsakiris et al., 2011) and enfacement illusions (Tajadura-Jiménez & Tsakiris, 2014), indicating that vicarious pain perception may also be associated with reduced interoception in addition to higher depersonalisation. Although, at present there does not appear to be a direct relation between interoception and depersonalisation: Sedeño and colleagues (2014) report reduced interoceptive accuracy for a single case study of an individual with depersonalisation disorder, while Michal and colleagues (2014) find comparable interoceptive accuracy and sensibility in a larger sample of participants with high depersonalisation. Of particular relevance to the present studies, individuals with higher interoceptive accuracy show greater difficulty in inhibiting the imitation of others’ actions when required (Ainley, Brass & Tsakiris, 2014). Prior work has indicated that imitation-inhibition is impaired in MTS (Santiesteban et al., 2015b), and it has been suggested that similar difficulties may be observed in conscious vicarious pain (Ward & Banissy, 2015; Derbyshire et al 2013). With this in mind, assessing interoception in conscious vicarious pain responders is of theoretical interest, and there is a need to identify the nature of any trait differences in interoception which may exist in conscious vicarious pain, since previous evidence leads to contradictory predictions (i.e., either improved or impaired interoceptive abilities in this group).

Alexithymia is a subclinical trait encompassing difficulties with identifying and describing emotions, as well as a tendency to reduce emotional experiences and focus attention externally (Bagby et al., 1994). Past research has shown that alexithymia is associated with impaired interoceptive accuracy (Herbert, Herbert & Pollatos, 2011; Shah, Hall, Catmur & Bird, 2016), but increased interoceptive sensibility (i.e,, a greater focus on internal sensations; Ernst et al., 2014). There is also evidence to suggest that individuals high in alexithymia show reduced imitation on imitation-inhibition tasks (Sowden et al., 2016) and reduced activity in neural networks linked to empathy for pain (Bird et al., 2010). This contrasts with suggestions that conscious vicarious perception may be linked to increased imitation (Santiesteban et al., 2015b) and that vicarious pain responders show greater activity in neural networks associated with empathy for pain (Osborn & Derbyshire, 2010; Grice-Jackson et al., 2017). Collectively, this provides rationale for studying alexithymia in conscious various pain responders, with a prediction of lower alexithymia and heightened interoception in individuals that experience conscious vicarious pain.

To summarise, prior literature suggests that there may be trait differences associated with conscious vicarious pain which have thus far not been studied. Here, the aim was to identify differences in self-reported traits relevant to bodily and emotional self-awareness in vicarious pain responders for the first time. This was carried out with a view to understanding the broader traits associated with conscious vicarious pain, and informing theoretical explanations of the condition. On the basis of previous research, heightened depersonalisation and reduced alexithymia were predicted in conscious vicarious pain responders compared with non-responders. Atypical interoceptive sensibility was also predicted in conscious vicarious pain responder groups, although a specific prediction was not made regarding the direction of this difference, based on prior research.

5.2. Materials and methods

5.2.1 Participants

183 healthy participants completed the online questionnaire. (131F, 52M; age 18-66 years, *M* = 28.1, *SD* = 10.9). Normal or corrected-to-normal vision was required to participate. Ethnicity was classified into Asian (*N* = 32), Black (*N* = 10), Caucasian (*N* = 131), or mixed/other ethnic background (*N* = 10) Participants were either recruited through Prolific.ac and paid £5, or recruited from undergraduate Psychology students at Goldsmiths in return for course credit. The project was approved by the Goldsmiths Psychology Department Ethics Committee.

5.2.2 Procedure

Testing was conducted online using Qualtrics online survey software. The online questionnaire was based on the procedure used by Grice-Jackson and colleagues (2017), and comprised four main sections. Participants were first given a description of mirror-sensory synaesthesia. Video screening procedures for the occurrence of conscious vicarious touch experience, and for vicarious pain experience, followed this. Lastly, self-report questionnaires of interoceptive sensibility, depersonalisation and alexithymia were completed. All participants completed the tasks in the order stated. The pain screening procedure was chosen to occur after the touch screening to avoid emotional or physical reactions to the mildly unpleasant stimuli affecting responses to later videos.

Vicarious touch video screening

To capture the subjective experience of vicarious touch, participants were required to view 15 short (3-5 second) videos of touch to a human body part or an object, delivered by the index finger of another human hand. Videos were displayed in pseudo-random order. Three videos contained touch to a female face, three to a male face, three to human hands shown from an egocentric perspective, and three from an allocentric perspective, and three videos showed touch to two cups placed adjacent to each other (selected stimuli are shown in Figure 5.1, and all videos can be viewed online using the following link: https://www.youtube.com/channel/UCL5K0hDB7fg9XdYPjAUw2qQ/videos?sort=dd&shelf_id=0&view=0). For each body part or object, touch was shown to the right cheek, hand or cup, the left, and both sides. Participants were asked to view each video in full screen and then respond ‘yes’ or ‘no’ to the question “Did you experience any bodily sensation of touch whilst observing this video”. Participants who responded ‘yes’ to the first question were given two further questions. The first asked them “Please rate the intensity of the touch sensation you experienced” on a 10-point scale from 1 (not at all intense) to 10 (highly intense). The second asked “Did you feel this pain in a specific location or was it a more general bodily feeling?” Participants could select either “Generalised”, “Localised but not in the same body part as the observed touch”, or “Localised to the same body part as observed touch”. If “localised to the same body part as the observed touch" was selected, the participant was also asked to indicate whether the touch sensation was on the left or the right side of their own body.

Vicarious pain video screening

The procedure for assessing vicarious pain experience matched the procedure for vicarious pain, with some minor differences. In this case 16 pseudo-randomised videos (10-13 seconds) were observed, each depicting painful events. Eight of these videos portrayed sports injuries (e.g., a cyclist falling from a bike) and eight showed injections to various parts of the body. Videos were obtained with permission from Grice-Jackson and colleagues (2017), and can be viewed using this link https://www.youtube.com/channel/UCT8goTgWGRsu14NjVaPCSGw/videos (example stimuli are shown in Figure 5.1). After each video participants were asked "Did you experience any bodily sensation of pain whilst observing the [e.g., arm injection]?" All participants were also asked to rate "How unpleasant did you find the experience of watching this video?" on a 10-point scale from 1 (not unpleasant) to 10 (highly unpleasant). If the response was 'yes', three further questions appeared. As for the touch videos, participants were asked to rate the intensity and the location (generalised vs. localised) of the vicarious pain they experienced. Finally, participants could select up to 23 descriptive words (10 affective, 10 sensory, 3 cognitive) from the McGill Pain Questionnaire (Melzack, 1975) to describe their experience. If the participant felt that none were appropriate there was also an option to add their own words.

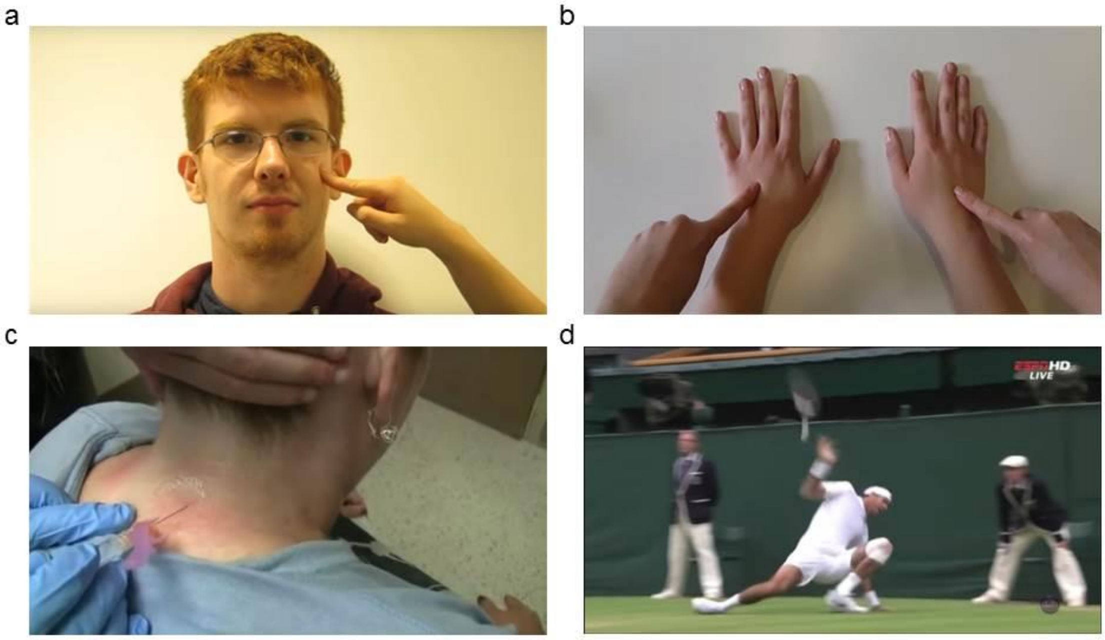

Figure 5.1: Stills from four of the video stimuli used in the online questionnaire. Shown are examples of touch to a) the face and b) the hands, and pain by c) injection and d) sports injury.

5.2.3 Self-Report Measures

Cambridge Depersonalisation Scale

The Cambridge Depersonalisation Scale (CDS; Sierra & Berrios, 2000) was administered to assess depersonalisation symptoms experienced in the past six months. Participants are presented with 29 statements, such as “Parts of my body feel as if they didn’t belong to me” and should rate the frequency of this experience on a five-point scale from “never” to “all the time”. Unless the participant responds “Never”, they then also rate of the typical duration of the experience, on a six-point scale from “few seconds” to “more than a week”. Possible scores range between 0 and 290, with higher scores indicating greater depersonalisation. Sierra and Berrios report good internal consistency (α = .89) and excellent split-half reliability (α = .92) for the scale as well as good validity, shown in a specific correlation (*r* = .80) with the depersonalisation subscale of the Dissociative Experiences Scale (Bernstein & Putnam, 1986). High internal consistency is also found in the current sample (α = .94).

Multidimensional Assessment of Interoceptive Awareness

Interoceptive sensibility was measured using the Multidimensional Assessment of Interoceptive Awareness (MAIA; Mehling et al., 2012). The scale contains 32 items, including "When I am tense I notice where the tension is located in my body". Participants respond to indicate the extent to which the statement applies to them, on a six-point scale from "never" to "always". Scores can be combined into eight subscales, including Noticing: "awareness of uncomfortable, comfortable and neutral body sensations"; Not-Distracting: "tendency to ignore or distract oneself from sensations of pain or discomfort" (reversed), Not Worrying: "emotional distress or worry with sensations of pain or discomfort" (reversed), Attention Regulation: "ability to sustain and control attention to body sensation", Emotional Awareness: "awareness of the connection between body sensations and emotional states", Self-Regulation: "ability to regulate psychological distress by attention to body sensations", Body Listening: "actively listens to the body for insight", and Trusting: "experiences one's body as safe and trustworthy". Scores on each subscale can range between 0 and 5, with a higher score indicating greater interoceptive awareness. Mehling and colleagues demonstrate construct validity for the scale and acceptable to good internal consistency on five of the eight subscales (α = .79 - .87). However, they note that for the 'Noticing', 'Not-Distracting', and 'Not-Worrying' subscales internal consistency was lower (α = .66 -

.69) Similar results are reported in the current sample, with good internal consistency on five subscales (α = .83 - .86), and questionable internal consistency on the 'Not-Distracting' subscale (α = .63), although for the 'Noticing' subscale, internal consistency in the present sample was acceptable (α = .71). Internal consistency for the 'Not-worrying' subscale was poor (α = .50), and so the present results for this subscale should be interpreted with caution.

Toronto Alexithymia Scale

Alexithymia was assessed with the twenty item Toronto Alexithymia Scale (TAS-20; Bagby et al., 1994). The questionnaire requires participants to indicate the extent which they agree with each of 20 statements on a five-point scale from "strongly disagree" to "strongly agree." Three subscales represent Difficulty Describing Feelings, e.g, "It is difficult for me to find the right words for my feelings", Difficulty Identifying Feelings, e.g., "I am often confused about what emotion I am feeling", and Externally-Oriented Thinking, e.g., "Looking for hidden meanings in movies or plays distracts from their enjoyment". Total scores range from 20 to 80, with a higher score representing greater alexithymia. Bagby and colleagues confirm the validity of the three-factor structure and report acceptable internal consistency for the Difficulty Describing Feelings (α = .75) and Difficulty Identifying Feelings (α = .78) subscales, although reliability for Externally-Oriented Thinking' was slightly lower (α = .66). The same pattern of results is found in the present sample (α = .60 - .82).

5.3 Results

5.3.1 Individual Variability in Vicarious Pain

Participants were assigned to pain responder groups according to their responses on the vicarious pain screening questionnaire, using a two-step cluster analysis, adapted from the procedure used by Grice-Jackson and colleagues (2017; see also Zhang et al., 1996). This involves an initial clustering of participants to produce cluster centroids, and then categorises participants into groups based on these centroids. Since this method produces optimal results using large data sets, data from the 183 participants was combined with previous responses from Grice-Jackson and colleagues.

The first step comprised a hierarchical cluster analysis using Ward's method (Ward, 1963) to identify the number of clusters and cluster centroids. This was based on three input variables: 1) Mean pain intensity (the average intensity rating across all 16 videos), 2) Sensory-Affective (the total number of sensory descriptors used to describe the pain – the total number affective descriptors, and 3) Local-General (the total number of localised pain responses – the total number of generalised responses). This step confirmed a three-factor solution, in line with prior work (Grice-Jackson et al., 2017). The second step involved a non-hierarchical k-means cluster analysis, which assigned participants into one of the three groups, based on the cluster centroids from the first step.

The analysis resulted in a non-responder group (*N* = 153; 107F, 46M; age *M* = 28.6, *SD* = 11.1), who did not tend to report conscious vicarious experiences, a Sensory-Localised responder group (*N* = 15; 13F, 2M; age *M* = 22.5, *SD* = 7.0) who tended to report conscious vicarious experiences localised to the same body part as the observed stimulus, and use sensory descriptors, and an Affective-Generalised responder group (*N* = 15; 11F, 4M; age *M* = 29.0, *SD* = 11.8), who tended to report conscious vicarious experiences more generalised over the whole body, and to use more affective than sensory descriptors.

Since the actors receiving pain in the video stimuli were all Caucasian, vicarious responses were compared according to participants' ethnicity. A chi-square analysis found no significant relation between ethnic group and pain responder cluster (χ^2 [6] = 6.70, p =.349). Vicarious responses to the stimuli do not therefore appear to have been influenced by whether the subject was of the participant's own or another ethnic background. In addition, responder groups did not significantly differ in age (F [2,180] = 2.33, p = .111, η_p^2 =.02) or gender (χ^2 [2] = 2.06, p =.356).

The relatively low number of conscious vicarious pain responders in the present sample (*N* = 15 in both Sensory-Localised and Affective-Generalised sub-types) precluded a systematic analysis of within-group differences in bodily self-awareness related to vicarious responses to touch. For this reason, individuals were classified only in terms of their vicarious pain responses, rather than creating further subgroups of, for instance, those who experience conscious vicarious pain and touch, and those who experience only conscious vicarious pain.

5.3.2 Trait Measures

Correlations for all participants between trait measures are reported in Table 5.1. Higher depersonalisation was associated with higher scores on the 'Describing Feelings' and 'Identifying Feelings' subscales of the TAS. A more mixed pattern of results was observed regarding the relation between depersonalisation and interoceptive sensibility. While a negative correlation was found between for the Trusting subscale, moderate positive correlations were found for the Noticing, Not-Worrying, and Emotional Awareness subscales. Between alexithymia and interoception, negative correlations were observed for the majority of subscales, indicating a general association between lower interoceptive sensibility and higher alexithymia (in line with previous work).

No significant associations were found with age for any of the self-report trait measures (*p*s > .06). However, gender differences were observed in the data. Correcting for multiple comparisons, a significant effect of gender was found on the Trusting subscale of the MAIA (t [181] = 3.82, $p < .001$, Cohen's $d = 0.61$), where male participants scored higher than females, indicating greater interoceptive sensibility.

Table 5.1: Pearson's coefficients for correlations between the self-report measures.

Self-Report Measure	1	2	3	4	5	6	7	8	9	10	11	12
1.CDS	-											
TAS												
2. Describing Feelings	$.43^{***}$	-										
3. Identifying Feelings	$.54^{***}$	$.65^{***}$	-									
4. Externally Oriented Thinking	-.05	$.24^{**}$	.04	-								
MAIA												
5. Noticing	$.18^{*}$	- .04	.13	$- .20^{**}$	-							
6. Not-Distracting	-.08	.07	- .02	- .01	.04	-						
7. Not-Worrying	$.20^{**}$	$.15^{*}$	.11	.10	.06	.01	-					
8. Attention Regulation	.07	$- .15^{*}$	$- .15^{*}$	- .08	$.49^{***}$	.05	.10	-				
9. Emotional Awareness	$.28^{**}$	- .04	$.25^{***}$	$- .22^{**}$	$.55^{***}$	.12	.00	$.38^{***}$	-			
10. Self-Regulation	.03	$- .16^{*}$	- .09	- .13	$.39^{***}$	.06	.02	$.59^{***}$	$.45^{***}$	-		
11. Body Listening	.12	$- .16^{*}$	.02	$- .23^{**}$	$.46^{***}$	.11	.01	$.47^{***}$	$.59^{***}$	$.52^{***}$	-	
12. Trusting	$-.17^{*}$	- .14	$- .29^{***}$	- .02	$.22^{**}$	- .01	- .05	$.49^{***}$	.18*	$.49^{***}$	$.38^{***}$	-

*$p<.05$, ** $p<.01$, ***$p<.001$

5.3.3 Trait Differences associated with Vicarious Pain

Depersonalisation

The distribution of depersonalisation scores showed a significant positive skew (z = 11.69). This pattern is typical for the CDS when administered in the general population rather than clinical groups (Sierra & Berrios, 2000). Due to the distribution of the data a Kruskal-Wallis H test was used to compare CDS scores in each of the pain responder groups (Sensory-Localised vs. Affective-Generalised vs. Control). In this case, the main effect of group was significant (H [2] = 6.28, p = .043). Pairwise comparisons, using a Bonferroni corrected alpha level of $p < .017$, show that this reflected significantly higher depersonalisation in Sensory-Localised group compared with controls (U = 35.92, z = 2.51, p = .012, r = .18) (see Figure 5.2). Depersonalisation in this group was also higher than the Affective-Generalised group, although this comparison did not reach significance (U = 33.40, z = 1.73, p = .084, r = .13). There was also no significant difference between the Affective-Generalised group and controls (U = 2.52, z = 0.18, p = .861, r = .01).

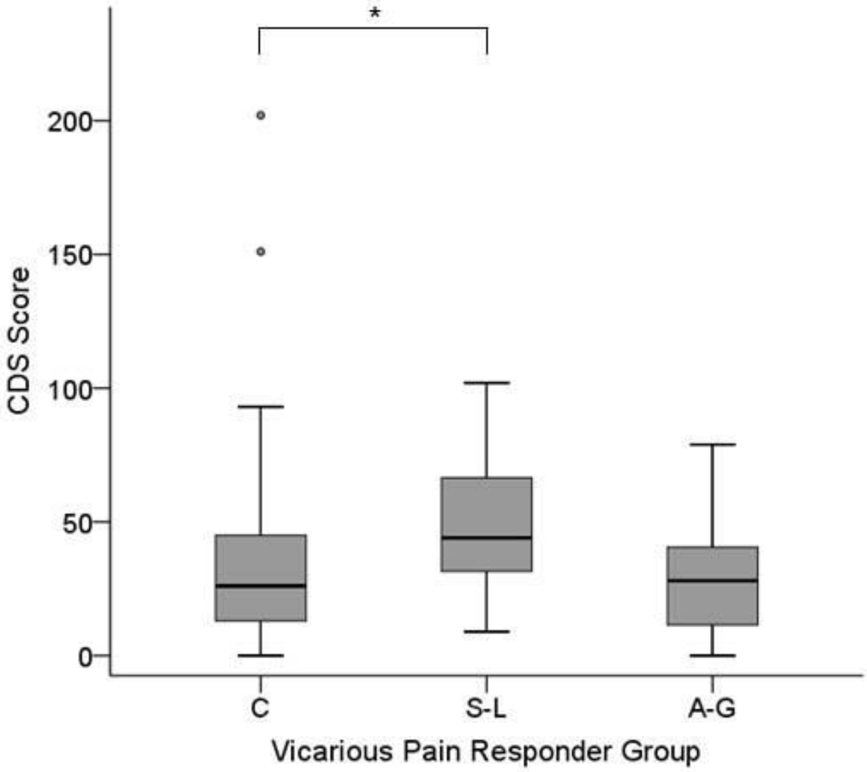

Figure 5.2: Self-reported depersonalisation in each of the pain responder groups. Higher CDS total scores were found for Sensory-Localised pain responders than for controls (p < .05). C, Control; S-L, Sensory-Localised; A-G, Affective-Generalised. Error bars represent +/- 1 S.E.M.*

<u>*Interoceptive Sensibility*</u>

A multivariate analysis of variance (MANOVA) was carried out to explore differences in interoceptive sensibility between the pain responder groups. Each of the eight subscales of the MAIA were entered as dependent variables in the analysis, with pain responder group (Sensory-Localised vs. Affective-Generalised vs. Control) as the independent variable. While there was not a significant effect of pain responder group on MAIA scores overall (F [16,348] = 1.02, p = .432, η_p^2 =.05), there was a specific effect on the ‘Noticing’ subscale (*F* [2,180] = 4.10, *p* = .018, η_p^2 =.04), which refers to the “awareness of uncomfortable, comfortable, and neutral body sensations” (Mehling et al., 2012, p.10). Post-hoc pairwise comparisons, using Games-Howell’s correction for unequal variances, demonstrate that the Sensory-Localised responder group obtained significantly higher scores on this subscale than controls (*t* [30] = 4.52, *p* < .001, Cohen’s *d* = 0.88). Responses in the Affective-Generalised group did not significantly differ from controls (*t* [169] = 1.68, *p* = .096, Cohen’s *d* = 0.46) or the Sensory-Localised group (*t* [19] = 0.64, *p* = .528, Cohen’s *d* = 0.25) (see Figure 5.3). Effects for all other subscales were not significant (*p*s > .15). Mean scores are shown in Figure 5.3.

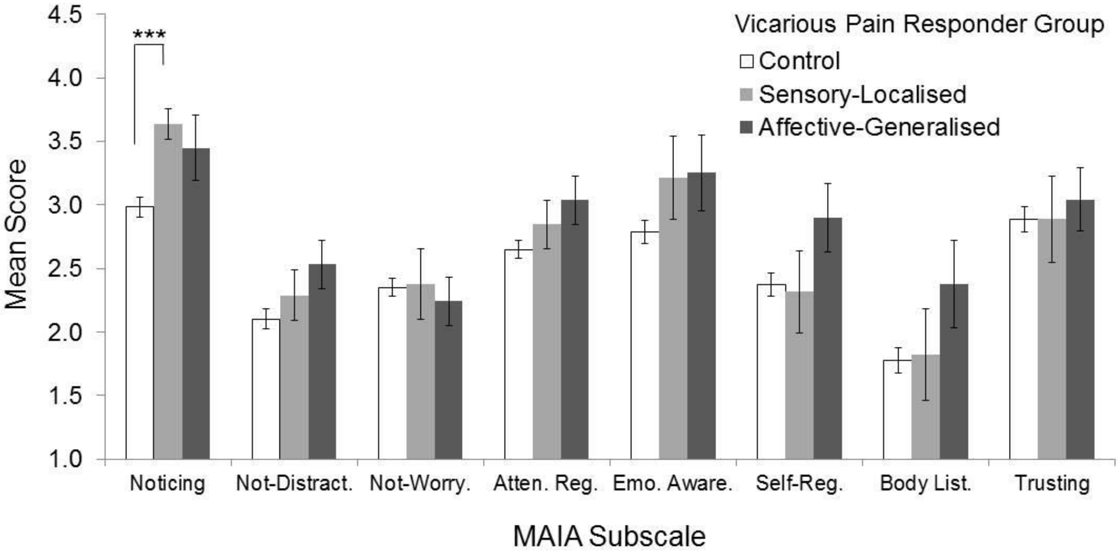

*Figure 5.3: Scores on each subscale of the MAIA in each pain responder group. Higher interoceptive sensibility was found on the ‘noticing’ subscale for Sensory-Localised pain responders compared with controls (*** p < .001). Error bars represent +/- 1 S.E.M.*

Alexithymia

A MANOVA was also used to compare TAS scores in each of the pain responder groups. The effect of group on TAS scores overall was not significant (*F* [6,358] = 1.06, p = .384, η_p^2 =.02) and there were no significant effects on the Describing Feelings (*F* [2,180] = 0.81, p = .445, η_p^2 =.01), Identifying Feelings (*F* [2,180] = 1.66, p = .192, η_p^2 =.02), or Externally-Oriented Thinking (*F* [2,180] = 1.36, p = .258, η_p^2 =.01) subscales.

5.4 Discussion

The present study provides evidence of heightened depersonalisation and interoceptive sensibility associated with Sensory-Localised vicarious pain. The findings support hypotheses that vicarious pain perception is associated with atypical bodily self-awareness.

The initial prediction that vicarious perception would be associated with increased depersonalisation was supported. Sensory-Localised pain responders reported greater experience of depersonalisation symptoms than non-responders. This result is in line with prior research linking both depersonalisation (Adler et al., 2016; Kanayama et al., 2009) and conscious vicarious pain perception (Derbyshire et al., 2013; Grice-Jackson et al., 2017) with impairments in self-other distinction and a tendency towards self-other merging of body-relevant information. The results also demonstrate increased interoceptive sensibility in Sensory-Localised pain responders compared with non-responders. This difference was present on the ‘noticing’ subscale of the MAIA (Mehling et al., 2012), which refers to the “awareness of uncomfortable, comfortable and neutral body sensations”, indicating a greater tendency for vicarious pain responders to focus attention on internal bodily states. The result complements previous work reporting an association between interoceptive accuracy and difficulty inhibiting imitation, in the motor domain (Ainley et al., 2014). However, it is important to note the distinction between interoceptive sensibility and accuracy. High interoceptive sensibility, referring to the tendency to focus on internal bodily states, does not necessarily imply accuracy, the ability to correctly identify these states (Garfinkel et al., 2015). Further research is therefore required to establish whether observed differences associated with conscious vicarious pain extend to other dimensions of interoception - for example using a heartbeat detection task (e.g., Schandry, 1981) to measure interoceptive accuracy - or are limited to interoceptive sensibility.

With this caveat in mind, the collective evidence of altered bodily self-awareness in conscious vicarious pain responders adds to growing evidence highlighting that individuals who experience conscious vicarious sensations show broader differences that extend beyond simple mirroring of sensorimotor consequences. As noted, Self-Other Theory (see Ward & Banissy, 2015) provides a potential framework from which to understand these broader differences in self-awareness experienced by vicarious pain responders. While the present results provide novel insight into the broader phenomenal experience of conscious vicarious pain, conclusions cannot be drawn regarding causal relationships from this data alone. In the case of depersonalisation, a sense of detachment from the bodily self may cause the individual to incorporate other-relevant information into the self-concept, leading to the conscious percept of pain when observing another person in pain. However, it is also conceivable that the shared experience of vicarious pain could lead to a self-other blurring (similar to that induced by synchronous touch in the rubber hand and enfacement illusions –

Botvinick & Cohen, 1998; Tsakiris, 2008), and that this could increase feelings of detachment from the self. Similarly, a greater focus on internal bodily states (interoceptive sensibility) could lead to increased detection of physical sensations induced by observing pain, leading to a conscious vicarious percept. Alternatively, individuals that experience vicarious pain may be more likely to attend to bodily states, due to increased sensation from both self- and other-focused stimulation. Future work should aim to establish the causal mechanisms underlying the associations between depersonalisation, interoceptive sensibility and vicarious pain are seen here.

It will also be interesting for future work to assess the extent to which the pattern of data that is observed in individuals who experience conscious vicarious pain is also observed in other groups linked to conscious vicarious perception. One example would be mirror-touch synaesthesia. While self-reported responses to vicarious touch were examined in the present questionnaire, there was not a large enough sample of individuals reporting conscious vicarious tactile responses to make systematic comparisons to the current conscious vicarious pain groups. Future work should seek to examine similarities and differences in the traits identified here between individuals who experience only conscious vicarious pain, individuals who experience only conscious vicarious touch, and individuals who experience both types of conscious vicarious experience.

Despite trait differences in bodily self-awareness in Sensory-Localised pain responders compared with controls, no such differences were found for Affective-Generalised responders, across both interoceptive sensibility and depersonalisation. This result is perhaps surprising, considering both subtypes of vicarious pain response are associated with increased grey matter in left AI compared with controls (Grice-Jackson et al., 2017), a region previously linked with bodily self-awareness and interoception (e.g., Craig, 2003, 2009, Critchley, 2005). In the current study, Affective-Generalised responders also showed a trend towards increased depersonalisation and interoceptive sensibility, with no significant differences found for these measures compared with either non-responders or Sensory-Localised responders. In this regard, Affective-Generalised responders appear to lie somewhere between Sensory-Localised responders and non-responders in terms of their bodily self-awareness and capacity for self-other distinction. However, the precise differences underlying these two forms of conscious vicarious pain responses remains a key question for future research.

Contrary to predictions, no significant differences in alexithymia were found between vicarious pain responder groups. It was hypothesised that individuals reporting vicarious pain may show fewer alexithymic traits than controls, since alexithymia is associated with reduced empathy for pain, driven by reduced activity in AI when observing pain (Bird et al., 2010). In fact, eight out of thirty conscious vicarious pain responders met the clinical cut-off for alexithymia in the current sample (TAS Total Score ≥ 61; Taylor, Bagby & Parker, 1999), slightly above the 17.9% prevalence rate reported in a British undergraduate sample (Mason, Tyson, Jones & Potts, 2005). The results suggest that although reduced vicarious pain response has previously been linked to high trait alexithymia (Bird et al., 2010), individuals who experience heightened or conscious vicarious perception may not necessarily score low on the TAS. It should also be noted that although Bird and colleagues report reduced vicarious activity in AI in individuals with high trait alexithymia, another study has reported the opposite pattern, where alexithymia is associated with greater activation in AI when explicitly viewing others' pain (Moriguchi et al., 2006). The relation between alexithymia and vicarious perception is therefore not so clear. Future research should study vicarious perception in individuals with both high and low levels of alexithymic traits to clarify any potential connection.

To summarise, the present results show increased depersonalisation and interceptive sensibility in Sensory-Localised conscious vicarious pain responders compared with Affective-Generalised or non-conscious responders. This has important implications for understanding the mechanisms contributing to conscious vicarious pain and vicarious perception in the wider population by indicating that processes related to maintaining the sense of bodily self, and relevant to self-other distinction, may be necessary to regulate vicarious perception of others' pain. The results highlight the need for future research into mechanisms of vicarious perception to take a broader focus, beyond sensorimotor mirroring.

Chapter 6

Effects of Stimulus and Perceiver Variability on Perception of Animacy

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Discriminating real human faces from artificial can be achieved quickly and accurately by face-processing networks, and may modulate vicarious perception of touch and pain. However, little is known about what stimulus qualities or inter-individual differences in the perceiver might influence whether a face is perceived as being alive. With this in mind, this chapter aimed to establish factors affecting the perception of animacy, with a view to informing future work regarding the role of animacy perception in modulating vicarious perception. Morphed stimuli differing in levels of animacy were created, and participants made judgements about whether the face appeared animate at different levels along the morph continuum. The faces varied in terms of emotional expression (happy vs. neutral) and gender. Male faces were judged to be animate at a lower threshold (i.e., closer to the inanimate end of the continuum) than female faces. Animacy was also perceived more readily in faces with happy expressions than neutral. These effects were observed across two separate studies involving different participants and different sets of stimuli. The influence of inter-individual variability on animacy perception was also examined. This revealed that an externally-oriented cognitive style, a component of alexithymia, was associated with lower thresholds for perceiving animacy, for animate faces morphed with dolls. MTS was not associated with systematic differences in the perception of animacy. The findings are discussed in relation to inter- and intra-individual variability in animacy perception and social interaction, and potential future directions for understanding individual variability in vicarious perception of touch and pain.

6.1 Introduction

Along with other mechanisms of self-other distinction, the accurate identification of animate (i.e., living beings capable of independent actions, thoughts, and emotions) human faces from inanimate objects is vital for social interaction and carries a key evolutionary advantage. Perception of animacy is thought to play a key role in action observation (Liepelt & Brass, 2010; Press, 2011) and mentalizing (Cross, Ramsey, Liepelt, Prinz & Hamilton, 2016), as well as vicarious tactile and pain perception. For instance, specific behavioural and neural responses have been reported for observed touch and pain to animate human bodies and to inanimate objects (Avenanti et al., 2005; Bolognini et al., 2013; Costantini, Galati, Romani & Aglioti, 2008). However, since this previous work has compared responses to animate body parts with objects rather than inanimate body parts, it remains unclear whether different response patterns are related to perception of animacy or to differences in visual form. One study by Deschrijver, Wiersema and Brass (2015) addresses this issue, showing SEP modulation while viewing the tapping finger of a wooden hand compared with an animate human hand. This indicates that vicarious somatosensory representations involve a process of distinction between other animate agents with the capacity for physical sensation and inanimate objects. However, in Chapter 3 of this thesis, the animacy of a hand being touched (i.e., human hand vs. dummy hand) did not modulate conscious vicarious perception. Further work is needed to identify the potential modulating effect of stimulus animacy in vicarious perception.

Previous experiments on the perception of animacy have used stimuli that are morphed between human and dolls’ faces, and report a threshold for perceiving life at 67% (Looser & Wheatley, 2010). Several studies also compare the ‘Point of Subjective

Equality' (PSE). This refers to the point on the morph continuum at which stimuli are judged to be 50% animate. A stimulus at this point on the continuum is therefore equally likely to be perceived as either animate or inanimate. This point consistently falls closer to the animate end of the stimulus continuum, and ranges between 56-68% (Balas, 2013; Balas & Horski, 2012; Hackel et al., 2014; Looser & Wheatley, 2010). Two stimulus factors that have been shown to influence the PSE are the social identity of the stimulus (e.g., Hackel et al., 2014; Swiderska, Krumhuber and Kappas, 2012) and stimulus gender (e.g., Balas, 2013). With regards to gender, Balas demonstrated that female faces are less likely to be perceived as animate than male faces; and animate faces less likely to be perceived as female than male. These results have led to suggestions that they reflect the dehumanisation or objectification of the faces of women (Balas, 2013), but this has not yet been empirically tested for animacy perception. A purely perceptual account of why the gender of a face may influence animacy judgments can also be made. Female faces are associated with narrower jawlines and lighter skin pigmentation compared with male faces (Brown & Perrett, 1993; Frost, 1988) and as such share a closer similarity with the doll faces typically used in animacy experiments than male faces do. This may result in female face stimuli being rated as less animate than male stimuli. These differing hypotheses are not mutually exclusive, and it is possible that both processes contribute to the reported gender differences in animacy perception. Experiment One in this chapter sought to investigate both the objectification and perceptual hypotheses of gender difference. Objectification is addressed by incorporating a measure of the extent to which participants objectify women's bodies. If objectification underlies the gender differences seen in animacy perception, then participants who demonstrate greater objectification of women should show higher animacy thresholds for female faces than those who score low on objectification of women.

In addition to gender and social identity a number of other factors may be important to animacy perception. For example, face perception research frequently uses achromatic stimuli to avoid confounding effects of differences in facial pigmentation. However, the majority of previous facial animacy perception studies (Balas, 2013; Hackel et al., 2014; Looser & Wheatley, 2010; Powers, Worsham, Freeman, Wheatley & Heatherton, 2014; Swiderska et al., 2012; Wheatley et al., 2011) have used chromatic stimuli. It is therefore unclear how important colour cues such as skin pigmentation are for detecting animacy in a face. This casts some doubt on the validity of comparing animacy thresholds for different stimulus faces (e.g., gender and racial groups) where colour cues have not been controlled. Where achromatic stimuli have been used (Balas & Koldewyn, 2013; Balas & Tonsager, 2014; Looser et al., 2013), there has been no direct comparison of achromatic and chromatic stimuli, and so it remains unclear whether the results can be applied to animacy judgements made with chromatic stimuli, either in previous studies or real-world perception.

Further, no published research on animacy perception has considered the effect of the emotional expression of the stimulus on animacy thresholds. The studies mentioned above have averaged together ratings for several different stimuli, regardless of the emotion expressed. Given the social significance of emotion expression (Keltner & Kring, 1998), it seems likely that this factor may influence animacy perception from faces. More specifically, if animacy reflects a capacity for experiencing emotion (Looser et al., 2013), it follows that a face expressing emotion would be more likely to be perceived as animate than a face with neutral expression. Two features of particular importance for animacy perception are the eyes and mouth (Looser and Wheatley, 2010), which lends further support to this hypothesis, since these features are also particularly relevant for conveying and perceiving emotion (Eisenbarth & Alpers, 2011; Emery, 2000; Langton, Watt & Bruce., 2000; Yuki, Maddux & Masuda, 2007). Collectively, this evidence indicates that emotional expression may influence animacy perception judgements.

In conjunction with properties of the stimulus, individual differences in the observer can influence animacy perception judgements. For example, the readiness with which facial animacy is perceived has recently been linked to the desire for social connection. In this study by Powers and colleagues (2014), scores on a Need to Belong Scale (NTBS; Leary, Kelly, Cottrell & Schreindorfer, 2013) correlated with animacy perception thresholds, such that individuals with a greater desire for social acceptance and belonging perceived animacy at a lower threshold. Further, participants subjected to an experimental manipulation to induce feelings of social disconnection also judged animacy to occur at a lower threshold than those who received a ‘socially connected’ induction. The authors proposed that these results reflect an adaptive strategy on the part of individuals who feel socially isolated, where perceiving animacy more readily increases the likelihood of valuable social interaction. This idea ties in with the suggestion that animacy is perceived more readily for in-group members than out-group due to a greater motivation for social interaction with the in-group (Hackel et al., 2014). If attributing animacy to an ambiguous stimulus indeed reflects a strategy to gain social interaction, then thresholds should also be lower for individuals with increased loneliness. Epley, Akalis, Waytz and Cacioppo (2008) report that self-reported loneliness correlates positively with mental state attribution in objects. In this study more lonely individuals were more likely to describe an inanimate object as having “a mind,” “intentions,” and “emotions.” Further, experimentally induced social disconnection led to greater attribution of anthropomorphic traits related to social connection to their pets. As yet the relation between loneliness and animacy perception has not been explored.

Previous results linking desire for social connection with increased animacy perception (Powers et al., 2014) suggest that other social factors may also influence how animacy is perceived. Individuals with high trait social anxiety appear to demonstrate attentional biases towards socially relevant stimuli. However, the direction of this bias is not yet clear, with increased attention observed in certain contexts, and avoidance in others (for reviews see Bogels & Mansell, 2004; Heinrichs & Hoffman, 2001). In either case socially anxious individuals could be predicted to demonstrate altered detection of animacy in human faces, compared with controls. In the case of increased attention, individuals with social anxiety may identify animacy more readily, leading to lower animacy thresholds; and in the case of avoidance individuals may be less likely to detect animacy in the face, leading to higher thresholds. Evidence from Epley and colleagues (2008) favours the former hypothesis, demonstrating that experimentally induced fear leads to greater likelihood of perceiving faces in ambiguous line drawings, compared with induced social disconnection. The hypothesised relation between social anxiety and animacy perception therefore provides an interesting research question, as well as a tool for understanding the cognitive biases associated with the condition.

A final trait factor that could be implicated in the detection of animacy is alexithymia. Alexithymia is a subclinical personality trait reflecting difficulties identifying and describing emotions, and the tendency to focus attention externally, while reducing emotional experiences (Bagby et al., 1994). It is reported in higher levels in males than females (Franz et al., 2008). Alexithymia is thought to involve deficits in processing emotion information (Lane et al., 1996) and in facial emotion recognition specifically, though studies of the latter have so far yielded mixed results (Cook, Brewer, Shah & Bird, 2013; Grynberg et al., 2012; Jongen et al., 2014; Pandey & Mandal, 2011; Parker, Taylor & Bagby, 1993). If, as hypothesised, emotion recognition is involved in detecting animacy, then it may follow that individuals high in alexithymia show differential facial animacy processing, compared with those who score low. Alexithymia has also been associated with impairments in empathy (Bird et al., 2010; Parker, Taylor & Bagby, 2001) and in 'mentalizing,' understanding the mental states of others (Moriguchi et al., 2006). Since animacy perception involves making a judgement about whether a stimulus has the capacity to possess mental states, this provides further support for the notion that alexithymia would be associated with reduced perceptions of animacy.

With the aforementioned studies in mind, the current online study compared the effect of stimulus qualities and individual differences of the perceiver on perception of animacy in ambiguous face stimuli. These stimuli were created by morphing images of human faces with visually matched doll faces that varied in colour (achromatic vs. chromatic), gender (male vs. female) and emotional expression (happy vs. neutral). The influence of individual differences in the perceiver relevant to social interaction on animacy judgements was also assessed. The relation between inter-individual variability in the following traits and facial animacy perception were examined: 'Need to Belong' (as per Powers et al., 2014), loneliness, social anxiety, alexithymia and objectification. Specifically, the following predictions were made:

1. Male faces would be judged to appear animate at a lower threshold than female faces.
2. Faces displaying emotion would be perceived to be animate at a lower threshold than faces with neutral expression.

3. Facial animacy judgements would rely on colour cues in the face, such as skin pigmentation.
4. Perception of animacy would be influenced by individual variability in traits including need to belong, loneliness, social anxiety, alexithymia and objectification.

6.2 Experiment One

The first experiment aimed to address each of the above hypotheses, using a novel stimulus set formed of doll-human morphs.

6.2.1 Materials and methods

Participants

The target sample size was 90. This target was calculated using an a priori power analysis for a within-subjects t-test with 0.8 power and 0.05 alpha level, based on the effect size previously obtained by Hackel and colleagues (2014; Cohen's *d* = 0.3) when comparing within-subjects animacy perception judgements of two stimulus types. 105 participants were then recruited online using the University College London Sona System, to account for some attrition from the online task. Volunteers were given a £7.50 Amazon voucher for completing the study. Data from one participant was excluded as the individual completed the study twice, leaving 104 participants (49 female, 55 male, age range 18-39 years, *M* = 26.6, *SD* = 6.7). Ethnicity was classified into Asian (*N* = 43), Black (*N* = 5), Caucasian (*N* = 48), or mixed/other ethnic background (N = 8). One participant chose not to complete the '*alive*' rating task, resulting in 103 participants for this section only. Some participants also missed or chose to omit items on the self-report scales, meaning that overall scores could not be calculated. This resulted in only 102 completing participants for the Need to Belong and Loneliness scales, and 103 participants for 'Difficulty Identifying Feelings' and total scores on the Toronto Alexithymia Scale. No further data was collected following analysis for these participants.

Stimuli

Face stimuli were created by morphing together images of human faces from the Radboud Faces Database (RaFD; Langner et al, 2010) with images of dolls, using FantaMorph software (Version 4; Abrosoft Co., Beijing, China). Dolls were selected to represent male and female faces, with happy and neutral expressions (Male, neutral N = 6; Male, happy N = 3; Female neutral N = 4; Female happy N = 6). All stimuli (both dolls and human faces) were Caucasian and human faces wore no cosmetics, piercings, facial hair or other distinguishing features. Stimuli were 596x736 pixels and displayed in an oval frame, removing external features (hair, ears, neck, etc.; see Figure 6.1a). All stimuli are available at http://dx.doi.org/10.5281/zenodo.204416.

Three rating tasks were completed. In each task still images were selected from each morph at 10% intervals, creating 11 still images representing different levels of animacy for each morph, and 209 stimuli in total per block. For animacy threshold judgements, stills were selected at 2% intervals, creating 50 images for each of the 19 morphs.

Procedure

The online experiment comprised five main sections, running as follows. All questionnaire measures and experimental tasks are listed here:

1. Self-report questionnaires (see details below for information on each)
    a. Demographic information
    b. Need to Belong Scale
    c. UCLA Loneliness Scale
    d. Toronto Alexithymia Scale
    e. Social Interaction Anxiety and Social Phobia Scales (short versions)
    f. Objectification Questionnaire (Male)
    g. Objectification Questionnaire (Female)
2. Rating Task 1: *Whether the face appears to be alive*
3. Animacy threshold judgements
4. Rating Task 2: *Whether the face is able to feel pain*
5. Rating Task 3: *Whether the face has a 'mind'*

All participants completed the tasks in the order above. The order of rating tasks followed that used by Looser and Wheatley (2010). As the authors suggest, ratings of whether the face had a mind were blocked last, to avoid this influencing other animacy judgements. The threshold task was given after the 'alive' rating task to avoid influencing these ratings, since a similar judgement is being made, but mid-way through the longer rating task blocks to prevent participant fatigue. All tasks followed the procedure used by Looser and Wheatley. On starting the experiment, participants were randomly assigned to either the chromatic (*N* = 53) or achromatic (*N* = 51) condition. In the chromatic condition stimuli were viewed in their original colour, and in the achromatic condition stimuli were seen at 0% saturation.

Animacy thresholds

To set thresholds for perceived animacy, participants were able to scroll through each morph at 2% intervals. They were asked to "scroll along until you find the point where you think the face changes from *having the appearance of being alive* to *not having the appearance of being alive*. Then select the first image on the *alive* side of that threshold" (see Figure 6.1b for an example). Faces were seen as fully inanimate when the scroll bar was on the left, and animate when on the right. Starting positions of the scrollbar were randomised so that they first appeared at each end point on 50% of trials.

Rating tasks

For each rating task participants were required to make a response on the given criteria for each of the 209 stimulus faces. Responses were given on a 7-point Likert scale, with 1 meaning definitely appears alive/feels pain/has a 'mind' and 7 meaning definitely doesn't appear alive/feel pain/have a 'mind'. Each face was shown on screen for 500 ms, after which participants responded by pressing 1-7 on their keyboard (see Figure 6.1c for an example trial).

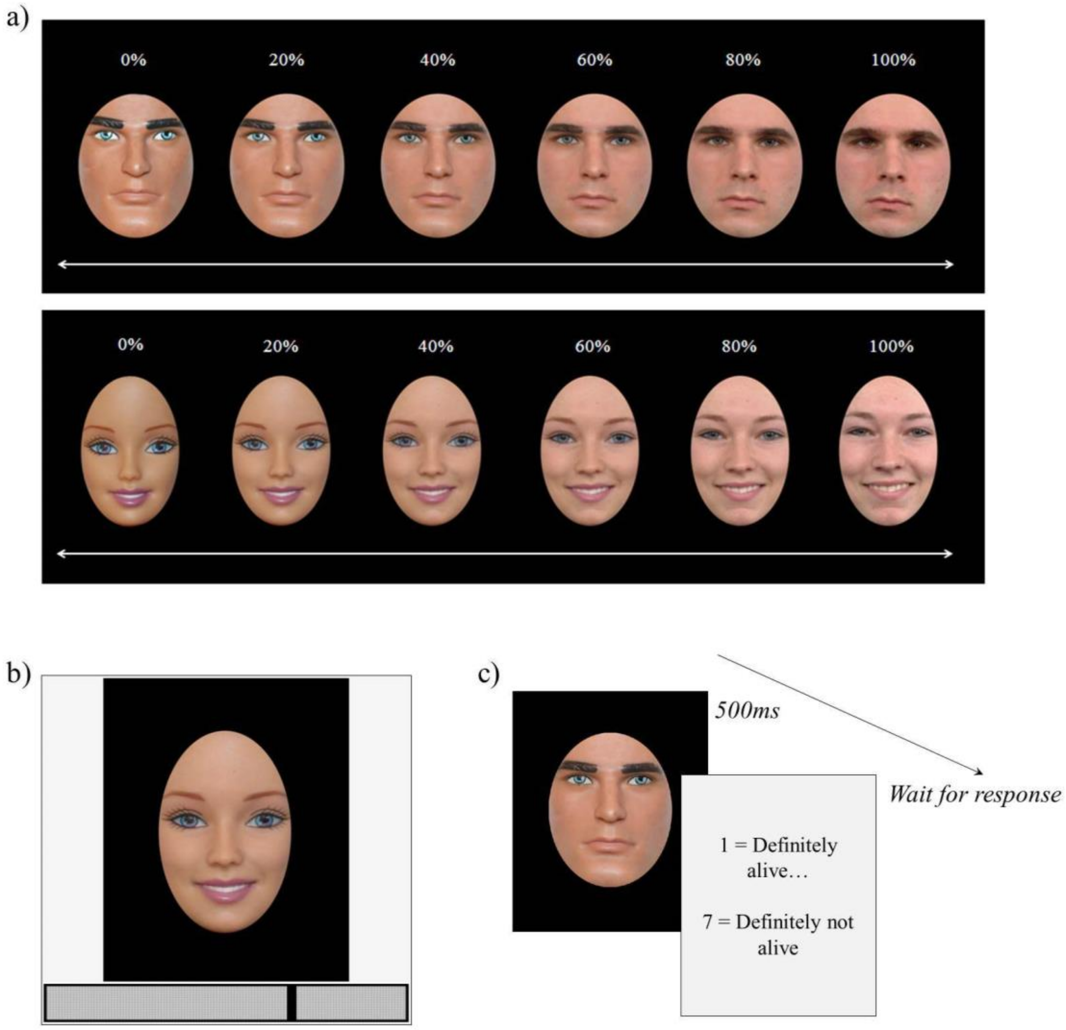

Figure 6.1: a) example male/neutral (upper row) and female/happy (lower row) morph stimuli used in Experiment One. Stimuli are shown here at 20% intervals along the morph continuum, and desaturated as seen in the achromatic condition. b) Example trial on the threshold task. Participants could use the slider to move up and down the morph continuum at 2% intervals, to select the threshold at which the face first appeared to be animate. c) Example trial on the rating task. Stimuli were displayed for 500 ms before a response was given using the 1-7 number keys.

Self-report measures

Need to Belong Scale

In an attempt to replicate the findings of Powers and colleagues (2014), the Need to Belong Scale (NTBS; Leary et al., 2013) was used as a measure of desire for social connections. Participants were required to rate the extent to which 10 statements, such as "I do not like being alone," were characteristic of them, using a 5-point scale ranging from 'Not At All' to 'Extremely.' Possible scores range from 10-50, with a higher score indicating greater desire for social connection. Leary and colleagues report good construct validity for the scale as well as good reliability ($\alpha = .81$). Internal consistency was also good in the current sample ($\alpha = .83$).

UCLA Loneliness Scale

To further assess the effect of social connection, the UCLA Loneliness Scale (Version 3; Russell, 1996) was used. Participants were shown 20 statements, such as "I lack companionship" and asked to indicate how often they felt the way being described, on a 4-point scale from 'Never' to 'Often.' Possible scores range from 20-80, with a higher score representing greater loneliness. The scale has been shown to have excellent reliability ($\alpha > .90$), as well as construct and convergent reliability. Internal consistency was also excellent in the current sample ($\alpha = .91$).

Social Interaction Anxiety and Social Phobia Scales

Short versions of the Social Interaction Anxiety and Social Phobia Scales (SIAS-6 & SPS-6; Peters, Sunderland, Andrews, Rapee & Mattick, 2012) were administered to account for other possible influences on motivation for social interaction. Each scale comprises six statements, and as for the NTBS, participants are required to rate the extent to which each is characteristic of them, using a 5-point scale ranging from “Not At All” to “Extremely”. Statements for the SIAS-6 included “I have difficulty making eye contact with others,” and for the SPS-6 included “When in an elevator I am tense if people look at me.” Each scale generates a score between 0 and 24, with a higher score indicating greater anxiety. Peters and colleagues demonstrate that the validity of these measures is not sacrificed in the shortened versions. In this sample, good internal consistency was found for both SIAS (α = .82) and SPS (α = .85).

Toronto Alexithymia Scale

The Toronto Alexithymia Scale (TAS; Bagby et al., 1994; see section 5.2) requires participants to indicate the extent which they agree with each of 20 statements, including “I often don’t know why I am angry,” on a 5-point scale from “Strongly Disagree” to “Strongly Agree.” Overall scores can range between 20 and 80, with a higher score indicating more alexithymic traits. Responses can be grouped into three subscales, measuring ‘Difficulty Describing Feelings’ (5 items), ‘Difficulty Identifying Feelings’ (7 items), and ‘Externally-Oriented Thinking’ (8 items), which refers to a tendency to focus attention outwards rather than inwardly and includes items such as “I prefer to just let things happen rather than to understand why they turned out that way”. The authors report good reliability (α = .81) as well as validity for the scale. The current sample also reports good internal consistency (α = .83).

Self-Objectification Questionnaire

Objectification of men and women was assessed separately with modified versions of the Self-Objectification Questionnaire (Noll & Fredrickson, 1998; Strelan & Hargreaves, 2005). In this task participants were required to rank 10 qualities in order of importance, first for men and then for women. These included 5 appearance-based, such as ‘physical attractiveness,’ and 5 competence-based traits, such as ‘physical coordination’. Ranks for competence items can be deducted from appearance items, to obtain an overall objectification score between -25 and 25, with a higher score representing increased objectification. Noll (1996, as cited in Noll & Fredrickson, 1998) reports that the Self-Objectification Questionnaire demonstrates acceptable construct validity.

6.2.2 Results

Self-report measures

Self-report questionnaires demonstrated a wide range of responses in all the measured constructs. Correlations between the measures are displayed in Table 6.1. Moderate to strong positive correlations were found between subscales of the TAS, between the social anxiety measures SIAS and SPS and between male and female objectification scores. In addition, a significant positive correlation was found between NTBS and male objectification, where those with a greater need to belong reported greater objectification of men. The same relation was not found for female objectification; however, this scale showed a significant positive correlation with the Externally-Oriented Thinking subscale of the TAS. Individuals who objectified women more also report a more externally-oriented cognitive style. Loneliness showed a significant positive correlation with both SIAS and SPS, with more lonely individuals reportedly more socially anxious. Loneliness, SIAS and SPS all correlated positively with total TAS scores, as well as the ‘Identifying’ and ‘Describing’ subscales. Increased loneliness and social anxiety appears to be associated with a difficulty labelling identifying and describing emotions. However, of the three, only SPS resulted in a significant positive correlation with EOT.

Table 6.1: Pearson's coefficients for correlations between the self-report measures.

Self-Report Measure	1	2	3	4	5	6	7	8	9	10
1.NTBS	-									
2.Loneliness	-.08	-								
3.SIAS	.07	$.51^{***}$	-							
4.SPS	.05	$.31^{**}$	$.62^{***}$	-						
Objectification										
5. Male	$.22^{*}$	-.02	.17	.13	-					
6.Female	.08	-.11	.04	.02	$.45^{***}$	-				
TAS										
7. Identifying Feelings	.05	$.40^{***}$	$.34^{***}$	$.31^{**}$	-.04	-.02	-			
8. Describing Feelings	-.01	$.43^{***}$	$.47^{***}$	$.38^{***}$	-.00	-.03	$.70^{***}$			
9. Externally-Oriented Thinking	-.12	.12	.10	$.21^{*}$	-.09	$.23^{*}$	$.23^{*}$	$.25^{*}$	-	
10.Overall Score	-.03	$.41^{***}$	$.39^{***}$	$.39^{***}$	-.05	.07	$.87^{***}$	$.83^{***}$	$.62^{***}$	-

* $p < .05$, ** $p < .01$, *** $p < .001$

Prior to examining the influence of trait differences on animacy perception, the influence of participant demographic (age and gender) on the trait measures were examined. Contrary to prior research (Franz et al., 2008), male and female participants showed no significant difference in overall alexithymia scores (t[101] = .30, p = .762, Cohen's d = 0.06). However, male participants received significantly higher scores on the EOT subscale (t[102] = 2.49, p = .014, Cohen's d = 0.49). No gender differences were found on the 'Identifying Feelings' (t[101] = -1.21, p = .230, Cohen's d = 0.24) or 'Describing Feelings' subscales (t[102] = -0.09, p = .929, Cohen's d = 0.02). Gender differences were found in NTBS (t[100] = -3.72, p < .001, Cohen's d = 0.74) and male objectification (t[102] = -3.01, p = .003, Cohen's d = 0.59) with female participants demonstrating higher scores than males in both cases. Female objectification did not significantly differ across male and female participants (t[102] = 1.25, p = .215, Cohen's d = 0.24). No further gender differences were found on the remaining measures (SIAS: t[102] = -1.26, p = .210, Cohen's d = 0.25; SPS: t[102] = -1.80, p = .076, Cohen's d = 0.35; Loneliness: t[100] = -0.26, p = .794, Cohen's d = 0.04). The effect of participant age on trait measures was significant only for female objectification, where objectification scores were negatively correlated with age, such that younger participants scored higher than older participants (r[102] = -.23, p = .018). Inspection of this effect in each gender group showed that this effect was driven by a highly significant correlation in the female participant group only (r[47] = -.39, p = .006), with a nonsignificant effect in the male group (r[53] = -.09, p = .521).

Threshold task

The point on the morph continuum (ranging from 0-100% human) at which the participant reported that the stimulus face first appeared to be animate on the threshold judgement task was combined for each of the 19 stimuli, to calculate a mean animacy threshold for each participant (*M* = 68.70, *SD* = 10.96)]. To analyse the effect of the gender and emotional expression of the stimulus on perceived animacy thresholds, mean thresholds were also calculated for each gender/emotion group, i.e., male/neutral (*M* = 68.29, *SD* = 12.82), male/happy (*M* = 63.63, *SD* = 13.96), female/neutral (*M* = 71.36, *SD* = 12.78), female/happy (*M* = 69.86, *SD* = 11.76).

Inter-individual variability in animacy perception

To examine how inter-individual variability on traits of interest influenced animacy perception, scores on each of the self-report questionnaires were correlated with mean animacy thresholds. Pearson's correlation coefficients are reported in Table 6.2. All correlations were nonsignificant, with the exception of the EOT subscale of the TAS, which showed a negative correlation with animacy thresholds (*r*[101] = -.29, *p* = .003). A more externally-oriented cognitive style was associated with a lower threshold for perceiving animacy, closer to the inanimate end of the continuum. To identify whether this relation was consistent for all subgroups of face stimulus, EOT was correlated with animacy thresholds in each group individually. Significant negative correlations were found for all stimulus subgroups (male/neutral: *r*[101] = -.26, *p* = .008; female/neutral: *r*[101] = -.24, *p* = .013; female/happy: *r*[101] = -.33, *p* = .001) except male/happy stimuli, although this correlation showed a negative trend (*r*[101] = -.13, *p* = .204).

Table 6.2: Pearson's correlations between self-report measures and animacy threshold judgements.

	Animacy Threshold	
Self-Report Measure	*df*	*r*
NTBS	99	-.04
Loneliness	99	.09
SIAS	101	.04
SPS	101	.02
Objectification		
Male	101	-.12
Female	101	.04
TAS		
Identifying Feelings	100	-.03
Describing Feelings	101	.06
Externally-Oriented Thinking	101	-.29**
Overall Score	100	-.15

** $p < .01$

A further analysis was conducted to assess the effect of participant demographics (gender and ethnicity) on animacy threshold judgements. Ethnicity was originally grouped into one of four broad categories: (Asian, Black, Caucasian, and mixed/other ethnic background. Since there were relatively few participants with black or mixed/other ethnic background, only Asian and Caucasian groups were compared in this analysis (N = 91, 20 Asian males, 23 Asian females, 27 Caucasian males, 21 Caucasian females). A 2 (gender) x 2 (ethnicity) x 2 (stimulus gender) mixed ANOVA was therefore used. Stimulus gender was added as a third factor to identify any interaction effects between the gender of the participant and stimulus. The analysis revealed a main effect of stimulus gender (*F*[1,87] = 25.82, $p < .001$, $\eta_p^2 = .23$), but no significant main effects or interactions for participant gender or ethnicity (*p*s > .05). The effect of stimulus gender was consistent across male and female participants. Participant gender and ethnicity variables were therefore removed from the remaining analyses.

Effects of stimulus variability on animacy perception

The effect of stimulus qualities on threshold judgements was analysed with a 2 (stimulus gender) x 2 (emotion type) x 2 (chromatic condition) mixed ANOVA, with stimulus gender and emotion as within-subjects factors, and chromatic condition as the between-subjects factor (*N* = 104). Main effects of both stimulus gender and emotion type were found, with thresholds for male faces closer to the inanimate end of the continuum than female faces (*F*[1,101] = 42.04, $p < .001$, $\eta_p^2 = .29$), and thresholds for happy faces closer to the inanimate end than neutral (*F*[1,101] = 13.88, $p < .001$, $\eta_p^2 = .12$). A further interaction effect was found between stimulus gender and emotion (*F*[1,101] = 5.00, $p = .027$, $\eta_p^2 = .05$). Post-hoc t-tests indicate that happy faces were judged to be alive at a significantly lower threshold than neutral faces, for male stimuli only (*t*[102] = 3.88, $p < .001$, Cohen's *d* = 0.38), and not for female stimuli (*t*[102] = 1.56, $p = .121$, Cohen's *d* = 0.16). A significant gender difference was observed in both neutral (*t*[102] = -3.11, $p = .002$, Cohen's *d* = 0.30) and happy stimuli (*t*[102] = -6.07, $p < .001$, Cohen's *d* = 0.62) (see Figure 6.2). All main effects and interactions involving chromatic condition were nonsignificant (*p*s > .05).

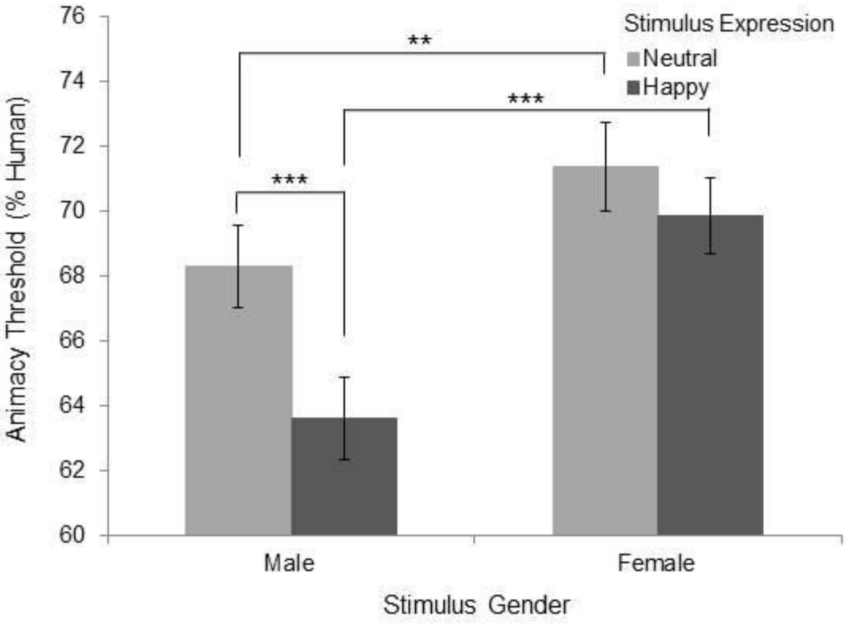

*Figure 6.2: Mean animacy thresholds for each stimulus subtype, according to emotional expression and gender. Male stimulus faces were perceived to be animate at a lower threshold than female faces, across both emotion groups. Animacy thresholds for male faces were also lower for stimuli with a happy than neutral expressions (*p<.05, ** p<.01, ***p<.001). Error bars represent +/- 1 S.E.M.*

<u>Rating tasks</u>

Participants' ratings for whether the stimulus face '*appears to be alive,' 'is able to feel pain'* and *'has a mind'* were first subject to a linear transformation to convert scores from a 1-7 Likert scale to a score between 0 and 1, with 1 representing most animacy, and 0 least animacy. Scores were then combined as for the threshold values, to give a mean rating for each participant, at each animacy level, in each gender/emotion group and overall.

Mean ratings across participants were fitted with a single-term Gaussian function in the curve fitting toolbox for Matlab, using the following equation:

$$f(x) = ae^{\left[-\left(\frac{x-b}{c}\right)^2\right]}$$

A good fit was achieved for all models ($\bar{R}^2 > .96$). This allowed the Point of Subjective Equality (PSE) to be calculated, reflecting the point on the morph continuum at which stimuli were judged to appear 50% animate.

Alive ratings

As found on the threshold judgement task, PSEs highlight that male faces were judged to appear alive at lower morph levels (i.e., when 'less human') than female faces, and happy faces at a lower level than neutral faces.

Figure 6.3a demonstrates that male stimuli were judged to appear more alive than female stimuli at the majority of morph levels, but this difference is not apparent when stimuli are 0% human or 80%-90% human. Holm-Bonferroni-corrected t-tests allowed for paired comparisons between ratings for male and female stimuli at each of the 11 animacy levels. This analysis confirmed that the gender difference in '*alive*' ratings was significant only for morph stimuli between 10 and 70% human (*p*s < .001), and also just reached significance at 100% human (t[102] = -2.63, p = .010, Cohen's d = -.22), although at this level female faces were judged to appear more animate than male faces.

Figure 6.3b illustrates a greater effect of emotion occurring at higher morph levels, i.e., when the stimuli were more human. This pattern is reflected in Holm-

Bonferroni-corrected t-tests, which demonstrate a significant emotion effects at 40% human and above (*p*s < .016).

Mind ratings

PSEs for the 'mind' task follow the same pattern as the 'alive' task, demonstrating that participants thought male stimuli and happy stimuli were perceived to 'have a mind' at a lower animacy level than for female or neutral stimuli.

As shown in Figure 6.3d, the gender difference in ratings to whether the face 'has a mind' follow the same pattern as 'alive' ratings, with male faces receiving higher ratings and differences decreasing as the stimulus becomes more human. Overall, the gender difference appears less pronounced than for the 'alive' ratings. Nevertheless, Holm-Bonferroni-corrected t-tests between ratings for male and female stimuli on the '*mind*' task report a significant gender difference between 0 and 70% human (*p*s < .002).

Similar to the gender difference data, emotion effects follow a similar pattern to ratings on the 'Alive' task, with larger differences observed for more human stimuli (Figure 6.3e). Again, the differences appear less pronounced on this task than for the 'Alive' task, but Holm-Bonferroni-corrected t-tests report significant differences at the same animacy levels as the previous task, at 40% and above (*p*s < .001).

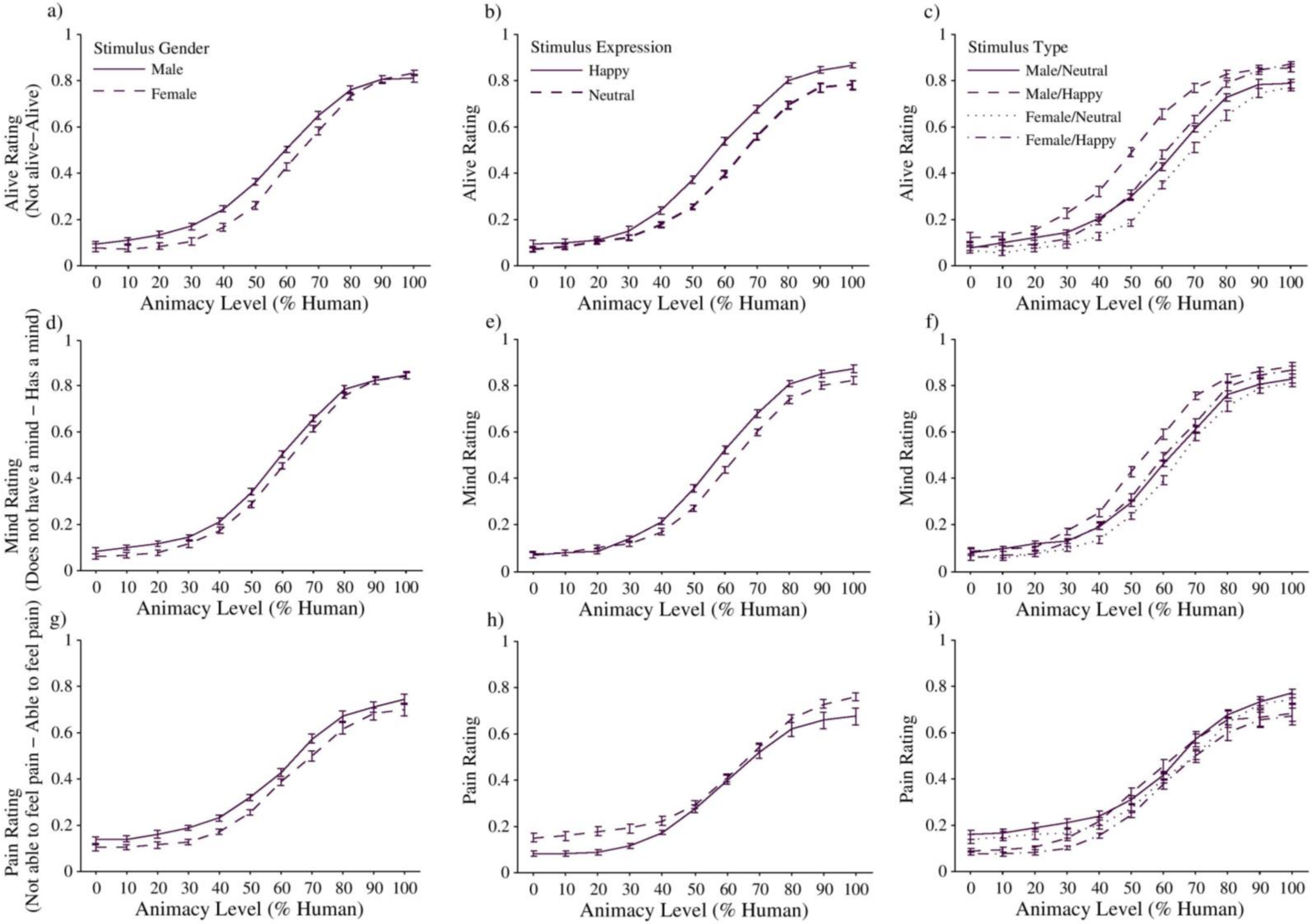
a)
Stimulus Gender
Male
Female
Alive Rating (Not alive–Alive)
b)
Stimulus Expression
Happy
Neutral
Alive Rating
c)
Stimulus Type
Male/Neutral
Male/Happy
Female/Neutral
Female/Happy
Alive Rating
d)
Mind Rating (Does not have a mind – Has a mind)
e)
Mind Rating
f)
Mind Rating
g)
Pain Rating (Not able to feel pain – Able to feel pain)
h)
Pain Rating
i)
Pain Rating
0
0.2
0.4
0.6
0.8
1
0 10 20 30 40 50 60 70 80 90 100
Animacy Level (% Human)

Figure 6.3 (previous page): Mean ratings from Experiment One of (a-c) "whether the face appears to be alive", (d-f) "whether the face has a mind" and (g-i) "whether the face is able to feel pain" at each level of animacy, from 0% human/100% doll to 0% doll/100% human. Y-axis shows ratings from 0 (completely inanimate, e.g., definitely not able to feel pain) to 1 (completely animate, e.g., definitely able to feel pain). Ratings are shown for a,d,g) each stimulus gender, b,e,h) each stimulus emotion c,f,i) each stimulus gender/emotion group. In both emotion groups, male stimuli were perceived to be more alive, more likely to have a mind, and more able to feel pain than female stimuli, from 0 to around 80% human. In both gender groups, happy stimuli were judged to appear more alive, and more likely to have a mind than neutral stimuli, from around 40% human. In contrast, neutral faces were perceived to be more able to feel pain than happy faces, at both extremes of the continuum. Error bars represent +/- 1 S.E.M.

Pain ratings

As for previous tasks, PSEs on the pain task indicate that male faces are judged to be animate at a lower level (less human) than female faces. However, in contrast with results from the threshold task and PSE analysis on the ‘Alive’ and ‘Mind’ tasks, in this task happy faces were judged ‘able to feel pain’ at a higher threshold than neutral faces.

Figure 6.3g highlights that in the case of the pain task, a more consistent gender effect appears, at all morph levels, rather than being more evident at mid-low morph levels. Holm-Bonferroni-corrected t-tests comparing the gender difference confirm a significant effect at every level (*p*s < .006).

The effect of emotional expression on stimulus ratings on the pain task also show a different pattern to the alive and mind tasks (Figure 6.3h). In this case a greater difference is observed at either end of the morph continuum than in the mid-range. This is confirmed by Holm-Bonferroni-corrected t-tests, which confirm a significant emotion effect at 0-30% human and 90-100% human only (*p*s < .007). The graph also illustrates that neutral faces were judged as being more ‘able to feel pain’ than happy faces.

6.2.3 Discussion

Experiment One demonstrates that the perception of animacy in stimuli morphed between human and doll faces is influenced by the gender and emotional expression of the stimulus face, but does not appear to rely on colour cues present in the stimulus. The present evidence also shows that Externally-Oriented Thinking is associated with reduced animacy perception thresholds.

The effect of stimulus gender on perceived animacy in this study supports the findings of Balas (2013). Balas proposed that the effect of stimulus gender may be driven by objectification of female faces. The present study provides the first attempt at testing this hypothesis. Scores on a scale of female objectification showed no significant correlation with animacy perception thresholds, and thus the current results do not support this account. In view of this, an alternative perceptual account of gender difference in animacy perception should also be considered. Human female faces share a closer similarity to the doll stimuli used in animacy experiments than male faces, due to narrower jawlines and lighter skin pigmentation than males (Brown & Perrett, 1993; Frost, 1988). This could be the factor that leads to increased animacy thresholds for female stimulus faces.

Male stimuli were also judged to appear more ‘alive’ and more likely to have a ‘mind’ than female stimuli at the majority of morph levels, but not when stimuli were 80% human or above. This is unlikely to represent a ceiling effect, since ratings do not reach 100% (consistent with Looser & Wheatley, 2010). The lack of gender difference at the more human end of the morph continuum can possibly be explained by differences in use of cosmetics. All human faces used to create the experimental stimuli wore no make-up. However, many of the female dolls used gave the appearance of wearing make-up, including lipstick and eyeliner, where male dolls did not. These cosmetics can increase the local contrast of the eyes and lips, and in this case could have affected female stimuli at the inanimate end of the spectrum (Balas, 2013). This could lead to female morphed stimuli appearing less realistic than male stimuli at the same animacy level. It is interesting to note that in Balas’ (2013) study following the same procedure, human faces were also photographed without removing cosmetics (i.e., cosmetics were present for both doll and human faces), this may explain why a consistent gender difference in animacy judgements was found across the morph continuum.

Experiment Two aimed to test this alternative perceptual explanation of gender differences in animacy perception, by creating a set of stimuli which overcame these potential biases.

6.3 Experiment Two

In Experiment Two the threshold and rating tasks from the first experiment were repeated using morphed stimuli that combined animate human faces with computer generated inanimate faces. This removed the issue of the exaggeration of feminine facial features and make-up cues present in doll faces, and so allowed an assessment of whether the observed gender differences in Experiment One were influenced by these perceptual factors.

6.3.1 Materials and methods

Participants

Target sample size for the second experiment was 103, to match those collected in Experiment One. 100 participants who did not take part in Experiment One (30 female, 70 male, age range 18-61 years, *M* = 29.2, *SD* = 9.2) were recruited online from the website Prolific.ac. Ethnicity was classified into Asian (*N* = 30), Black (*N* = 4), Caucasian (*N* = 60), or mixed/other ethnic background (*N* = 6). All participants were paid £5 for taking part.

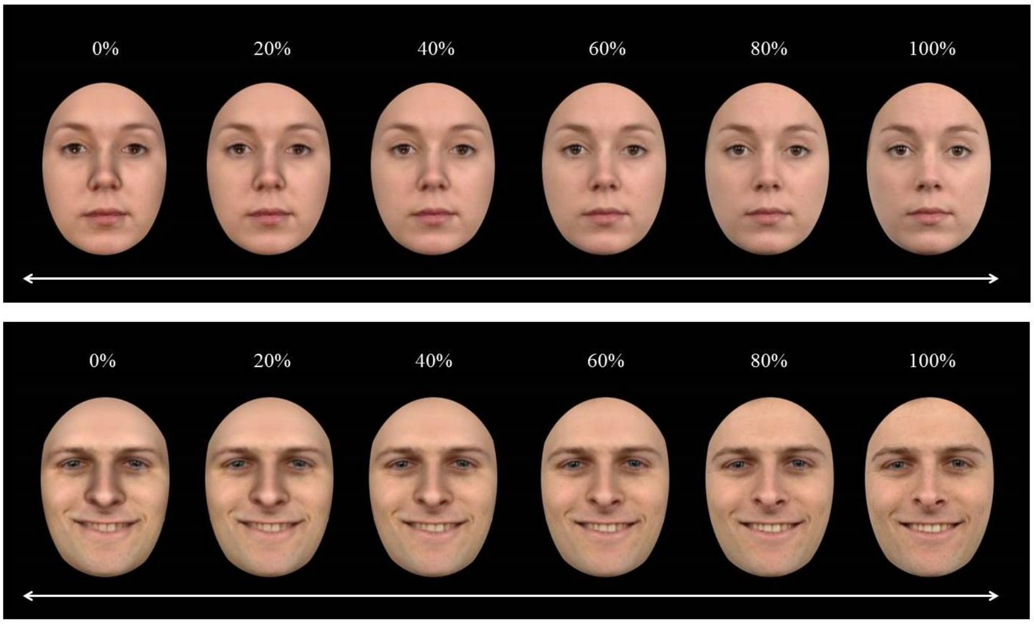

Figure 6.4: Example stimuli as used in Experiment Two. The upper row depicts female/neutral stimuli and the lower row male/happy. Stimuli are shown here at 20% intervals along the morph continuum, and desaturated as seen in the achromatic condition.

<u>Stimuli</u>

For Experiment Two, a new set of stimuli were created using FaceGen Modeller (Singular Inversions, Toronto, Canada). FaceGen was used to create computer generated inanimate versions of human faces from the RaFD (Langner et al, 2010). These inanimate versions were then morphed with the originals to make a set of stimuli highly controlled to match features across the morph continuum (see Figure 6.4). As in Experiment One, stimuli were selected to represent four categories: male, neutral expression (*N* = 4), male happy expression (*N*=4), female neutral expression (*N* = 4), female happy expression (*N* = 4). Faces were all Caucasian and without make up or other distinguishing features, and were displayed in a frame removing external features. All stimuli were 400x400 pixels. All stimuli are available at http://dx.doi.org/10.5281/zenodo.204453.

Procedure

Participants completed all tasks as described in Experiment One, in the same order, with two exceptions. Since in the previous experiment the Externally-Oriented Thinking subscale of the TAS (Bagby et al., 1994) was the only trait variable found to be correlated with animacy thresholds, only this questionnaire measure was retained for the second experiment. Additionally, as colour condition (chromatic vs. achromatic) did not significantly influence animacy judgements in the previous experiment, stimuli were displayed in colour for all participants.

6.3.2 Results

Self-report measures

Internal consistency on the TAS (Bagby et al., 1994) was again shown to be good in this second sample of participants (α = .83). Overall scores on the TAS (*M* = 51.09, *SD* = 11.97), and scores on the describing feelings (*M* = 14.29, *SD* = 4.35), identifying feelings (*M* = 17.24, *SD* = 6.23), and Externally-Oriented Thinking (*M* = 19.56, *SD* = 4.45) subscales were calculated for each participant. Firstly, individual differences in TAS scores were analysed in terms of age and gender. Pearson’s correlation analyses showed no significant relation between age and overall TAS scores

($r[98] = -.14$, $p = .165$), or with Externally-Oriented Thinking ($r[98] = .07$, $p = .498$), but scores on the describing feelings subscale did reach significance ($r[98] = -.20$, $p = .043$), and for identifying feelings was marginally significant ($r[98] = -.18$, $p = .079$). In both cases TAS scores decreased with age. Gender differences in TAS scores were compared with independent t-tests. This revealed no significant gender differences in overall scores ($t[99] = 1.05$, $p = .298$, Cohen's $d = 0.22$) or any of the subscales (Identifying Feelings: $t[99] = 0.92$, $p = .363$, Cohen's $d = 0.19$; Describing Feelings: $t[99] = 1.45$, $p = .151$, Cohen's $d = 0.30$; Externally-Oriented Thinking: $t[99] = 0.12$, $p = .904$, Cohen's $d = 0.03$).

Threshold task

Mean threshold judgements were calculated for all stimuli ($M = 58.96$, $SD = 15.76$), and for each stimulus category, including male/neutral ($M = 58.46$, $SD = 17.67$), male/happy ($M = 59.06$, $SD = 21.71$), female/neutral ($M = 59.64$, $SD = 17.02$), and female/happy faces ($M = 58.67$, $SD = 21.57$).

Comparison of threshold judgements with those made in Experiment One showed heterogeneity of variances between the two groups, according to Levene's test ($F[1,201] = 8.78$, $p = .003$). With degrees of freedom adjusted for unequal variances, an independent samples t-test showed that thresholds for perceiving animacy were significantly lower (closer to the inanimate end of the continuum) in Experiment Two than in Experiment One ($t[176] = 5.10$, $p < .001$, Cohen's $d = .73$). This indicates that the FaceGen faces used to create the second set of stimuli appeared more animate than the previous doll faces, shifting thresholds closer to the centre of the morph.

Inter-individual variability in animacy perception

Scores on the TAS (Bagby et al., 1994) were correlated with mean animacy thresholds to identify the relation between these variables. Pearson's correlation coefficients were not significant for total scores (r[98] = -.04, p = .705), or for the describing feelings (r[98] = -.01, p = .978), identifying feelings (r[98] = -.10, p = .309) or Externally-Oriented Thinking subscales (r[98] = .04, p = .668). Animacy perception thresholds do not appear to be related to traits of alexithymia in this sample.

As in Experiment One, the effect of participant age, gender and ethnicity on animacy thresholds was analysed. Pearson's correlation coefficient between participant age and mean threshold was not significant (r[98] = -.16, p = .104), indicating that threshold judgements were consistent across age groups. An ANOVA was carried out to compare thresholds across male and female participants, and across ethnic backgrounds. Firstly, participants were grouped into categories based on ethnicity, resulting in Asian, Black, Caucasian and mixed/other background. As in Experiment One, Asian (male N = 21, female N = 9) and Caucasian (male N = 41, female N = 19) participants represented the largest groups, and were compared in this analysis due to the very limited number of participants in other categories (N = 10). A 2 (participant ethnicity) x 2 (participant gender) x 2 (stimulus gender) mixed ANOVA showed no significant main effects of ethnicity (F[1,86] = 0.46, p = .499, η_p^2 = .01) or participant gender (F[1,86] = 0.51, p = .479, η_p^2 = .01), or interaction between the two (F[1,86] = 1.25, p = .267, η_p^2 = .01). There were also no significant main effects or interactions with stimulus gender (ps > .27). The results suggest that participants perceived similar thresholds for animacy whether they had the same or other gender and ethnicity to the stimulus face.

Effects of stimulus variability on animacy perception

To identify the effect of stimulus gender and emotional expression on threshold judgements a 2x2 repeated-measures ANOVA was carried out comparing responses for male and female, and happy and neutral stimuli. Neither the effect of stimulus gender ($F[1,99] = 0.15$, $p = .702$, $\eta_p^2 < .01$) or emotion ($F[1,99] = 0.01$, $p = .919$, $\eta_p^2 < .01$) were significant in this analysis. The interaction term was also nonsignificant ($F[1,99] = 0.63$, $p = .428$, $\eta_p^2 = .01$). Threshold judgements appear to be fairly consistent across stimulus categories.

Rating tasks

Following the procedure for Experiment One, ratings of the extent to which the stimulus '*appears to be alive,' 'is able to feel pain'* and *'has a mind'* were linearly transformed to give a score between 0 and 1, with 1 representing most, and 0 least animacy. Mean ratings in each of the stimulus and emotion categories, at each animacy level were then calculated for each participant. Data from three participants was excluded from the 'mind' task prior to analysis, as they had given either the maximum or minimum rating possible to every stimulus face within one or more gender/emotion categories. This was taken as an indication of a technical difficulty or fatigue on the task. This resulted in 100 participants for the 'alive' and 'pain' rating tasks, and 97 participants on the 'mind' task only (30 female, 67 male, age range 18-61 years, $M = 29.3$, $SD = 9.4$).

As shown in Figure 6.5, ratings on all three dimensions showed relatively little change across the animacy morph continuum. This meant that PSE values could not be calculated from the data. Comparison of mean ratings at each animacy level are therefore described below.

Alive ratings

Ratings of the extent to which the stimulus face appeared to be alive were compared in a 2 (gender) x 2 (emotion) x 11 (animacy level) repeated-measures ANOVA. This revealed significant main effects of gender ($F[1,99] = 31.90$, $p < .001$, $\eta_p^2 = .24$), with male faces rated as appearing more alive than female faces, and emotion ($F[1,99] = 200.41$, $p < .001$, $\eta_p^2 = .67$), with happy faces appearing more alive than neutral faces. The main effect of animacy level was also significant ($F[1,99] = 21.51$, $p < .001$, $\eta_p^2 = .18$), with faces rated as appearing more alive towards the animate end of the continuum, although it should be noted that this effect was smaller than that of emotion or gender. The analysis also revealed a significant interaction between gender and emotion ($F[1,99] = 10.34$, $p = .002$, $\eta_p^2 = .10$), and between gender and animacy ($F[10,990] = 2.76$, $p = .002$, $\eta_p^2 = .03$). Holm-Bonferroni-corrected post-hoc t-tests demonstrate that the effect of gender on ratings for happy faces was significant only at the 70% level of animacy ($t[99] = 3.23$, $p = .002$, Cohen's $d = .35$). However, the gender effect was significant for neutral faces at 0-50 and 70-80% human (ps $< .009$), indicating that the effect of gender was present more for neutral faces, towards the inanimate end of the continuum.

Mind ratings

Ratings for whether the stimulus face appeared to have a mind also showed a main effect of gender ($F[1,96] = 5.04$, $p = .027$, $\eta_p^2 = .05$), with higher ratings associated with male stimuli than female, and emotion ($F[1,96] = 54.22$, $p < .001$, $\eta_p^2 = .36$), with higher ratings given to stimuli with happy expressions than neutral. The main effect of animacy level was also significant, with ratings increasing across the morph continuum ($F[10,960] = 32.46$, $p < .001$, $\eta_p^2 = .25$). In this task no significant interactions between the three variables were found (ps > .11).

Pain ratings

For the rating task requiring participants to decide whether the stimulus face was capable of experiencing pain, again a main effect of gender ($F[1,99] = 16.69$, $p < .001$, $\eta_p^2 = .14$), and emotion ($F[1,99] = 51.50$, $p < .001$, $\eta_p^2 = .34$) were observed. However, in this case the effects were reversed compared with previous tasks, where a greater capacity to experience pain was attributed to neutral faces than happy, and to female faces than to male. The main effect of animacy was also significant ($F[10,990] = 3.11$, $p = .001$, $\eta_p^2 = .03$). Again, no significant interaction effects were shown (ps > .13).

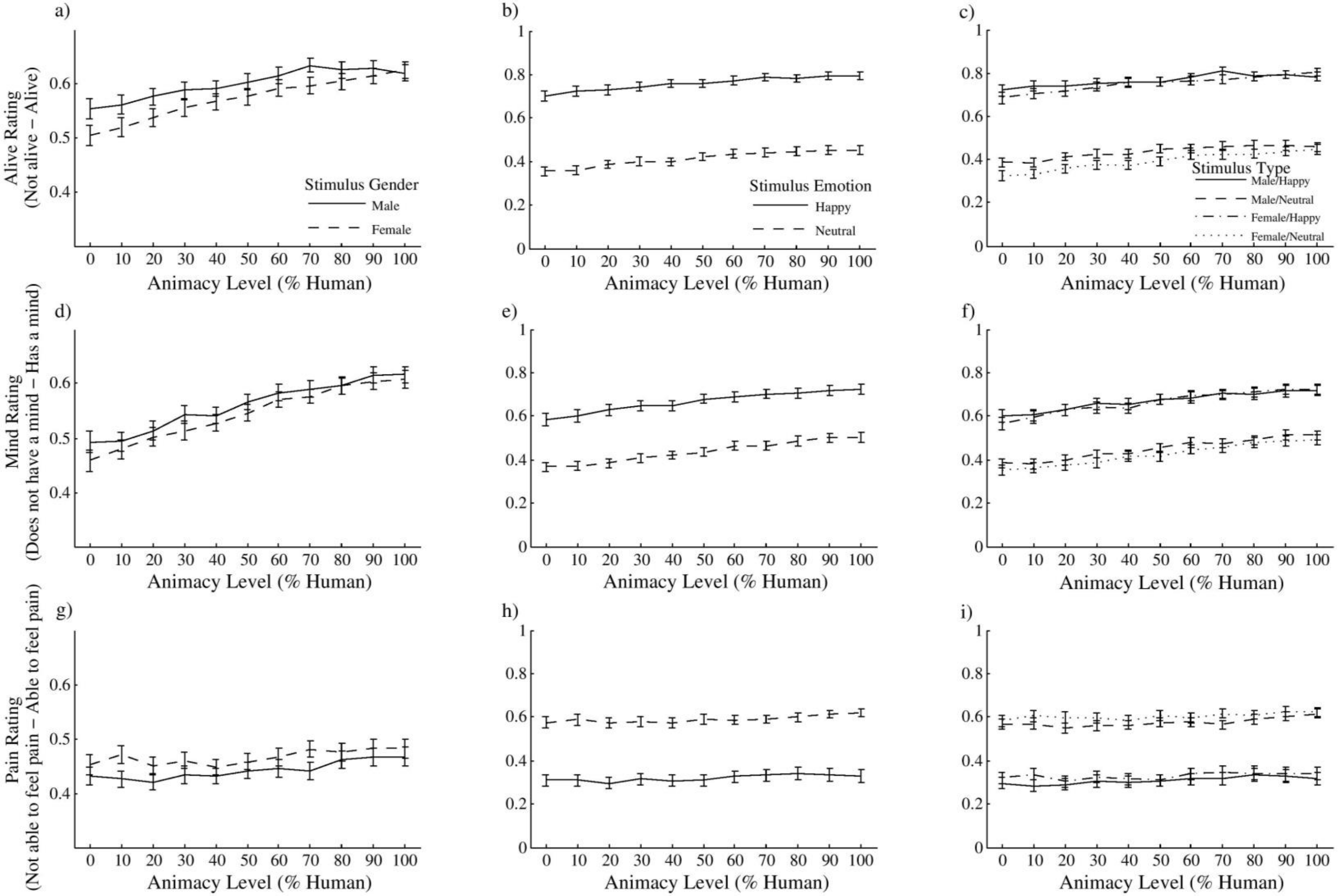
a)
Alive Rating
(Not alive – Alive)
0.4
0.5
0.6
Stimulus Gender
Male
Female
0 10 20 30 40 50 60 70 80 90 100
Animacy Level (% Human)
b)
0
0.2
0.4
0.6
0.8
1
Stimulus Emotion
Happy
Neutral
Animacy Level (% Human)
c)
Stimulus Type
Male/Happy
Male/Neutral
Female/Happy
Female/Neutral
Animacy Level (% Human)
d)
Mind Rating
(Does not have a mind – Has a mind)
Animacy Level (% Human)
e)
Animacy Level (% Human)
f)
Animacy Level (% Human)
g)
Pain Rating
(Not able to feel pain – Able to feel pain)
Animacy Level (% Human)
h)
Animacy Level (% Human)
i)
Animacy Level (% Human)

Figure 6.5 (previous page): Mean ratings from Experiment Two of (a-c) "whether the face appears to be alive", (d-f) "whether the face has a mind", and (g-i) "whether the face is able to feel pain, at each level of animacy from 0% human/100% computer generated to 0% computer generated/100% human. Y-axis shows ratings from 0 (completely inanimate, e.g., definitely not able to feel pain) to 1 (completely animate, e.g., definitely able to feel pain). Ratings are shown for (a,d,g) each stimulus gender, (b,e,h) each stimulus emotion (c,f,i) each stimulus gender/emotion group. Male faces were perceived as more likely to be alive and to have a mind than female faces, but (in contrast with Experiment One) less likely to be able to feel pain. Faces with happy expression were also perceived as more likely to be alive and to have a mind than neutral faces, but less likely to be able to feel pain. Error bars represent +/- 1 S.E.M.

6.3.3 Discussion

The results of Experiment Two partially replicate the findings from Experiment One and show that the effects of stimulus gender and emotional expression on animacy perception are consistent across varying stimulus types. In this regard, the hypothesis that gender differences in animacy judgements are driven by exaggeration of facial features and apparent cosmetics present in female dolls was not supported. When participants were required to rate the extent to which stimulus faces appeared to be alive, or to have a mind, female faces were again perceived as less animate using highly controlled computer generated stimuli without the bias of feminised facial features or apparent cosmetics. This reaffirms a small but robust effect of gender in animacy perception, although the cause of this effect remains unclear.

One may note that the effects of gender and emotion were only found on the rating tasks, and not on the threshold setting task in which participants could freely select the point at which animacy was first perceived. The realistic nature of the inanimate stimuli used in Experiment Two may suggest a reason for the lack of gender and emotion effects on this task. Thresholds were strikingly consistent across each gender and emotion category, with animacy first perceived when the stimulus was approximately 58-59% human. Thresholds for the morphed FaceGen stimuli were significantly lower (closer to the inanimate end of the continuum) than for the morphed doll stimuli in Experiment One. This is perhaps unsurprising, since programs such as FaceGen aim to create a more realistic face stimulus than the dolls used in the previous experiment. A more realistic stimulus at the inanimate end would therefore shift thresholds closer to this end of the continuum. As can be observed from the rating task results (see Figure 6.5), stimuli were rated fairly consistently across each level of animacy. This indicates that it may have been difficult for participants to distinguish between the animacy levels, and therefore to select the point at which animacy was first perceived. Participants may then have been more likely to select a similar threshold on every trial, closer to the middle of the continuum, if they found the stimuli too similar to distinguish between.

In the case of rating whether the stimulus face was able to feel pain, effects of gender and emotion were also observed in Experiment Two. However, female stimuli were rated as more able to feel pain (i.e., more animate) than male faces, in contrast with the ‘alive’ and ‘mind’ tasks, and with the results of Experiment One. This effect may have arisen from pre-existing assumptions regarding gender differences in sensitivity to pain. Research using the Gender Role Expectations of Pain (GREP) questionnaire (Robinson et al., 2001) demonstrates that both male and female participants rate women as more sensitive to, and less enduring of pain than men. Perhaps this gender bias influenced rating judgements on the task. While this bias did not appear to influence ‘pain’ judgements in the first experiment, perhaps this discrepancy can also be attributed to differences in the perceived animacy of the two stimulus sets. If participants found it difficult to distinguish faces at different animacy levels in Experiment Two, then perhaps they were more likely to rely on gender information than animacy to make rating judgements.

The relation between higher levels of Externally-Oriented Thinking and lowered animacy perception thresholds was not replicated in Experiment Two. This does not seem to be a result of the range of TAS scores obtained from the second participant group, as this was consistent with those in Experiment One. Again, since this correlation measure was based on threshold judgements, the relation between variables may have failed to arise in this case if participants found the stimuli too difficult to distinguish between. Further research is necessary to clarify the link between animacy perception and Externally-Oriented Thinking.

6.4 Experiment Three

Experiments One and Two established variability in animacy perception thresholds related to both stimulus and perceiver. This inter-individual variability in the readiness with which animacy is perceived could underlie differences in vicarious responses to inanimate objects and body parts within MTS and conscious vicarious pain (see section 1.3 and Chapter 3 of this thesis). In typical adults vicarious tactile perception is enhanced for animate compared with inanimate body parts (Deschrijver et al., 2015). Vicarious perception may therefore vary between individuals according to individual animacy perception thresholds, where perception should be heightened for stimuli above the threshold for animacy compared with below-threshold stimuli. As noted previously, a minority of individuals with MTS report vicarious sensations of touch for inanimate body parts (Banissy & Ward, 2007; Banissy et al., 2009). Individual differences in the perception of animacy could therefore underlie this variability. In order to investigate this potential moderating effect, it is important to first examine whether MTS is associated with general differences in the perception of animacy, compared with typical adults. Individual difference factors related to social cognition have previously been linked to variability in animacy perception thresholds (i.e., alexithymia, Experiment One; need to belong, Powers et al., 2014, but see Experiment One). Given that MTS has been linked to broader changes in social perception and cognition associated with some of these characteristics (see Banissy, 2013 for a review) there is potential for variability in animacy perception in MTS compared with typical adult controls. In Experiment Three, participants with MTS completed the Threshold Task using the doll-human morph stimuli from Experiment One, to identify whether animacy perception differed in this group compared with non-synaesthetes.

6.4.1 Materials and Methods

Participants

Seven participants who report experiencing MTS were recruited from an existing database at Goldsmiths, University of London. All participants had previously had their experiences verified on a visuotactile interference task (described in section 1.3).

Procedure

Participants completed only the Threshold Task described in Experiment One. The experiment was again completed online. Again, since colour condition did not affect animacy perception thresholds in Experiment One, chromatic stimuli were displayed for all participants.

6.4.2 Results

Mean threshold judgements were calculated for all stimuli (*M* = 69.11, *SD* = 7.90), and for each stimulus category, including male/neutral (*M* = 67.54, *SD* = 11.00), male/happy (*M* = 66.08, *SD* = 12.26), female/neutral (*M* = 72.08, *SD* = 13.68), and female/happy faces (*M* = 70.21, *SD* = 10.11). Mean animacy thresholds are displayed with those made by controls (in Experiment One) in Figure 6.6. This figure demonstrates the same pattern of results obtained from control participants in the previous experiment, with higher thresholds obtained for female faces than male, and for faces with neutral expressions than happy expressions.

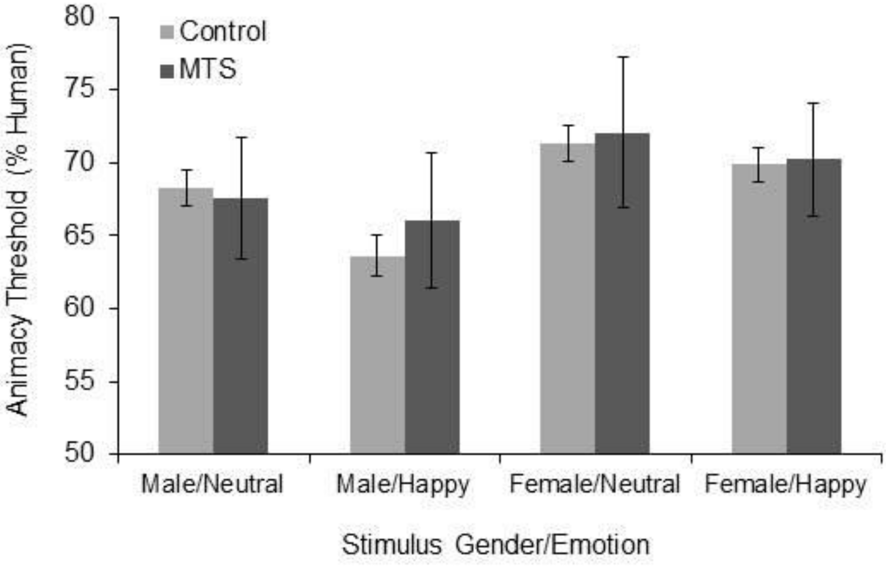

Figure 6.6: Mean animacy thresholds for each stimulus type in MTS participants (Experiment Three) and controls (Experiment One). MTS participants did not significantly differ from controls for any stimulus type.

Comparison of overall threshold judgements with those made by control participants in Experiment One showed no significant effect of participant group (*t*[108] = 0.10, *p* = .922, Cohen's *d* = .04). Again, no significant differences were found for male/neutral (*t*[108] = 0.15, *p* = .880, Cohen's *d* = .06), male/happy (*t*[108] = -0.45, *p* = .651, Cohen's *d* = -.19), female happy (*t*[108] = -0.14, *p* = .886, Cohen's *d* = -.05) or female neutral (*t*[108] = -0.08, *p* = .938, Cohen's *d* = -.03) stimulus faces specifically.

The results therefore indicate that participants with MTS did not differ from control participants in the threshold at which they perceived animacy to occur.

6.4.3 Discussion

The results of Experiment Three extend the findings reported in Experiments One and Two of this chapter to confirm typical animacy perception thresholds in individuals with MTS. The same pattern of variability in animacy thresholds is observed for MTS participants as controls, with animacy perceived more readily in male faces than female, and in happy faces than neutral.

The present results provide useful implications for further research into the role of animacy perception in vicarious tactile response. Variability in conscious vicarious response has been observed within individuals with MTS, where some report vicarious sensations in response to inanimate stimuli while others do not (Banissy & Ward, 2007; Banissy et al., 2009). Individual variability in the perception of animacy therefore provides a candidate mechanism by which this heterogeneity within MTS may occur. The results of Experiment Three establish that animacy perception in MTS does not differ in a systematic fashion. Research should now focus on examining whether conscious vicarious responses differ as a function of individual animacy thresholds, using morphed stimuli such as those created here.

6.5 General Discussion

The present research aimed to elucidate the extent to which facial animacy judgements are influenced by a) the gender of the face, b) the emotional expression of the face, c) colour cues and d) inter-individual variability relevant to social interaction, across varying stimulus sets. The results demonstrate for the first time that the emotional expression of the stimulus face modulates animacy perception, with happy male faces perceived as being animate at a lower level than neutral male faces. The present results also provide further evidence that animacy is perceived more readily in male faces than in female faces. This effect was not driven by objectification of female faces or by cosmetic features associated with inanimate female stimuli that have been used in the past. Animacy judgements were also not affected by whether the stimulus was chromatic or achromatic, but were found to correlate with an externally-oriented cognitive style. Together the results provide important implications for understanding variability in animacy perception and social interaction.

6.5.1 Stimulus Variability Factors that Contribute to Animacy Judgments

The mean animacy perception threshold across all stimuli in Experiment One was 69%. This lies very close to the 67% threshold reported by Looser and Wheatley (2010). The sigmoid function observed in animacy ratings across the morph continuum, and PSE values shifted towards the animate end of the continuum also align with results from previous studies (Balas, 2013; Balas & Horski, 2012; Hackel et al., 2014; Looser & Wheatley, 2010). The similarity between animacy thresholds and PSE values in this study and previous studies indicates a reliable and consistent animacy boundary across experimental procedures, and testing environments (either online or in the laboratory).

However, animacy thresholds using morphed computer generated stimuli in Experiment Two were significantly lower, around 58% human. This suggests that threshold values previously reported may be limited to stimuli morphed from dolls or statues, as have been consistently used in previous literature. Research should now be extended to other types of inanimate stimuli to identify the extent to which this perceptual threshold may vary.

The hypothesis that animacy perception from faces would be enhanced for stimuli expressing emotion was supported in both experiments. It appears that emotional expressions indicate a capacity to experience emotions. This evidence provides an additional suggestion of why the eyes disproportionately influence animacy judgements, as they convey information about emotional state (Eisenbarth & Alpers, 2011; Yuki, Maddux & Masuda, 2007). The role of emotional expression highlights the importance of social cues, in addition to the featural and structural properties of the face, in perceiving animacy. This finding does come with a caveat, as the current study used only happy and neutral expressions. It therefore cannot be determined whether the observed effect was a product of emotion expression in general; or of positively-valenced emotion specifically. Future research should aim to establish the role of positive and negative emotion in attributing animacy to faces.

Across both experiments evidence is provided in support of the effect of stimulus gender in animacy perception (Balas, 2013), with male faces tending to appear more animate than female faces. These findings are extended to show that both male and female participants judge male faces to appear more animate than female. No support was found in this study for Balas' suggestion that gender differences may be caused by objectification of female faces, as animacy threshold judgements were not significantly correlated with individual variability in objectification. The effect of gender also cannot be reduced to biases in the doll stimuli used by Balas, or in Experiment One of this paper. It was proposed that the appearance of cosmetics present in female dolls, or the feminine facial features of doll stimuli, such as lightened skin pigmentation and narrow jawlines could have driven the gender effects observed in these experiments. However, in Experiment Two comparable gender effects were found for computer generated inanimate stimuli without such biases. Further research is needed then, to identify the mechanisms behind the influence of gender in animacy perception.

When rating whether a stimulus was able to feel pain, the effect of emotional expression was reversed compared with ‘alive’ and ‘mind’ judgements, with lower ratings given to happy faces than neutral. Participants were less likely to attribute the capacity to feel pain to faces that were expressing an emotion incongruent with the experience of pain. In Experiment Two, female faces were judged to be more able to experience pain than male faces, also in contrast with judgements of animacy on the ‘alive’ and mind’ tasks. This difference may reflect a gender bias in the perception of others’ sensitivity to pain, since both men and women tend to attribute greater pain sensitivity to women than to men (Robinson et al., 2001). While these explanations seem straightforward, the findings suggest that deciding whether or not a face is capable of experiencing pain relies on different stimulus cues to deciding whether the face appears alive or has a mind, and therefore these may reflect two distinct processes. Gray, Gray and Wegner (2007) propose two core dimensions to mind perception: experience and agency. This account fits with the results of the ‘alive’ and ‘mind’ rating tasks. If a face was perceived as *experiencing* emotion, then it was associated with appearing more alive, and more likely to have a mind. However, if the capacity to feel pain is to be considered an aspect of the mind, then the experience of emotion should also increase mind perception in this aspect, according to Gray and colleagues. In the current stimuli the opposite effect was observed, with emotion expression resulting in reduced perception of the capacity for pain. Further investigation is required to establish whether animacy and the capacity to feel pain reflect separable perceptual judgements.

Finally, in Experiment One, animacy judgements were not significantly affected by whether the stimulus was chromatic or achromatic. This suggests that skin pigmentation is not a vital cue for animacy perception. It should be noted that pigmentation is not the only cue that can be gained from the skin. Texture and shading details are also relevant for other aspects of face processing (Bruce & Langton, 1994; Meinhardt-Injac, Persike & Meinhardt, 2013), suggesting that these cues may have influenced animacy judgements on the task. However, Looser and Wheatley (2010) show that while animacy ratings for the eyes alone accounted for 75% of the variance of whole-face ratings in their experiment, ratings for skin patches did not account for a significant proportion of this variance. In fact, animacy ratings for the morphed skin patch stimuli increased only by around 10% between 100% inanimate and 100% animate stimuli. This indicates that skin properties do not provide a particularly useful cue to animacy. Overall, the present findings support the validity and generalisability of previous studies which have used chromatic images to compare animacy judgements for different stimulus groups (Balas, 2013; Hackel et al., 2014; Looser & Wheatley, 2010; Powers et al., 2014; Swiderska et al., 2012; Wheatley et al., 2011). This provides useful implications for future animacy research, as it appears equally valid to present chromatic or achromatic stimulus faces.

6.5.2 Perceiver Variability Factors that Contribute to Animacy Judgments

Prior work has suggested that an individual's desire for social connection may influence the threshold at which animacy is perceived. Powers and colleagues (2014) report a negative correlation between scores on the NTBS and animacy thresholds, indicating that animacy was perceived more readily by participants with a greater need to belong. This correlation was not replicated for the participant sample in Experiment One. It is worth noting that the present sample was larger (104 vs. 30) and showed a wider range of NTBS scores than the sample recruited by Powers and colleagues. It is possible that the extra anonymity provided by an online experiment increased the honesty of participants' responses on this self-report measure. Comparison of Internet and lab-based self-report measures indicates that online tests are as reliable as those conducted under controlled conditions (Buchanan & Smith, 1999) and are likely to result in more honest self-disclosure (Joinson, 1999). There was also no significant correlation between self-reported loneliness and animacy perception, as predicted based on the research of Epley and colleagues (2008). However, the studies conducted by Epley and colleagues focussed on the attribution of anthropomorphic traits to animals and objects, rather than human faces. It appears that the modulating effect of loneliness may be limited to these kinds of stimuli. Overall, while the present findings contradict those previously reported, further research is necessary to establish the link between desire for social interaction and the readiness with which animacy is perceived.

In Experiment One, higher levels of Externally-Oriented Thinking, a subscale of the TAS measure of alexithymia (Bagby et al., 1994) were associated with increased likelihood of perceiving animacy. However, this effect was not replicated in Experiment Two, which may be related to the difficulty of making threshold judgements using this stimulus set. The Externally-Oriented Thinking subscale is associated with focussing attention on external events rather than inner feelings and emotions (Bagby et al., 1994). It is possible that individuals scoring highly on this subscale may be less influenced by the emotional and social cues in the stimuli, and more influenced by low-level perceptual differences when making animacy judgements. This could result in reduced thresholds for perceiving animacy. The second point to consider is that a lower animacy PSE is also closer to the true point of equality (50%) than a higher PSE. An alternative explanation of the data is therefore that lower animacy thresholds reflect more accurate animacy judgements. Those with an externally-oriented cognitive style may therefore be more accurate at animacy perception as a result of relying more on perceptual than social cues. In this study, for instance, a stimulus face that was smiling was no more likely to be animate than a stimulus with neutral expression. Therefore allowing social cues to influence animacy judgements would not improve accuracy. One way of exploring this hypothesis would be to design an animacy task with ‘correct’ responses. This could involve, for example, a sorting task in which participants must arrange stimulus faces at different animacy levels into the correct answer. This would allow conclusions to be made regarding whether cognitive style and stimulus qualities modulate the accuracy, as well as the likelihood, of animacy perception. At present, however, the link with animacy perception indicates wider differences in face processing in alexithymia than previously thought, which carries important implications for understanding underlying mechanisms of the condition.

6.5.3 Implications for vicarious perception of touch and pain

The present results provide interesting future directions for the study of vicarious perception. Evidence of individual variability in thresholds for perceiving animacy (e.g., in relation to Externally-Oriented Thinking) suggests that this variability may be an important factor in modulating vicarious responses to touch and pain, given that the vicarious somatosensory responses appear to be enhanced for animate compared with inanimate agents (Deschrijver et al., 2015). If vicarious perception is enhanced for stimuli that are perceived as animate, then it may also vary according to individual animacy thresholds, where vicarious responses to an ambiguous stimulus may be enhanced for individuals with lower animacy thresholds. Further, prior evidence of individuals with MTS who experience conscious vicarious sensations in response to inanimate dummies (Banissy & Ward, 2007; Banissy et al., 2009) may reflect these individual differences in the readiness with which animacy is perceived. Experiment Three identified that MTS is not associated with general differences in animacy perception thresholds. Future research should next examine animacy perception in MTS at the individual level, by comparing vicarious tactile experiences for morphed stimuli above and below individual animacy thresholds.

6.5.4 Conclusions

Across two experiments, effects of both stimulus and individual variability in making animacy judgements are established. The findings corroborate previous evidence that the threshold at which animacy is perceived along a continuum is influenced by the gender of the stimulus face (Balas, 2013). In addition, novel evidence is provided to suggest that this threshold is also influenced by the emotional expression of the stimulus, with happy faces perceived as being animate at a lower threshold than neutral faces. With regards to individual variability, some evidence was found to suggest that an Externally-Oriented Thinking style was associated with lower animacy thresholds. However, animacy perception did not significantly differ for participants with MTS compared with typical adults. Taken as a whole, these findings provide vital guidance for the careful control of stimuli in future facial animacy perception research. They also give rise to broader implications for the role of cognition, emotion and gender in social perception, and future directions for the study of vicarious touch and pain.

Chapter 7

Conclusions

This chapter provides an overview of empirical findings regarding the contribution of self-other distinction to vicarious perception of touch and pain reported in this thesis. Each of the main aims of the thesis will be addressed, along with possible limitations of the present research and future directions for the field.

7.1 Introduction

This thesis has investigated two important processes for social interaction: self-other distinction and vicarious perception of touch and pain. Previous research has indicated that self-other distinction may modulate typical vicarious perception (e.g., Adler et al., 2016; Deschrijver et al., 2015; de Guzman et al., 2015; Serino et al., 2008, 2009), and that atypical self-other distinction may underlie conscious vicarious perception (e.g., Derbyshire et al., 2013; Santiesteban et al., 2015b; but see Chapter 1 for a full discussion). However theoretical questions remain regarding the extent to which mechanisms of self-other distinction are required for vicarious perception of touch and pain. With these in mind, the main aims of this thesis were as follows:

1. To examine the extent to which vicarious tactile perception can be modulated by increasing excitability in primary somatosensory cortex or the right temporo-parietal junction with transcranial current stimulation (Chapter 3)

2. To clarify the contribution of self-other control and domain-general inhibitory control mechanisms to vicarious perception by comparing the performance of conscious

vicarious pain responders and controls on an imitation inhibition and a domain-general task (Chapter 4).

3. To assess the involvement of self-other distinction processes with regard to bodily self-awareness in vicarious pain perception, comparing trait levels of depersonalisation and interoceptive sensibility in conscious vicarious pain responders and controls (Chapter 5).

4. To identify individual and stimulus factors which contribute to the distinction between animate and inanimate human faces, with the aim of designing future studies to examine the role of animacy perception in modulating vicarious perception (Chapter 6).

In this chapter, the results of these research questions will be discussed in relation to theories of conscious vicarious touch and pain perception, and implications for understanding vicarious perception and social cognition more generally. Future directions for the field are also considered.

7.2 Modulating vicarious tactile perception with transcranial current stimulation

Chapter 3 addressed the question of whether vicarious tactile perception on a visuotactile interference task could be modulated using transcranial current stimulation (tDCS or tRNS) to increase excitability at either primary somatosensory cortex or the right temporo-parietal junction. In this way, assumptions of both the Threshold Theory and Self-Other Theory of MTS (see Ward & Banissy, 2015 for a review) were investigated across two experiments. Behaviourally, greater vicarious perception was found for individuals with higher self-reported perspective taking, when observing a spatially congruent human hand being touched (compared with a dummy hand or object). However, modulation of vicarious perception was not observed following tDCS over rTPJ. While some evidence indicating enhancement of vicarious tactile perception as a result of tDCS (but not tRNS) targeted at right hemisphere somatosensory cortex emerged, this was only found using liberal statistical thresholds. The evidence therefore does not provide convincing support for the potential to enhance vicarious tactile perception by enhancing somatosensory excitability. Nevertheless, the effect is interesting given that it fits the pattern of results of prior work (Bolognini et al., 2013). The question of whether vicarious tactile perception can be modulated with transcranial current stimulation therefore seems worthy of further investigation.

Future research using this experimental paradigm could identify potential individual variability factors which may moderate the effects of stimulation on vicarious perception. In the present studies, trait empathy was not found to moderate stimulation effects. However, recent research in other cognitive domains has highlighted the variability of tCS responsiveness in relation to several factors, such as (but not limited to) trait differences, anatomy and baseline ability (see Krause & Cohen Kadosh, 2014 for a review). It therefore seems likely that certain factors could influence the modulating effects of stimulation on vicarious perception. Further, variability between experimental participant samples could potentially account for the different results observed in the current work and those previously reported (Bolognini et al., 2013).

The lack of convincing stimulation effects in the present experiments could also be related to structural brain differences associated with MTS outside of somatosensory cortex (Holle et al., 2013). It may be over-simplistic to attempt to induce conscious vicarious perceptual experiences in control participants by targeting one brain region in isolation, these additional differences considered. In this regard, the present results do not necessarily contradict a Threshold Theory of MTS (see Ward & Banissy, 2015). Although boosting somatosensory excitability was not sufficient to induce conscious vicarious tactile perception, somatosensory activity may represent only one of several mechanisms which contribute to the experience.

A candidate mechanism proposed within Self-Other Theory is an impairment in the ability to control representations of the self and others, a process which appears to be enhanced by tDCS targeted at the rTPJ (Santiesteban et al., 2012; Hogeveen et al., 2015). However, vicarious tactile perception was not modulated by tDCS over this region in the current study, therefore contrasting with the assumptions of Self-Other Theory. However, it should be noted that there were no explicit self-other control demands in the vicarious perception task. While vicarious perception in everyday scenarios involves a distinction between self and other, participants may incorporate the visual stimuli in the visuotactile interference task into their own self-concept, since they were presented in a first-person perspective (see arguments in section 1.2), resulting in a lack of self-other conflict. Further, task instructions did not create additional self-other control demand, for example by asking participants to imagine that the viewed body part belonged to either themselves or to a stranger (see Vistoli et al., 2016). The requirement of self-other control mechanisms in completing the current task may therefore have been insufficient to be modulated by stimulation of rTPJ. Further, it should be noted that in order to best match the procedure of Bolognini and colleagues (2013) the present stimulation parameters differed from those used in prior work which has effectively modulated self-other control ability following tDCS over rTPJ (see Coll et al., 2017; Santiesteban et al., 2012, 2015a; Sowden et al., 2015). Future work should consider manipulations to task instructions and design to increase self-other control demands and follow guidance from prior research for stimulation protocol, in order to identify whether performance can be modulated according to excitability of rTPJ.

7.3 Inhibitory control in vicarious pain responders

The lack of support for mechanisms of self-other control in vicarious perception found in Chapter 3 was followed up using a behavioural design in Chapter 4, comparing self-other control ability in conscious vicarious pain responders and control participants. No further support was provided by the results of this next experiment. Neither Sensory-Localised nor Affective-Generalised conscious vicarious pain responders showed impairments in self-other control ability on imitation inhibition or perspective-taking tasks. Further, no significant differences in domain-general inhibitory control ability were observed between the groups, as proposed by Task Control Theory (Heyes & Catmur, 2015). These results contrast with past evidence indicating that both conscious vicarious pain responders (Derbyshire et al., 2013) and individuals with MTS (Santiesteban et al., 2015b) show a specific impairment in inhibiting other-relevant representations. The task used by Derbyshire and colleagues has been criticised for assessing domain-general mechanisms rather than self-other control. However, the fact that significant between-group differences were also not observed on a domain-general inhibitory control task in the present study indicates that this cannot fully account for the discrepancy between the current and previous results regarding self-other control. Further research is needed to establish the reason for this discrepancy with prior work, and whether previously reported effects reflect domain-general or specifically self-other control mechanisms.

On a visuotactile interference task involving observed pain, again no between-group differences were found, contrasting with the results of previous work (Vandenbroucke et al., 2013, 2014). It is possible that subtle differences in tactile stimulation in the present experiment accounted for this discrepancy. However, for control participants greater vigilance to pain was associated with increased vicarious pain perception. This finding supports suggestions made by Fitzgibbon and colleagues (2010) that conscious vicarious pain is driven by hypervigilance to painful stimuli, in individuals with a history of traumatic injury or chronic pain. However, since no between-group differences in vigilance to pain were detected, this trait may be sufficient to modulate vicarious perception on the interference task but not to induce conscious perception of the stimulus. As discussed above, additional factors are likely to be involved in conscious vicarious perception.

It is possible that the method of participant recruitment could explain why predicted differences in self-other control and visuotactile interference in vicarious pain responder groups were not found in this experiment. One issue could be the sample sizes of Sensory-Localised (N = 10) and Affective-Generalised responders (N = 3). Conscious vicarious touch and pain responders are relatively rare, which makes recruitment of large sample sizes challenging. A full discussion of the impact of statistical power on the experimental results contained in this thesis is provided in section 7.3. Alternatively, differences between groups may not have been detected due to the lack of an objective measure of conscious vicarious pain experience. The classification measure used in Chapter 4 relies on self-report rather than an objective measure as used to verify MTS in previous studies (Banissy & Ward, 2007; Santiesteban et al., 2015b). It is important to note that self-report classification measures of MTS have not been found to be sensitive in the past (although see Ward et al., 2018).

For instance, Banissy and colleagues (2009) identify a self-reported prevalence rate of MTS of 10.8%, compared with an objectively-verified prevalence of 1.6%. Self-report measures rely on accurate introspective ability, and these results indicate that many individuals who self-report conscious vicarious perception may not meet objective cut-offs. The current self-report measure involves responses to visual stimuli and more in-depth questions than previous studies of conscious vicarious pain (e.g., Vandenbroucke et al., 2013, 2014), providing a more nuanced investigation of participants' experiences. Previous research into conscious vicarious pain has typically made a distinction only between conscious responders and controls. The distinction between Sensory-Localised and Affective-Generalised responders according to this classification method has only been made recently, and thus received limited confirmation of the validity and reliability of this classification structure. Nevertheless, responder groups based on the current screening measure have shown quantitative differences in brain structure and function (Grice-Jackson et al, 2017), adding validity to the three-factor structure. Specifically, while both responder groups show structural differences in the insula, somatosensory cortex and rTPJ compared with controls, only the Sensory-Localised group demonstrate sensorimotor mu suppression when viewing others in pain. The cluster analysis reported in Chapter 5 of this thesis replicated the original three-factor structure identified by Grice-Jackson and colleagues in a new sample, highlighting the reliability of the method. Collectively, this evidence of the validity and reliability of the scale provides support for its sensitivity to identify pain responder groups in the current thesis. Future work should focus on consistency in the recruitment of conscious vicarious pain responders to allow comparison between studies. Combining self-report with objective measures of vicarious pain, as is considered best practice in the study of

MTS (Banissy & Ward, 2007) could also be effective in identifying conscious responders.

7.4 Atypical bodily self-awareness in vicarious pain responders

In addition to impairments in self-other control ability, Self-Other Theory (see Ward & Banissy, 2015) proposes that conscious vicarious perception of touch and pain may be related to an extension of bodily self-awareness. To address this proposition in Chapter 5, individuals with Sensory-Localised or Affective-Generalised conscious vicarious pain, and control participants without conscious vicarious pain, were asked to complete a battery of self-report measures related to bodily self-awareness. Atypical responses were found for Sensory-Localised vicarious pain responders, specifically heightened depersonalisation (related to a detachment from the bodily self) and interoceptive sensibility (related to a focus on internal bodily sensations). This evidence supports Self-Other Theory, suggesting that broader differences beyond somatosensory mirroring may contribute to atypical conscious vicarious perception. Specifically, a detachment from one's own body as observed in depersonalisation is thought to be associated with impairments in self-other distinction, and a greater tendency to extend representations of the bodily self to incorporate others (Adler et al., 2016; Kanayama et al., 2009). Impairments in self-other distinction have previously been linked to conscious vicarious pain perception (Derbyshire et al., 2013; Grice-Jackson et al., 2017), suggesting that this could mediate the relation between depersonalisation and conscious vicarious perception reported here. In terms of interoceptive sensibility, a heightened focus on internal bodily sensations could increase detection of vicarious physical sensations induced by observing others' pain, leading to conscious perception.

Future work is necessary to further explore the trait differences found in this study. For instance, while this data provides evidence of broader trait differences associated with conscious vicarious pain, it cannot inform theory regarding the direction of the relation between these variables. It is conceivable that atypical bodily self-awareness could be either a cause or a consequence of conscious vicarious perceptual experience. Causal relationships regarding interoception could potentially be assessed by training attention towards bodily states, and examining subsequent changes in vicarious pain experience. For instance, some mindfulness-based therapies involve a focus on internal bodily sensations, and have been shown to increase neural activity associated with interoceptive attention (e.g., in anterior insula; Farb, Segal & Anderson, 2012). Increased grey-matter density in the TPJ has also been reported following long-term mindfulness training, suggesting potential implications for self-other control (Hölzel et al., 2011). This form of training could therefore provide a useful avenue for future research on vicarious perception.

Before extending these findings beyond conscious vicarious pain responders, it will be important to also assess bodily self-awareness in individuals with MTS. Following evidence of vicarious body ownership and agency in MTS (e.g., Aimola Davies & White, 2013; Cioffi et al., 2016), Self-Other Theory predicts that vicarious touch may also be associated with the sense of bodily self-awareness, but this is yet to be examined in terms of trait differences in depersonalisation and interoception, and the sample of individuals reporting conscious vicarious responses to touch in the present study was not large enough to make systematic comparisons with conscious vicarious pain responders. The extent to which vicarious perception of touch and pain involve overlapping mechanisms requires further examination.

7.5 Effects of stimulus and perceiver variability on perception of animacy

Perception of animacy is an important factor for self-other distinction, and previous work has indicated that vicarious perception of touch and pain may be modulated by whether an observed body part is perceived as animate or inanimate (Deschrijver et al., 2105; see section 1.2). This is a pertinent research question, since vicarious perception is thought to act as a mechanism for social cognition and empathy (e.g., Bird & Viding, 2014; de Guzman et al., 2016; Gallese and Goldman, 1998). If vicarious perception facilitates the representation and understanding of the states of others, then these responses should be specific to other animate beings. Given the proposed link between animacy and vicarious perception but the relative lack of direct evidence, Chapter 6 aimed to first investigate the processes underlying how animacy is perceived, in order to inform future research. This chapter explored stimulus and perceiver characteristics which may modulate perception of animacy from faces. Two separate studies revealed that animacy is perceived more readily in male faces than female faces, and in human faces displaying emotional expressions. Higher Externally-Oriented Thinking (a component of alexithymia) was also associated with perceiving animacy more readily.

The present studies provide interesting future directions regarding the role of animacy perception in modulating vicarious perception, giving rise to testable hypotheses for future research. For instance, individual variability was present in the threshold at which animacy is perceived. If, as previous evidence has suggested (e.g., Deschrijver et al., 2015) vicarious perception is enhanced for animate compared with inanimate body parts, then it should also be enhanced for individuals who perceive animacy more readily in ambiguous stimuli (i.e., morphed faces around the threshold for detecting animacy). Further, in Experiment One individuals with higher Externally-Oriented Thinking scores showed lower animacy thresholds, and so it follows that vicarious perception in response to ambiguous stimuli may be greater for individuals with higher Externally-Oriented Thinking. In Chapter 5 of this thesis self-reported conscious vicarious pain was not associated with differences in alexithymia or Externally-Oriented Thinking specifically. However, observed pain stimuli in this chapter were either clearly human body parts or objects. Responses to ambiguous morphed stimuli may be more closely linked to alexithymic traits. In this way, inter-individual differences in animacy thresholds and Externally-Oriented Thinking provide potential explanations for why some (but not all) individuals with MTS report vicarious sensations to dummy body parts (Banissy & Ward, 2007; Banissy et al., 2009). Future research should consider trait differences such as these in assessing the effect of perceived animacy in modulating vicarious perception of touch and pain.

7.6 Theoretical implications for vicarious perception of touch and pain

The experimental work reported in this thesis contributes to understanding the role of self-other distinction in vicarious touch and pain. Support is provided for the suggestion that vicarious pain is associated with broader mechanisms beyond somatosensory mirroring, as proposed by the Self-Other Theory of MTS (see Ward & Banissy, 2015). In particular, processes relevant to maintaining the sense of bodily self, discussed in Chapter 5, may play an important role in modulating vicarious pain perception.

Less support is provided for the involvement of other self-other distinction processes in modulating vicarious pain perception. Stimulus variability factors, specifically animacy (human vs. dummy) and visual perspective (1st vs. 3rd person) were not found to modulate performance on an objective measure of conscious vicarious tactile perception in a bottom-up way, in Chapter 3. However, this lack of modulation may be explained by the non-synaesthete participant sample who took part in the study. Since these individuals were not expected to experience conscious vicarious sensations of touch under sham stimulation conditions, any modulating effect of animacy or perspective may not be detected on this particular task. Indeed, previous research which has recorded neural responses to stimuli varying in animacy (Deschrijver et al., 2015) and visual perspective (Canizales et al., 2013) has indicated a modulating effect on unconscious vicarious perception of touch and pain. Future research should continue to vary self-other distinction factors such as animacy in both a bottom-up (e.g., using visibly inanimate body parts) and a top-down way (e.g., using a gloved hand and instructing participants that the hand belongs to either a human or a robot, see Liepelt & Brass, 2010), and also incorporate individual variability factors relevant to animacy perception to effectively assess the modulating effect on vicarious perception.

Furthermore, in Chapter 4 self-other control ability was comparable across conscious vicarious pain responders and controls, on a task requiring the inhibition of other-relevant and promotion of self-relevant representations. Investigating the functional role of rTPJ in modulating vicarious tactile perception also provided little support for the involvement of self-other control processes. Increasing excitability in this region with tDCS has previously been linked with improved self-other control ability (Santiesteban et al., 2012; Hogeveen et al., 2015), but did not have a significant effect on conscious vicarious tactile perception in Chapter 3. These results contrast with predictions based on Self-Other Theory, and with prior evidence indicating impairments in self-other control associated with MTS (Santiesteban et al., 2015b) and conscious vicarious pain (Derbyshire et al., 2013).

Evidence for Threshold and Task Control theories was lacking in the present studies. While vicarious pain responder groups did not show differences in self-other control ability, these groups also performed comparably on a domain-general inhibitory control task. The question of whether previously observed impairments in self-other control in conscious vicarious responder groups (Derbyshire et al., 2013; Santiesteban et al., 2015b) reflect domain-general deficits in inhibitory control, as proposed by Task Control Theory (Heyes & Catmur, 2015), therefore remains unclear.

Additionally, attempts to modulate vicarious perception using transcranial current stimulation in Chapter 3 did not provide strong support for a Threshold Theory of conscious vicarious experience (see Ward & Banissy, 2015). Conscious vicarious perception of touch did not significantly increase (after correction for multiple comparisons) following tDCS or tRNS aimed at increasing cortical excitability in primary somatosensory cortex. However, this result does not necessarily conflict with Threshold Theory. Factors such as individual variability in responsiveness to transcranial current stimulation (see Krause & Kadosh, 2014) may have influenced the effectiveness of stimulation in this case. Additionally, even if hyper-excitability in somatosensory cortex is involved in MTS, this may not be sufficient to induce the condition if other neural mechanisms (such as self-other distinction) are involved.

The lack of significant effects reported in the experiments of Chapters 3 and 4 (as discussed above) must be considered in light of a potential lack of statistical power with which to identify these effects. In Chapter 3, for instance, data from 22 participants was analysed for Experiment 1 and 23 for Experiment 2. While in each case this is fewer than participated in the study being replicated (*N* = 32; Bolognini et al., 2013), in this previous study participants were divided into two groups in terms of the hemisphere targeted with tDCS (left or right) whereas in the current experiments all participants received stimulation on the same hemisphere. Further, the number of experimental trials was increased in the current experiments (180 per task compared with 144), further increasing statistical power. Nevertheless, achieved power for the crucial t-test comparison between SI and sham RTs in Experiment 2 was only 0.51, insufficient to detect significance. Power calculations indicate that a sample size of 44 would be required to achieve a 0.80 level of power. With this in mind, it should be noted that although the effects reported by Bolognini and colleagues were not replicated here, the current results alone do not provide strong evidence for the null hypothesis.

In Chapter 4 similar problems arise. Power calculations indicate that sufficient power (0.96) was achieved for the interaction effect between pain responder group and congruency on the imitation-inhibition task where between-group differences were predicted, despite a null result being found. While this indicated a sufficient overall sample size, the analysis does not account for the unequal groups in the study (Controls N = 24, Sensory-Localised N = 10, Affective-Generalised N = 3). Certainly, more than 3 participants would be required to detect significant differences in the Affective-Generalised group versus controls. With the obtained ratio of Sensory-Localised to control participants, estimated sample sizes of 38 Controls and 16 Sensory-Localised responders would be required to achieve 0.8 power for paired comparisons, based on effect sizes obtained with mirror-touch synaesthetes in prior work (Santiesteban et al., 2015b). Again, we can conclude that despite the null results obtained in this Chapter, strong evidence for the null hypothesis is not provided. Across both areas of investigation (Chapters 3 and 4) further work with larger sample sizes is warranted in order to clarify discrepancies with prior work.

Based on the evidence presented in this thesis and reviewed here, mechanisms associated with the sense of bodily self-awareness appear to be of relevance to conscious vicarious perception (at least of painful stimuli). Chapter 5 of this thesis presents only a preliminary investigation of bodily self-awareness in relation to depersonalisation and interoception, but provides a promising avenue for future research. Both MTS and conscious vicarious pain have previously been linked to greater plasticity of body representations (Aimola Davies & White, 2013; Cioffi et al., 2016; Maister et al., 2013; Osborn & Derbyshire, 2010), with these individuals more likely to incorporate others into their own bodily self-concept. In line with Self-Other Theory, it has been suggested that this broader plasticity of the bodily self may underlie conscious vicarious experiences of touch and pain (see Banissy & Ward, 2013; Ward & Banissy, 2015). Plasticity of the bodily self in MTS and conscious vicarious pain could be further studied using existing paradigms from the body representations literature. For instance, visual adaptation to a distorted version of one’s own arm (e.g, larger or smaller) alters perceived tactile distances on the arm, indicating a rescaling of the implicit body model (Taylor-Clarke, Jacobsen & Haggard, 2004; see also Longo, Azañón & Haggard, 2010). For individuals with MTS or conscious vicarious pain, an extended plasticity of bodily representations to incorporate others may mean that similar effects are observed following visual adaptation to another person’s arm. Methods such as these provide interesting future directions for research and may provide further insight into bodily self-awareness and vicarious perception.

The theories discussed above, while originally developed to explain vicarious tactile perception, have also been adopted to explain vicarious perception of pain. While substantial evidence has been provided in support of these theories in relation to both touch and pain (see section 1.3 for an overview), the extent to which underlying mechanisms overlap is not clear. For instance, differences in the prevalence rates of MTS (approximately 1.6%) and Sensory-Localised vicarious pain (approximately 19%) indicate additional factors are relevant in modulating responses to touch and pain stimuli. In addition, Chapter 4 of this thesis found no significant impairment in self-other control ability in conscious vicarious pain responders, while Santiesteban and colleagues (2015b) have found that individuals with MTS have a difficulty inhibiting representations of others and promoting representations of the self. Future work should aim to directly compare these groups to identify the extent to which underlying mechanisms (such as those proposed by Threshold Theory and Self-Other Theory) are shared in the two conditions, and what individual variability factors dictate whether a person will experience, for example, vicarious perception of pain but not touch.

7.6.1 Summary

The collected evidence presented in this thesis points towards the involvement of atypical self-other distinction processes relevant to the bodily self in conscious vicarious perception of touch and pain. This evidence supports previous suggestions of broader mechanisms, beyond somatosensory mirroring, involved in these experiences (see Self-Other Theory; Ward & Banissy, 2015). The results have implications for understanding vicarious perception more generally, suggesting that an ability to distinguish between self and other and to maintain a stable sense of bodily self-awareness allows typical individuals, without vicarious touch or pain, to maintain appropriate levels of vicarious perception. The extent to which these mechanisms contribute to other mechanisms of vicarious perception (e.g., for action) and more complex social cognitive processes (e.g., empathy) was beyond the scope of this work, but remains a necessary avenue for future research.

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