

**Bodily pleasure and the self:
Experimental, pharmacological and clinical studies
on affective touch**

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Abstract

In the last decade, neuroscience and psychology alike have paid increasing attention to the study of affective touch, which refers to the emotional and motivational facets of tactile sensation. Some aspects of affective touch have been linked to a neurophysiologically specialised system, namely the C tactile (CT) system. While the role of this system for affiliation, social bonding and communication of emotions have been investigated, less is known about the potential role of affective touch in the awareness of the body as our own, i.e. as belonging to our psychological ‘self’.

This thesis attempted to contribute to the knowledge on affective touch and its relation to body awareness, by exploring the potential role of this modality to the way we perceive and make sense of our body as our own. Specifically, this work aimed to advance the current state of knowledge by investigating: 1) the effect of affective touch on the sense of body ownership, which is a fundamental aspect of body awareness; 2) the relation between interoceptive modalities, originating both internally (i.e. cardiac awareness) and peripherally (i.e. affective touch), and exteroception in body awareness; 3) the effect of intranasal oxytocin on the perception of affective touch and bodily awareness; 4) the perception and social modulation of affective touch in psychiatric patients who show difficulties in body awareness, namely patients with Anorexia Nervosa, and 5) the modulating role of self-other distinction and of self-other relation in the perception of affective touch and body awareness.

In a first experiment (N = 52) the rubber hand illusion paradigm was used to investigate the role played by CT-optimal, affective touch in the sense of body ownership. The results showed that slow, pleasant touch enhanced the experience of embodiment in comparison to faster, neutral touch, suggesting that affective touch might uniquely contribute to the sense of body ownership. The following study (N = 75), used a similar methodology to test whether interoceptive sensitivity as measured by a heartbeat counting task would modulate the extent to which affective touch influences the multisensory process taking place during the rubber hand illusion. The results could not confirm a systematic relation between interoceptive sensitivity and the perception of affective touch, nor its influence on body ownership. The next study (N = 41) included a double-blind, placebo-controlled, randomised, cross-over design testing the effect of intranasal oxytocin on the perception of affective touch and body ownership, as measured by means of the rubber hand illusion. There was no evidence supporting the

hypothesis that intranasal oxytocin could influence the CT system as tested in this study. The next study (N = 55) applied some of the above methodologies to investigate the perception of CT-optimal touch in patients with anorexia nervosa and its emotional modulation by top-down factors. The results confirmed the hypothesis that people with anorexia nervosa show a reduced perception of affective touch compared to healthy controls, but its perception was not influenced by top-down affective modulation, in the sense that both patients and healthy controls perceived touch as more pleasant when presented concurrently with positive facial expressions compared to neutral and negative faces. Finally, the last two studies (N = 76 and 35 healthy volunteers, respectively) focused on the relationship between affective touch and body awareness in the context of social cognition. These studies used both online and offline social modulation paradigms to investigate the role of self-other distinction and of self-other relation in the perception of affective touch. The results showed that positive top-down social information can enhance the perceived pleasure of tactile stimulation.

Taken together, these studies point to the central role of affective touch in body awareness and social cognition. Finally, they also pave the way for future studies examining the role of disruptions of the CT system in the development of neuropsychiatric impairments of body awareness and social cognition.

Declarations

I declare that this thesis represents my own work and it has not previously been submitted successfully for an award.

Aspects of Chapters 1, 2 and 5 are under review for publication in:

Gentsch, A., Crucianelli, L., Jenkinson, P., & Fotopoulou, A. (under review). *The Touched Self: Affective Touch and Body Awareness in Health and Disease*. In H. Olausson, J. Wessberg, I. Morrison, F. McGlone (Eds.), *Affective Touch and the Neurophysiology of CT Afferents*. Springer.

The study presented in Chapter 2 has been published in:

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Table of Contents

Abstract	1
Declarations	3
Aknowledgments	4
Table of Contents	5
List of Tables	10
List of Figures	11
List of Appendices	123
Abberviations	13
Chapter 1: General introduction	14
1.1. Background.....	14
1.2. A specialised pathway for affective touch: The C tactile system	16
1.3. Bodily pleasure: Affective touch as an interoceptive modality	18
1.4. Multisensory integration and bodily self-consciousness	20
1.5. The role of interoception in body representation and the sense of body ownership	22
1.6. Role of others in the construction of the bodily self-consciousness	24
1.7. The neurobiological basis of affective touch	27
1.8. Aims and outline of this thesis.....	29
Chapter 2: Bodily pleasure matters: Velocity of touch modulates body ownership during the rubber hand illusion	32
2.1. Introduction	32
2.2. Materials and Method.....	35
2.2.1. Participants	35
2.2.2. Design and statistical analysis	35
2.2.3. Materials	37
2.2.4. Procedure	38
2.3. Results	39

2.3.1. Pleasantness ratings	39
2.3.2. Embodiment questionnaire – Composite Score of Ownership, Location and Agency	39
2.3.3. Sub-component analysis	41
2.3.4. Proprioceptive drift	43
2.4. Discussion	43
2.5. Limitations and future directions	45
Chapter 3: Integration of interoceptive and exteroceptive modalities during the Rubber Hand	
Illusion: An experimental study on the sense of body ownership	47
3.1. Introduction	47
3.2. Methods	50
3.2.1. Participants	50
3.2.2. Design and Statistical analysis	51
3.2.3. Apparatus and Materials.....	52
3.2.4. Experimental procedures	53
3.3. Results	55
3.3.1. Interoceptive sensitivity	54
3.3.2. BMI and pre-RHI measures	55
3.3.3. Rubber Hand Illusion	56
3.3.4. Correlational analysis	60
3.4. Discussion	61
3.5. Limitations and future directions	64
Chapter 4: The effect of oxytocin on the perception of affective touch and body awareness	66
4.1. Introduction	66
4.2. Methods	73
4.2.1. Participants	73
4.2.2. Experimental design and statistical analysis	74
4.2.3. Materials.....	78

4.2.4. Procedure.....	80
4.3. Results	82
4.3.1. Heartbeat baseline and interoceptive sensitivity	82
4.3.2. Affective touch task.....	82
4.3.3. Rubber hand illusion.....	83
4.4. Discussion	85
4.5. Other limitations	89
Chapter 5: The perception of affective touch in anorexia nervosa	90
5.1. Introduction	90
5.2. Methods	93
5.2.1. Participants	93
5.2.2. Design and data analysis	94
5.2.3. Stimuli and apparatus	95
5.2.4. Procedure.....	97
5.3. Results	97
5.3.1. Demographics and mood	97
5.3.2. Pleasantness ratings.....	98
5.3.3. Correlations	100
5.4. Discussion	101
5.5. Limitations and future directions	104
Chapter 6: Look into the mirror: The effect of self vs. other-mirror observation on interoception	106
6.1. Introduction	106
6.2. Methods	111
6.2.1. Participants	111
6.2.2. Experimental design and statistical analysis	112
6.2.3. Materials	113
6.2.4. Experimental procedure	114

6.3. Results	115
6.3.1. Interoceptive sensitivity	115
6.3.2. Pleasant touch	116
6.3.3. Correlational analysis	118
6.4. Discussion	118
6.5. Limitations and future directions	121
Chapter 7: The effect of shared touch on bodily pleasure	123
7.1. Introduction	123
7.2. Materials and methods	128
7.2.1. Participants	128
7.2.2. Experimental design and statistical analysis	128
7.2.3. Control procedure	130
7.2.4. Materials and set-up	131
7.2.5. Procedure.....	132
7.3. Results	133
7.3.1. Pleasantness ratings	133
7.3.2. Control embodiment questionnaire.....	135
7.4. Discussion	136
7.5. Limitations and future directions	138
Chapter 8: General discussion	140
8.1. Introduction.....	140
8.2. Summary of the main findings	141
8.3. Methodological discussion.....	145
8.3.1. Affective touch task.....	145
8.3.2. Rubber hand illusion.....	148
8.3.3. Heartbeat detection task.....	149
8.3.4. Social modulation: facial expressions, mirror observation and synchronous experiences	151

8.4. The role of affective touch in the representtaion of the bodily self	152
8.5. Integration of interoceptive and exteroceptive signals in bodily self-consciousness.....	155
8.6. A neurobiological basis for interoceptive bodily signals.....	159
8.7. The social modulation of bodily pleasure.....	161
8.8. Conclusion.....	165
References.....	167
Appendices.....	191

List of Tables

Table 1.1. <i>Summary of Aβ and C touch characteristics</i>	18
Table 2.1. <i>Table summarising the experimental design</i>	35
Table 3.1. <i>Means and standard deviations are reported for illustrative purposes only</i>	56
Table 3.2. <i>Summary statistics and test results for Proprioceptive Drift</i>	59
Table 3.3. <i>Summary statistics and test results for Temperature Change</i>	60
Table 5.1. <i>Summary of demographic and clinical measures</i>	98
Table 5.2. <i>Summary of experimental measures</i>	100
Table 7.1. <i>Summary of the experimental design</i>	129
Table 7.2. <i>The embodiment questionnaire</i>	131

List of Figures

Figure 2.1. <i>A schematic representation of the experimental set-up.</i>	37
Figure 2.2. <i>Median and interquartile range of pleasantness rating scores and change in embodiment</i>	39
Figure 2.3. <i>Median and interquartile range of change in ownership, location, agency and affect.</i>	40
Figure 3.1. <i>Materials and experimental procedure.</i>	53
Figure 3.2. <i>Main effect of stroking velocity on embodiment.</i>	57
Figure 4.1. <i>Study design and flowchart.</i>	77
Figure 5.1. <i>Experimental set-up</i>	96
Figure 6.1. <i>Means and standard errors of interoceptive sensitivity in the different visual conditions</i>	116
Figure 6.2. <i>Means and standard errors of pleasantness ratings in the different visual conditions</i>	117
Figure 7.1. <i>Plan view of the experimental setup</i>	132
Figure 7.2. <i>The experimental set-up</i>	132
Figure 7.3. <i>Means and standard errors of the pleasantness ratings across visual conditions</i>	134
Figure 7.4. <i>Correlations between embodiment and pleasantness ratings of slow/CT optimal and fast/CT non-optimal touch.</i>	135

List of Appendices

Appendix 1. *Pre embodiment questionnaire for studies in Chapters 2, 3 and 4*191

Appendix 2. *Post embodiment questionnaire for studies in Chapters 2, 3 and 4*194

Appendix 3. *Depression Anxiety Stress Scale (DASS 21) for the study in Chapter 5*197

Abbreviations

AN	Anorexia Nervosa
BMI	Body Mass Index
CT	C Tactile
DA	Dopaminergic circuits
DASS	Depression Anxiety Stress Scale
DSM-IV	Diagnostic and Statistical Manual of Mental Disorders, 4 th Edition
fMRI	Functional Magnetic Resonance Imaging
HB1, 2, 3	Heart-rate Baseline 1, 2, 3
HC	Healthy Controls
HR	Heart Rate
IQR	Interpersonal Range
IS	Interoceptive Sensitivity
IU	International Units
LMM	Linear Mixed Model
M	Mean
NHS	National Health Service
NRES	National Research Ethics Service
OT	Oxytocin
RHI	Rubber Hand Illusion
SCID	Structured Clinical Interview for DSM-IV Axis I Disorders
SD	Standard Deviation
SE	Standard Error
SSRIs	Selective Serotonin Reuptake Inhibitors
VRT	Visual Remapping of Touch

General introduction

“A person’s own body, and above all its surface, is a place from which both external and internal perceptions may spring. It is seen like any other object, but to the touch it yields two kinds of sensations, one of which may be equivalent to an internal perception. Psychophysiology has fully discussed the manner in which a person’s own body attains its special position among other objects of the world of perception ... - The self is first and foremost a bodily self”

(Freud, S. The Ego and the ID. 1895, pp. 25–6)

1.1. Background

Starting from our early sensorial experiences in the womb, touch is one of the first routes by which we receive information from the external world and make sense of what is ‘other from us’. In fact, it has been hypothesised that touch plays a pivotal role in developing a sense of self as separate from the other (see Field, 2010 for a review). Somewhat paradoxically, touch is also our most social sense since it seems central in how we bond with other people and form interpersonal attachments. The communicative power of a caress and the wellbeing derived by a hug are examples of the sociality of touch, and research has widely discussed the importance of tactile interactions with others in order to develop healthy social relationships (Morrison, Löken & Olausson, 2010).

In the last decade, neuroscience and psychology alike have paid increasing attention to the study of emotional and motivational aspects of touch, which has been referred to as affective touch (see McGlone, Wessberg & Olausson, 2014, for a review). The peculiarity of affective touch is its interpersonal nature and the fact that it is

mediated by the skin, our oldest and widest organ in terms of dimension and functions (Field, 2001; Montagu, 1971). Increasingly, research has been supporting the existence of a specialised tactile system for affective touch (i.e. the CT system; see the following section 1.2.) and more studies stress how important this modality could be for the development of the social brain (see Walker & McGlone, 2013 for a review).

While the characteristics and role of the affective touch system for affiliative behaviours, social bonding and communication of emotions has been widely described and discussed in recent research (see Olausson, Lamarre, Backlund, Morin, Wallin et al., 2002; Löken, Wessberg, Morrison, McGlone & Olausson, 2009; Morrison et al, 2010; Walker and McGlone, 2013, for reviews), less is known about the potential role of affective touch in making sense of ourselves as embodied beings. In fact, affective touch has been re-conceptualised as a modality providing information about the internal states of the body. This channel is referred to as interoception (Craig, 2002; 2008) and it seems to contribute to maintaining the homeostasis of the body, as well as having an important role in the awareness of ourselves as feeling entities (the so called ‘sentient self’) at any given time (Craig, 2003; 2009).

In the wake of these recent conceptualisations, this thesis attempts to contribute to the knowledge on affective touch, by providing experimental, pharmacological and clinical evidence supporting the importance of this modality to the way we recognise and make sense of our body as our own. In particular, this thesis seeks to investigate the interoceptive facet of affective touch (by measuring subjective bodily pleasure) and its importance - in isolation and in combination with exteroceptive information - to the development of the sense of body ownership, which is a fundamental aspect of bodily self-consciousness (Blanke, 2012; see below section 1.4.).

This introduction aims to provide an overview of the current state of research on affective touch, with a particular focus on its interoceptive nature. Theories around interoception and its relationships to body representation and affective touch are described. Then, a review of the recent research on bodily self-consciousness is given with a focus on the potential role played by affective touch. The integration and relationship between interoception and exteroception in the context of body

representation, a fundamental aspect of bodily self-consciousness, is then examined. Subsequently, a critical examination of factors that could modulate the perception of affective touch is discussed, with particular attention to social and neurobiological (e.g. oxytocin) aspects.

1.2. A specialised pathway for affective touch: The C tactile system

Research on the sense of touch has identified two distinct modalities; a discriminative and an affective one (see McGlone et al., 2014, for a review). The sensory-discriminative dimension supports the detection and identification of external stimuli, providing information about the physical characteristics and spatial location. By contrast, the motivational-affective dimension is involved in the valence and motivational nature of the stimuli, such as hedonic and emotional relevance. While the discriminative aspects of touch have been well-studied, the system responsible for the affective aspects has only recently been investigated (Olausson et al., 2002; McGlone, Vallbo, Olausson, Löken & Wessberg, 2007; Olausson, Cole, Vallbo, McGlone, Elam et al., 2008; Löken et al., 2009). This thesis will focus on the latter one. The affective dimension of touch can be investigated by means of a low-pressure, slow, caress-like tactile stimulation delivered at velocities between 1 and 10 cm/s (Löken et al., 2009). Studies conducted applying a neurophysiological method called microneurography, which allows recording of the activity of single peripheral nerves on the skin, showed an activation of C tactile (CT) afferents when touch presents the aforementioned characteristics (Vallbo, Olausson & Wessberg, 1999). These fibers are present only on the hairy skin of the body, and when activated, individuals report a pleasant percept. Indeed, Löken and colleagues showed that there is a linear correlation between the activation of the CT fibers and the subjective report of pleasantness (Löken et al., 2009).

To better clarify how affective touch gives rise to the pleasant percept, it is useful to explain first what is hypothesised about the pathway of the tactile stimulation from the periphery (skin) to the brain, and then how these signals are thought to be

modified by and integrated with top down information (Ellingsen, Leknes, Loseth, Wessberg & Olausson, 2015).

The human skin is innervated by a group of thin, slow-conducting afferents, C fibers and A δ fibers, which are defined as thermo-, noci- or chemo-receptive (Burgess & Perl, 1967) and by thick, fast-conducting (A β) afferents, described as mechanoreceptive (see Table 1.1). However, over the last few decades research has supported the hypothesis that CT afferents constitute a distinct system, both from the anatomical and functional point of view, which may be activated specifically in response to slow, caress-like types of touch and provides pleasant sensations (Vallbo et al., 1999; Olausson et al., 2002; Löken et al., 2009). Moreover, CT afferents seem to respond more actively to touch stimuli that are close to the typical skin temperature compared to colder or warmer stimuli, and also this activation correlates to subjective pleasantness ratings (Ackerley, Backlund-Wasling, Liljencrantz, Olausson, Johnson et al., 2014). Although the A β and C tactile systems act in parallel and respond to cutaneous stimulation, the latter one may specifically “pick out” a range of velocities likely to have social-affective relevance, for the purposes of further affective processing (Morrison et al., 2010).

Table 1.1. Summary of A β and C touch characteristics (see Björnsdotter, Morrison and Olausson, 2010, for a review)

	A β touch	C touch
Preferred stimulus (Basbaum, 2007; Löken et al., 2009; Ackreley, 2014)	Any kind of non-noxious touch.	Soft, light, skin-temperature touch.
Firing rates (Löken et al. 2009)	Correlate positively with stimulus intensity and velocity of a constant-force brush stimulus.	Form a \cap -shaped curve with a maximal response for brush velocities of 1-10 cm/s.
Electrophysiological properties (Basbaum, 2007)	The large diameter of A β afferents combined with a thick myelin sheath ensures high transmission speeds (around 35-37 m/s).	The thin, unmyelinated C afferents are substantially slower (around 1 m/s).
Temporal resolution (Basbaum, 2007)	40ms	1000ms
Spatial resolution (Vallbo et al., 1999).	The A β fiber system innervates the entire body.	C tactile afferents have been identified exclusively in the hairy skin and are lacking in the palms.
Pathway (Björnsdotter, et al., 2010 for a review)	Projects through posterior column to somatosensory cortices for discriminative processing	Projects through spinothalamic tract to insular cortex for affective and interoceptive processing
Percept (Vallbo et al., 1999; Olausson et al., 2002; Löken et al., 2009)	Acute, informative of the spatial and physical characteristics of the stimulus	Diffuse, informative of the affective (i.e. pleasant/unpleasant) valence of the stimulus

1.3. Bodily pleasure: Affective touch as an interoceptive modality

Given the distinct anatomical and physiological characteristics of the tactile systems mediated by A β and CT afferents, it has been argued that the two systems also have distinct functional properties (Morrison et al., 2010, McGlone et al., 2014 for reviews). As outlined in the previous section, the A β pathway seems to mediate

discriminative information, whereas the CT pathway signals the affective-motivational aspect of touch. Additionally, according to Craig (2002), affective touch can be re-defined as an interoceptive modality, since it provides information about the internal states of the body. The re-definition of affective touch as an interoceptive modality has important implications for some potential functions of the mediating CT afferents system.

Given the importance and the peculiar physiological characteristics of this affective touch system, theories suggest the presence of a specialised peripheral and central neurophysiological system, which seems to take a different pathway compared to the discriminative, emotionally neutral touch from the peripheral nerves of the skin to the posterior insular cortex (Olausson et al., 2002, but see Gazzola, Spezio, Etsel, Castelli, Adolphs et al., 2012). In fact, functional imaging studies in humans suggest the posterior insular cortex as a primary cortical target for C fibers (Olausson et al., 2002); an area strongly interconnected with the amygdala, hypothalamus and orbital frontal cortex. Further evidence comes from the study of two unique patients suffering from a neuropathy syndrome (Serman, Schaumburg & Asbury, 1980), which left intact only the CT afferents of the body. Functional magnetic resonance imaging (fMRI) of soft brush stroking on the hairy skin of these patients showed activation in the posterior insular cortex; in contrast, no activation in somatosensory cortices was recorded (Olausson et al., 2002). Therefore, the posterior insula may support an early convergence of sensory and affective signals. Following on from this, in the insular cortex, there seems to be a progressive integration - which follows a posterior to anterior pattern - of this interoceptive information (including signals derived from affective cutaneous stimulation) with exteroceptive information, and cognitive and social factors (Craig, 2009). This integration of interoceptive/affective and exteroceptive/sensory information seems to be responsible for the awareness of our whole body at any given time, and the construction of the subjective experience of the self (Critchley, Wiens, Rotshtein, Ohman & Dolan, 2004; Craig, 2008). Such integration is crucial for the homeostasis of the body, but it may also contribute critically to the formation of coherent representation of the body, the sensory environment, and motivational

conditions. Further support for the pivotal role of interoception in the sense of body ownership comes from neuropsychological findings. Karnath and colleagues described patients who, following lesions involving the right insular cortex (which is a key area for the processing of interoceptive signals), showed disorders of body ownership and self-awareness (Karnath, Baier & Nagele, 2005; Karnath & Baier, 2010).

1.4. Multisensory integration and bodily self-consciousness

How do we become aware of our body as our own? And what is the relationship between owning a body and the sense of self? These questions have been widely discussed in philosophy and psychology (e.g. Gallagher, 2000; James, 1890); indeed the body can be studied from multiple perspectives and there seem to be different systems for representing the body. However, an extended discussion of these issues lies beyond the scope of this thesis. The position embraced in this thesis is the one highlighted by Gallagher, and involves the distinction between body schema and body image (Paillard, 1999; Gallagher, 2005). The body schema involves sensory-motor capacities and it does not necessarily have to be conscious; it is involved in our interaction with the environment and therefore with action. In contrast, body image involves a conscious process to identify the body as our own, and therefore it is closely related to our sense of body ownership. It includes visual perceptions and beliefs about our own body, and it is not necessarily related to our ability to take actions in the environment. This thesis mainly addressed the conscious representation of the body which derives from the experience of owning a body, and which is considered to be a fundamental aspect of bodily self-consciousness (see Blanke, 2012 for a review; Dijkerman, 2015). Additionally, different components of bodily self-consciousness such as the perceived location of the body and the first-person perspective have been identified and experimentally manipulated using multisensory conflicts (for review see Blanke, 2012). However, this dissertation focuses only on the sense of body ownership.

Another concept that should be clarified in relation to this thesis is the one of the self, which has been extensively debated in literature since James first hypothesised the

existence of different senses of self (James, 1890). According to Gallagher, the different approaches can be divided in two main categories supporting the existences of the ‘minimal self’ and the ‘narrative self’ (Gallagher, 2000). The first one comprises a pre-reflective, non-conceptual form of bodily self-consciousness and it is thought to relate to sensory experiences associated with the sense of agency (i.e. the experience of initiating and controlling bodily movement and physiological states) and the sense of body ownership (i.e. the experience of belonging of our own body). The ‘narrative self’ is a concept of the self based on beliefs, intentions and autobiographical knowledge (Gallagher, 2000, Conway, 2001). However, the extensive debate around the definition of self in the context of embodied cognition is beyond the scope of this work. Instead, this thesis primarily explored representations of the bodily self in relation to the sense of body ownership.

The development of experimental paradigms that allow the controlled manipulation of limb ownership in laboratory settings, such as the rubber hand illusion (Botvinick & Cohen, 1998), provides a unique tool to investigate the malleability of the sense of body ownership and the bodily boundaries between self and other. In this illusion, synchronous touch between a visible rubber hand and the participant’s hidden hand, produce the illusion of ownership over the fake hand. The rubber hand illusion takes place as a result of a multisensory, three-way interaction between vision, touch and proprioception. Abundant research has replicated and extended the original finding (Botvinick & Cohen, 1998) and the rubber hand illusion has now been accepted as a reliable model of body ownership. Furthermore, it has been proposed that the subjective experience of body ownership is supported by activation of the posterior insular cortex (Tsakiris, 2010), a cortical target for the CT afferents and bodily interoceptive sensations more generally (Craig, 2002). Thus, this network seems to play a fundamental role in linking sensory stimulation to one’s own body, and therefore in bodily self-consciousness.

1.5. The role of interoception in body representation and the sense of body ownership

According to recent theories (Craig, 2002; 2008; Damasio, 2010), all affective feelings from the body are represented in a novel pathway which converges signals from the body to the posterior insular cortex and maintains the integrity of the body. These feelings seem to represent a sense of the physiological condition of the entire body, which Craig refers to as “interoception” (Craig, 2002). The interoceptive system is associated with the autonomic nervous system and has been related to the generation of subjective feelings and self-awareness (Craig, 2009; Chritcley et al., 2004; Damasio, 2010). Key sensations from the body such as pain, itch, temperature, hunger, cardiac signals and pleasant touch have been re-classified as interoceptive feelings and clearly separated from other discriminatory, exteroceptive sensations, such as information about the external environment, but also about the body in relation to the outside world.

Traditionally, the majority of studies investigating interoception attempted to quantify individual differences in the ability to perceive one’s own internal bodily signals by means of tasks measuring the perception of cardiac activity. In heartbeat perception tasks, participants are asked to count their own heartbeat silently under resting conditions, without taking their pulse or feeling their chest (Schandry, 1981; Pollatos, Kirsch & Schandry, 2005). The extent to which participants are able to perceive their cardiac signals, therefore, has been proposed as a measure of “interoceptive awareness”. The relation between cardiac awareness and the perception of signals from other interoceptive modalities, such as pain and affective touch, remains to be specified, particularly in relation to multisensory integration and bodily self-consciousness. In fact, interoception comprises signals from the body which can originate both peripherally from the skin (cutaneous signals such as itch, pain and pleasant touch) and internally to the body, such as heartbeat, hunger, distention of the bladder and taste.

Apart from heartbeat perception, which has traditionally been used to assess and ‘quantify’ interoceptive sensitivity, there are other objective methods to measure the

extent to which individuals are aware of their interoceptive signals, such as sensitivity to gastric functions (i.e. gastrointestinal distention) and adrenergic stimulation. However, these methods are not easy to implement and the relationships among these methods has only been partially established (Herbert, Muth, Pollatos & Herbert, 2012).

Given the centrality of bodily representation for our self-consciousness, special emphasis should be given to the role of internal bodily signals (i.e. interoception) in mediating this relation. Experimental paradigms using the aforementioned rubber hand illusion have documented the mechanisms of integrating visual, vestibular, proprioceptive and tactile input that give rise to higher level representation of our body (Blanke, 2012). This dynamic, multisensory integration process is considered to be at the core of the sense of body ownership. However, despite the important role of interoceptive signals for bodily self-consciousness in the sense of having a conscious experience of being a 'unitary entity' (Blanke, 2012), visceral afferent signals have long been neglected in body representation processes. Only recently have studies begun to explore the role of interoceptive, emotional and social factors, in bodily self-consciousness. Specifically, it has been proposed that the integration between interoceptive signals and exteroceptive information lies at the core of bodily self-consciousness. Craig (2009; 2010) argues that in the insula interoceptive information about the internal state of the body is progressively integrated with information from the exteroceptive senses (e.g. vision, audition, olfaction). Evidence shows that the exteroceptive and interoceptive modalities interact and can influence each other, contributing ultimately to the experience of a coherent self (e.g. Critchley et al., 2004). Recently, more studies attempted to investigate the relationship and the interplay between interoceptive and exteroceptive signals in body representation. For example, Tsakiris and colleagues (2011) showed that interoceptive sensitivity, in the sense of how well participants perform in the Heartbeat Counting Task (Schandry, 1981), can predict the malleability of the sense of body ownership in the rubber hand illusion paradigm (Tsakiris, Tajadura-Jimenez & Costantini, 2011). This finding has been partially replicated and extended also in the context of the virtual body illusion (Aspell et al., 2013) and virtual rubber hand illusion (Suzuki, Garfinkel, Critchley & Seth, 2013).

Although these studies addressed the interoception-exteroception debate, the extent to which interoception and exteroception contribute to body representation in isolation and in combination, and their reciprocal modulation, is still an open question.

1.6. Role of others in the construction of the bodily self-consciousness

As early as when William James (1890) discussed the different categories of the self, the *social Self* was assigned a key role in what constitutes a conscious being. Indeed, extensive evidence showed that the interaction with the outer world plays a pivotal role in the origin and development of bodily self-consciousness from the very beginning. Evidence suggests that the development of a sense of body ownership, and differentiation of self from other, are processes involving multisensory integration and are important precursors to more sophisticated social behaviors, such as imitation and empathy (Gallese, 2003; Chaminade, Meltzoff & Decety, 2005). In fact, the development of a sense of body ownership seems to be crucial also for social and cognitive abilities that necessitate differentiation of self from other (Schütz-Bosbach, Mancini, Aglioti & Haggard, 2006) and comparisons between self and other (Meltzoff, 2007). This process of identification, differentiation, and comparison between self and other is believed to be important for understanding others as thoughts and intentions (Gallese, 2003), and thus for the development of social relational behaviors (Gallese et al, 2004; Chaminade et al., 2005).

The connection between social contact with others and wellbeing has been firstly supported by studies conducted on primates. For example, Harlow and Zimmermann (1958) showed that infant monkeys seek social contact for reasons that go beyond nutrition and thermoregulation, and there seems to be a fundamental affective motivation related to ‘contact comfort’. On the same line, Zazzo (1975) showed how chimpanzees brought up in complete isolation are not able to recognise themselves in the mirror; however, after 3 months of social experience and physical contact with other chimpanzees, they started to recognise themselves in a mirror. This finding supports the vital importance of others in the development of the representation of the self and ultimately self-consciousness (Zazzo, 1975). In a similar way, in humans, it has been

argued that the bodily self is not something that depends only on mental and brain processes that belong to the singular individual; quite the contrary, the self and particularly bodily self-consciousness is shaped by the encounter with others and hence our self is seen as intrinsically intersubjective (Mead, 1913, 1982; Damasio, 1994). This idea is supported, among others, by studies highlighting the vital role of others in the case of premature infants (Feldman and Eidelman, 2003; Field et al., 2010 for a review) but also the protective role of social support and physical contact with others early in life for psychological wellbeing (House, Landis & Umberson, 1988; Eisenberger & Cole, 2012; Sharp, Pickles, Meaney, Marshall, Tibu et al., 2012).

Given its interpersonal and emotional nature, affective touch seems to be a suitable candidate to offer an explanation of how we perceive the world through our body and the social nature of the self. In fact, being mediated by the skin, which is the physical body's boundaries between the inside and outside, affective touch presents certain characteristics to simultaneously capture information about the self and the outside world. For example, the affective aspect of touch represents an essential part of early mother-infant interactions, and therefore it could have a unique developmental role in establishing the physical boundaries of the psychological self.

There is some evidence from developmental psychology suggesting that multisensory integration, including the integration of tactile stimuli with vision and proprioception, contributes to the establishment of the psychological distinction between one's body and that of others (Casco, Moana-Filho, Guest, Nebel, Weisner et al., 2012). In fact, the ability to integrate vision, touch and proprioception seem to be disrupted in children with Autism Spectrum Disorders (Casco et al., 2012). These children seem to rely more on proprioceptive input in the presence of competitive stimuli from other modalities, and they show a reduced multisensory integration in the context of the rubber hand illusion paradigm. Because of the important role of body ownership in the acquisition of social skills, such as imitation and empathy, this evidence may underlie an altered representation of the bodily self (Lombardo, Chakrabarti, Bullmore, Sadek, Pasco et al, 2010), and in turn it may give rise to diminished social abilities such as imitation and empathy.

If on the one hand hedonic tactile interaction is important in establishing and maintaining a healthy self-other distinction, on the other hand it may also be crucial in mediating the psychological connection between self and other (Morrison, Löken and Olausson, 2010). In fact, affective touch has a pivotal role in affiliative behaviour, which is the predisposition of seeking close contact with others. The motivational dimension of social touch can promote the positive consequence of tactile stimulation, by reinforcing the connection between the hedonic experience of affective touch ('liking') and seeking these kind of social interactions ('wanting') (Morrison et al., 2010; see Berridge & Kringelbach, 2008 for clarification on the "liking-wanting" distinction). Through this mechanism, which could facilitate and promote tactile interactions, affective touch might constitute the base for the formation and maintenance of social bonds in the same way as grooming (Dunbar & Schults, 2007) as well as tickling and other playful behaviours (Panksepp & Burgdorf, 2003) in other mammals.

Furthermore, affective touch seems to have a non-verbal communicative function. Hertenstein and colleagues (2006) demonstrated that individuals were able to discriminate and identify different categories of emotions on the basis of how someone touched them. Participants were able to distinguish between positive and negative categories of emotions. Remarkably, a slow caress was associated with the emotion of love (Hertenstein et al, 2006; 2009).

As discussed above (section 1.2), the hedonic value of touch is intrinsically related to the physical characteristics of tactile stimuli, like softness (Rolls et al., 2003), temperature (Ackerley et al., 2014) and velocity (Löken et al., 2009). However, the cutaneous signals are also processed and modulated by several "top-down" mechanisms to give rise to the subjective experience of touch in the brain (see Ellingsen et al., 2015 for a review). Recent experimental studies showed that the recipient's belief about the person giving the touch modulated the perceived pleasantness of slow touch (Gazzola et al., 2012; Scheele, Kendrick, Khouri, Kretzer, Schläpfer et al., 2014). Male participants rated slow touch as more pleasant when they believed that they were caressed by a female experimenter, but unpleasant when they believe that they were touched by a male experimenter. In all the conditions the experimenter was, in fact, always the same

(Scheele et al., 2014). This finding supports the social nature of affective touch, and how social top-down factors (such as the gender of the toucher) can modulate the meaning and desirability of the touch, and also the positive experience of it.

1.7. The neurobiological basis of affective touch

It has been proposed that in primates, grooming is a social activity, the function of which seems to be associated mainly with social bonding and facilitation of relationships, by providing a psychopharmacological environment that enhances commitment to the other animal (Dunbar, 2010). Given the soft touches and the gentle movements involved in social grooming, it could be argued that the CT afferent system can be potentially associated with this practice.

Grooming seems to be so important since it provides the psychological substrate for trust, and therefore is at the base of reciprocal support in case of need (Dunbar, 1988). According to Dunbar (2010), grooming creates the ideal environment for trust to flourish by triggering the release of neuroendocrines that create an internal psychological environment that facilitates onset and maintenance of social bonds. The mechanism that has been suggested as being the best candidate at the origin of social bonding involves oxytocin (OT). OT is a neuropeptide involved in mammalian reproduction, enabling the birth process and, subsequently, lactation. It is also observed to play a role in the process of pair bonding in mammals. Just like endorphin, OT seems to have analgesic and reward proprieties.

Studies suggest that one potential mechanism through which OT facilitates social interactions and affiliative behaviours is by modulation of the dopaminergic circuits (DA), usually associated with motivation. The interaction between DA and OT seems to promote socially relevant behaviour, such as social gaze and face recognition (see Lee, Macbeth, Pagani & Young, 2009, for a review), and to increase the motivational salience of social stimuli (Love, 2014). If the DA system seems to mediate the motivational aspect of social interactions, the hedonic experience seems to be associated by the endogenous opioids system (Berridge, 1996). In support of this idea, animal studies provide evidence that endogenous opioids mediate the rewarding effects of a number of

social behaviours which involve tactile social interactions, such as maternal behaviour, social play and allogrooming (Panksepp, Herman, Vilberg, Bishop & DeEsquinazi, 1981). Furthermore, some evidence supports the association of oxytocin and tactile stimulation. Caress-like stroking of rats' abdomens raised plasma oxytocin levels, and an association with reduced perception of pain was observed (Agren, Lunderberg, Uvnäs-Moberg & Sato, 1995). Newborn rodents receiving maternal grooming through tactile stimulation following a brief period of separation show, in adult age, lower stress reactivity. This includes lower levels of corticotropin-releasing factor compared with individuals who receive less maternal grooming, supporting the protective effect of maternal grooming on stress responses in the offspring (Liu, Diorio, Tannenbaum, Caldji, Francis et al., 1997; Weaver, Richardson, Worlein, & Waal Laudenslager, 2004).

In a similar way, studies in humans show that the reported frequency of physical contact with partners is correlated with elevated oxytocin level and lowered blood pressure in women (Light, Grewen & Amico, 2005), and supportive physical contact from a partner has been shown to reduce the response to an acute stress (Ditzen, Neumann, Bodenmann, von Dawans, Turner et al., 2007). Therefore, there is some evidence supporting the role of tactile stimulation, probably paired with oxytocin release, in reducing stress and promoting a healthy development in humans too (for a review, Walker & McGlone, 2013). Also, a recent study showed that self-reported frequency of maternal stroking over the first weeks of life reduced the association between prenatal depression and adverse mental health outcomes in infancy (Sharp et al., 2012). Accumulating clinical evidence supports the beneficial role of affective touch delivered through massage in healthy individuals as well as clinical populations, in promoting psychological and physical well-being (see Field, 2010, for a review). For example, woman diagnosed with Anorexia Nervosa who undertook 5 weeks of massage therapy, showed reduced salivary cortisol level (stress) and increased dopamine levels, as well as reporting reduced anxiety and lower mood. Remarkably, these patients also reported a decrease in body dissatisfaction as assessed by means of the Eating Disorders Inventory (Garner, Olmsted & Polivy, 1983), suggesting a potential implication for body representation and self-awareness (Hart, Field, Hernandez-Reif, Nearing, Shaw et al.,

2001). In conclusion, human tactile contact, just like grooming and tickling behaviors in other mammals, is increasingly understood to be central to a healthy emotional, cognitive and physical development.

1.8. Aims and outline of this thesis

The main aim of the present dissertation was to explore the role of affective touch to the representation of bodily self-consciousness. In order to do so, experimental, psychopharmacological and clinical methodologies were used. Specifically, on the basis of evidence highlighting the importance of tactile interaction in distinguishing the self from the other, (1) experimental studies were run to investigate the specific effect of slow/CT optimal touch on the sense of body ownership. These results were taken a step further to investigate the effect of self-other distinction and self-other togetherness to the bodily pleasure experience. In this context, the relationship between affective touch and cardiac awareness has also been explored. (2) Pharmacological studies have been run to investigate the effect of intranasal oxytocin on the perception of affective touch and bodily awareness. Finally (3), a clinical study was run to investigate the perception of affective touch in Anorexia Nervosa, a clinical population which presents social isolation, body image distortion and anhedonia.

To specifically address these objectives, in **Chapter 2** the rubber hand illusion paradigm (Botvinck & Cohen, 1998) was used to investigate the role played by affective touch to the sense of body ownership. Specifically, the velocity of touch during the illusion was manipulated (slow/CT-optimal vs. fast/no-CT optimal) in order to observe the effect of affective vs. emotionally neutral touch on the multisensory integration process taking place during the illusion. Furthermore, given the intimate nature of interoceptive signals (i.e. bodily pleasure) as belonging to the self and differentiate from the other, the type of hands used in the illusion was modulated. Half of the sample looked at a rubber hand whereas half of the sample looked at a real hand (of a person who was seated next to the participant). This manipulation was introduced to observe

whether the presence of another person, who has her/his own feelings and interoceptive experiences, would reduce the effect of affective touch on the embodiment processes.

Interoception is a term used to describe several modalities which provide information about the internal states of the body. To better understand the role of affective touch to bodily self-consciousness, the relation between affective touch and cardiac awareness has been examined in **Chapter 3**. In fact, although these two modalities both provide interoceptive information and contribute to the awareness of the body from within, they are fundamentally different. Affective touch originates peripherally from the skin, whereas the heartbeat finds its origin within the body. In this study, the heartbeat counting task and the affective touch task were combined in the context of the rubber hand illusion in order to explore their relationship, but also how they get integrated with exteroception (i.e. vision) in a multisensory integration paradigm.

Chapter 4 presents an investigation of the neurobiology of affective touch and its potential role in body representation. This double-blind, placebo-controlled, randomised, cross-over study aimed to explore the effect of intranasal oxytocin on the perception of affective touch and body awareness in healthy controls, by means of the heartbeat detection task and the rubber hand illusion. Participants were asked to rate the pleasantness of brush strokes applied at either slow or fast velocities to their forearm, both before and after self-administration of oxytocin or placebo. Subsequently, they were asked to complete the heartbeat counting task to establish interoceptive awareness both after oxytocin and placebo. The rubber hand illusion was also completed after oxytocin or placebo, in order to investigate the effect of the compound on the sense of body ownership.

Chapter 5 applied some of the above methodologies to investigate affective touch on a clinical population characterised by body image distortions, lack of awareness and social difficulties; i.e. Anorexia Nervosa. Patients with this psychiatric disorder present with reduced pleasure from social interactions (social anhedonia); however, studies showed that their symptomatology, in the sense of anxiety, low mood and body dissatisfaction, can be improved by massage therapy. Therefore, this clinical

population offers the unique opportunity to investigate and specify the potential role of the CT system on healthy body representation. Participants were asked to rate the pleasantness of the touch that they perceive on their forearm while looking at faces displaying different facial expressions, known to differently engage the attentional resources of individuals with Anorexia Nervosa. This manipulation also allowed the top-down social modulation of touch in both Anorexia Nervosa and healthy controls to be studied.

The relationship between affective touch and body awareness in the context of social cognition was investigated and discussed in Chapters 6 and 7, which is divided into two parts. In **Chapter 6**, the focus was on the *distinction* between self and other and the modulation of affective touch and cardiac awareness. Participants completed a heartbeat counting task and an affective touch task while they were looking at themselves or someone else in the mirror. In contrast, in **Chapter 7**, the effect of the *togetherness* of self and other on bodily pleasure was investigated. Namely, participants were asked to rate the pleasantness of touch while perceiving it together (synchronously or asynchronously) with someone else.

In summary, this work aimed to advance the current state of knowledge by investigating: 1) the effects of affective touch on the sense of body ownership, which is a fundamental aspect of bodily self-consciousness; 2) the relation between two interoceptive modalities, affective touch and cardiac awareness, in multisensory integration and body representation; 3) the effect of intranasal oxytocin on the perception of affective touch and bodily awareness, 4) the perception of affective touch, and its social modulation, in Anorexia Nervosa and, 5) the modulating role of self-other distinction and relation in the perception of affective touch and body awareness.

Bodily pleasure matters: Velocity of touch modulates body ownership during the rubber hand illusion

2.1. Introduction

The sense of body ownership refers to the feeling that our physical body is our own and a part of our psychological self (Gallagher, 2000; see Chapter 1). Scientific interest in body ownership has been intense since Botvinick and Cohen (1998) first reported the now well-known Rubber Hand Illusion (RHI), during which participants experience a lifelike rubber hand as part of their body, when their own unseen hand is synchronously stroked. This paradigm is considered one of the few viable ways to experimentally investigate body ownership, because it allows an external object to be subjectively experienced as part of one's body, rather than being simply visually recognised (Tsakiris, 2010). Thus, an abundance of research has sought to reveal the neurocognitive constituents of body ownership during the RHI, revealing that both low-level multisensory integration and high-level body representations contribute to our sense of body ownership (Makin, Holmes & Ehrsson, 2008; Tsakiris & Haggard, 2005; Tsakiris, 2010). However, the focus of such studies has mainly been on how the brain integrates different exteroceptive signals, such as vision and touch, to produce the sense of body ownership. Little attention has been paid to how the illusion may be affected by interoceptive bodily signals (defined here as afferent signals that track the physiological state of all tissues of the body, Craig, 2009; see Chapter 1), such as temperature, pain or pleasant touch. By contrast, in other domains of psychology and cognitive neuroscience, the recent influential discovery of a specialised, interoceptive system that represents the internal, homeostatic state of the body (Craig, 2003) has generated a lot of interest, particularly as regards the scientific study of emotion and self-consciousness. Recent influential accounts of self-awareness link interoception with how we become aware of

our body *from within* (Craig, 2009; Critchley et al., 2004; Damasio, 2010; Seth, Suzuki & Critchley, 2012).

In the context of the RHI, Tsakiris et al. (2011) showed that individuals who scored lower in a trait measure of interoceptive sensitivity (heart beat detection task) experienced a stronger RHI compared to individuals who scored higher, possibly reflecting an over-reliance on exteroceptive signals in the former group. It has also been shown that exteroceptive, multisensory integration can have an effect on the physiological regulation of the body during the illusion (Moseley, Olthof, Venema, Don, Wijers et al., 2008; but see Guterstam, Petkova & Ehrsson, 2011). Nevertheless, at the time that this study was conceptualised, only one study had attempted to study the reverse relationship, namely what is the specific contribution of interoceptive signals to the illusion and ultimately body ownership. Schütz-Bosbach and colleagues (2009) used a RHI paradigm to investigate whether participants' perception of tactile stimulation on their own hidden arm was modulated by simultaneously watching the rubber hand being touched by either the same or a different material (i.e. soft and rough fabric). The results showed that participants' interpretation of the perceived roughness of the fabric on their own arm was not modulated by the perceived visual stimulation of the rubber hand, and therefore touch perception seems to be resistant to top-down manipulation. However, the degree to which this study activated specific interoceptive pathways was unclear, as it manipulated the materials used to stimulate the hands (cotton versus sponge), and not the velocity of stroking (Schütz-Bosbach, Tausche & Weiss, 2009).

As introduced in Chapter 1, the latter is in fact particularly important for engaging a specialised interoceptive modality, defined as affective, or pleasant, touch. Pleasant touch is coded by specialised, unmyelinated CT afferents, found only in hairy skin (Vallbo et al., 1999; Olausson et al., 2002). These afferents respond to slow (between 1-10 cm/s), soft touch, and at such velocities the touch on hairy skin is perceived as most pleasant, with a linear correlation between CT firing rates as measured by microneurography and pleasantness ratings on visual-analog scales (Löken et al., 2009). Moreover, CT afferents are distinct from the well-characterised, myelinated tactile fibres that code for discriminative touch (Löken et al., 2009; McGlone et al.,

2007). In fact, CT afferents take a distinct ascending pathway from the periphery to the posterior insular cortex (Olausson et al., 2002; Morrison, Björnsdotter & Olausson, 2011), which is understood to support an early convergence of sensory and affective signals about the body that are then re-represented in the mid and anterior insula, the proposed sites of interoceptive awareness (Craig, 2009; Critchley et al., 2004). Interestingly, the insular cortex has also been linked with the experience of body ownership during the RHI (Tsakiris, Hesse, Boy, Haggard & Fink, 2007).

However, the question of how affective touch modulates body ownership in the RHI remains unanswered, as the velocity of tactile stimulation has never been manipulated in previous RHI studies. Moreover, the reporting of the related single velocity procedures in existing RHI studies vary considerably; some authors report only the location and overall duration of stroking (e.g. Maister, Sebanz, Knoblich & Tsakiris, 2013), while others report the duration of each individual stroke (e.g. Tsakiris & Haggard, 2005), or report no specific details of stroking velocity (e.g. Costantini & Haggard, 2007). Interestingly, in studies reporting velocity details, single frequencies of touch between 1 Hz (Longo, Schüür, Kammers, Tsakiris & Haggard, 2008; Tsakiris et al., 2011) and 3 Hz (e.g. Bekrater-Bodmann, Foell, Diers & Flor, 2012) are typical, corresponding roughly to velocity within the range of pleasant touch. In the current study, stroking velocity during the RHI paradigm was manipulated, by providing light, dynamic tactile stimuli in speeds known to elicit feelings of pleasantness (3cm/s) versus speeds known not to elicit such feelings (18cm/s) (Löken et al., 2009). Slow velocity stroking was predicted to be perceived as more pleasant and lead to greater ownership of the rubber hand than fast velocity stroking.

In addition, while the RHI is not induced when the rubber hand is replaced by a non-corporeal object such as a wooden stick (Tsakiris & Haggard, 2005), it occurs when the rubber hand is replaced by another person's real hand (Schütz-Bosbach et al., 2009). However, it is unclear whether the latter effect would apply when the multisensory integration that underlies the RHI involves integrating vision of another person's hand, with interoceptive signals that are usually used to represent one's own body from within.

This study thus investigated whether seeing another person’s hand versus a rubber hand would reduce the illusion in slow versus fast stroking conditions.

2.2. Materials and methods

2.2.1. Participants

Fifty-two, right-handed women (mean age = 21.04 years, SD = 4.05) took part in a single, 45-minute testing session. Three participants were later excluded from the data analysis; one did not complete all trials, and two failed to comply with experimental instructions. Institutional ethics approval was obtained and the experiment was conducted in accordance with the Declaration of Helsinki.

2.2.2. Design and statistical analysis

The experiment used a 2 (Seen Hand: rubber vs. real) x 2 (Stroking Mode: synchronous vs. asynchronous) x 2 (Stroking Velocity: slow vs. fast) mixed factorial design, with repeated measures on the latter two factors (see Table 2.1.). The order of conditions was randomised across participants. For the first, between-subjects manipulation, twenty-four participants watched a confederate’s hand being stroked during the relevant four conditions, whereas twenty-five participants watched a rubber hand.

Table 2.1. Table summarising the experimental design. The dotted line represents the between-subjects factor (Seen Hand), the continuous lines represent the within-subjects factors (Stroking Mode and Stroking Velocity)

	Rubber Hand		Real Hand	
	<i>Slow Stroking</i>	<i>Fast Stroking</i>	<i>Slow Stroking</i>	<i>Fast Stroking</i>
<i>Synchronous</i>	Slow/Synchronous	Fast/Synchronous	Slow/Synchronous	Fast/Synchronous
<i>Asynchronous</i>	Slow/Asynchronous	Fast/Asynchronous	Slow/Asynchronous	Fast/Asynchronous

Dependent variables comprised: (1) A subjective *pleasantness rating* (7-point Likert-type scale; -3 = not at all pleasant, +3 = extremely pleasant) of stroking per

condition was used to test whether slow touch was perceived as more pleasant than fast touch. (2) An *embodiment questionnaire* (Longo et al., 2008) was used to capture the subjective experience of the illusion (13 statements rated on a 7-point Likert-type scale; -3 = strongly disagree, +3 = strongly agree). In each condition, the questionnaire was administered pre- (i.e. embodiment due to the visual capture effect; see Appendix 1) and post-stroking (see Appendix 2) and their difference was calculated to obtain a measure of subjective embodiment due to visuo-tactile integration. This questionnaire consisted of four sub-components: *felt ownership*, that is related to the feeling that the rubber hand was part of one's body; *felt location* of own hand, that related to the feeling that the rubber hand and one's own hand were in the same place; *felt agency*, that is related to the feelings of being able to move the rubber hand; *affective component*, that included items related to the experience being interesting, pleasant and enjoyable (Longo et al., 2008). This difference between pre- and post- stroking for each of these components was examined, separately, as well as for an overall 'embodiment of rubber hand' (Longo et al., 2008) score, that was obtained by averaging the three subcomponents scores, namely ownership, felt location and felt agency that did not relate to affect. The study included this composite measure in order to examine whether the slow touch, which was predicted to be rated as subjectively more pleasant than fast touch, would have an overall effect on aspects of the subjective embodiment of the rubber-hand that were not primarily pleasantness-based. Lastly, the study employed (3) a *proprioceptive drift* measure, defined as the degree to which the hand is perceived to be closer to the rubber/real hand after the stroking. In each condition the value corresponding to the *actual* position of the participant's index finger was subtracted from the value corresponding to the *felt* position (see Procedures below), before ('pre' value) and after ('post' value) stroking and their difference was calculated to obtain a measure of proprioceptive drift due to multisensory integration, as in the case of the embodiment measure explained above. All analyses were conducted using non-parametric tests, as the data were not normally distributed. For confirmatory purposes, the same analyses were also run with parametric tests (ANOVA), revealing the same pattern of findings, but not reported here for brevity.

2.2.3. Materials

A black, wooden box measuring 34 cm x 65 cm x 44 cm was used to control visual feedback of the participants' arm/hand and the rubber, or the confederate's (real) arm/hand during the experiment (see Figure 2.1.). The box was placed approximately 15 cm in front of the participant's torso, with the centre of the box in alignment with the participant's left shoulder. The box was divided into two equal parts by a perpendicularly placed piece of opaque glass. Two circular holes (14 cm in diameter) on either side of the box allowed the participant and experimenter to place their arms inside; the left half of the box accommodated the participant's left forearm and hand, and the right half the rubber, or confederate's forearm and hand. A wooden lid prevented visual feedback of the participant's own arm. The top side of the box on the right was uncovered, allowing direct vision of the rubber/confederate's forearm and hand. The participant also wore a black cape to occlude vision of the proximal end of the rubber/real (confederate) arm and participant's left arm. Tactile stimulation (i.e. stroking) was applied using two, identical, cosmetic make-up brushes (Natural hair Blush Brush, N°7, The Boots Company).

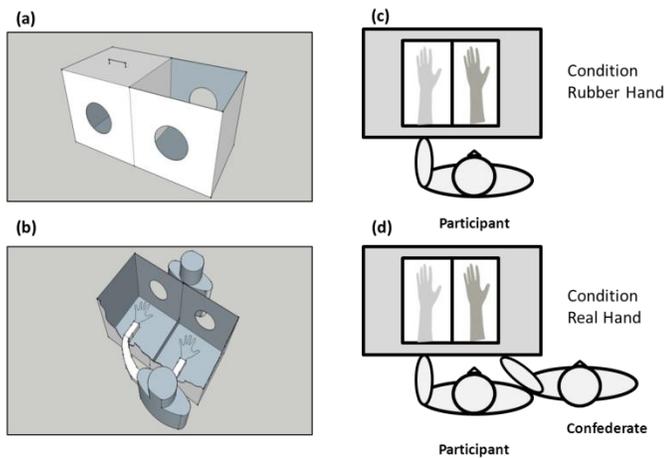


Figure 2.1. A schematic representation of the experimental set-up. A black wooden box measuring 34 cm x 65 cm x 44 cm (a) was placed approximately 15 cm in front of the participant's torso, with the centre of the box in alignment with the participant's left shoulder (b). The box was divided into two equal parts by a perpendicularly placed piece of opaque glass. Two circular holes (14 cm in diameter) on either side of the box allowed the participant and experimenter to place their arms inside; the left half of the box accommodated the participant's left forearm and hand, and the right half the rubber (c) or confederate's real (d) forearm and hand. A wooden lid (shown in a) prevented visual feedback of the participant's own arm. The top side of the box on the right was uncovered, allowing direct vision of the rubber/confederate's forearm and hand.

2.2.4. Procedure

Prior to the main experimental phase, participants were familiarised with procedures and all rating scales. Two adjacent stroking areas, each measuring 9cm long x 4cm wide were identified and marked with a washable marker on the hairy skin of participants' left forearm (wrist crease to elbow, McGlone, Olausson, Boyle, Jones-Gotman, Dancer et al., 2012). Stimulation was alternated between these two areas to minimise habituation, and congruent stroking area changes were applied to the rubber/confederate's hand in all instances.

In each condition, the experimenter placed the participant's left hand (palm facing down; fingers pointing forwards) at a fixed point inside the wooden box. A pre-stroking estimate of finger position was obtained using a tailor's tape measure placed on top of the box lid, above the participant's left hand, and in alignment with the coronal (frontal) plane. The section of tape laid across the box was varied across trials to avoid number repetition effects. The participant was asked to report a number on the tape to indicate where they thought their left index finger was located. The experimenter then measured and recorded the actual position of the participant's index left finger. Subsequently, the rubber or the confederate's left arm was positioned in the right half of the box, in front of the participant's body midline, and in the same direction as the participant's actual left arm. The distance between the participant's left arm and the visible arm (on the sagittal plane) was approximately 25 cm. The participant was then instructed to look at the visible arm continuously for 15 seconds, before completing the pre-stroking *embodiment questionnaire*.

The experimenter then sat opposite the participant and stroked the previously identified stroking areas (McGlone et al., 2012) for three minutes using a speed of either 3cm/s (slow/pleasant) or 18cm/s (fast/neutral). In the synchronous conditions, the participant's left forearm and the rubber/confederate's forearm were stroked such that visual and tactile feedback were congruent, whereas in the asynchronous conditions, visual and tactile stimulation were temporally incongruent.

After the stimulation period, the felt and actual location of the participant's left index finger was again measured. Participants then completed the post-stroking

embodiment questionnaire. Prior to commencing the next condition, they were given a 60s rest period, during which they were instructed to freely move their left hand.

2.3. Results

2.3.1. Pleasantness ratings

To establish whether slow stroking was generally perceived by participants as more pleasant than fast stroking, the main effect of Stroking Velocity on pleasantness ratings was examined (Figure 2.2.a). A Wilcoxon signed rank test confirmed that participants rated slow stroking (median = 4.5) as significantly more pleasant than fast stroking (median = 3.5, $Z = -4.94$, $p < 0.001$, $r = -0.5$).

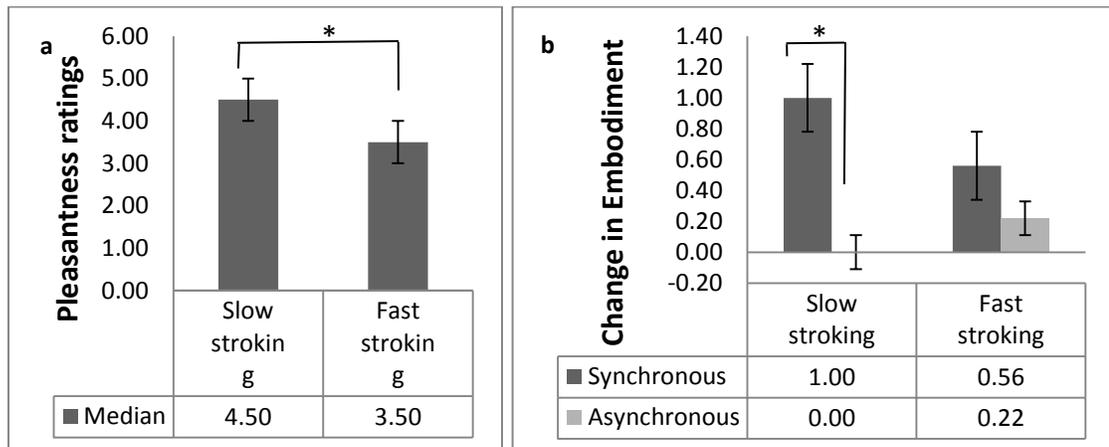


Figure 2.2. (a) Median and interquartile range (error bars) of pleasantness rating scores for slow and fast stroking. (b) Median and interquartile range (error bars) of change in embodiment of the rubber/real hand for synchronous (dark grey bars) and asynchronous (light grey bars) stroking.

2.3.2. Embodiment questionnaire – Composite Score of Ownership, Location and Agency

2.3.2.1. Main effects

A Wilcoxon signed rank test revealed a main effect of Stroking Mode, with synchronous stroking (median = 0.78) producing significantly higher embodiment scores than asynchronous stroking (median = 0.16; $Z = -3.44$, $p < 0.001$, $r = -0.35$), confirming

the classic RHI effect. A Mann-Whitney U test on the main effect of Seen Hand revealed that participants embodied the real hand (median = 0.79) to a significantly greater extent than the rubber hand (median = 0.33; $Z = -2.77$, $p = 0.005$, $r = -0.28$). The main effect of Stroking Velocity on embodiment was not significant ($Z = -1.64$, $p = 0.1$, $r = -0.17$).

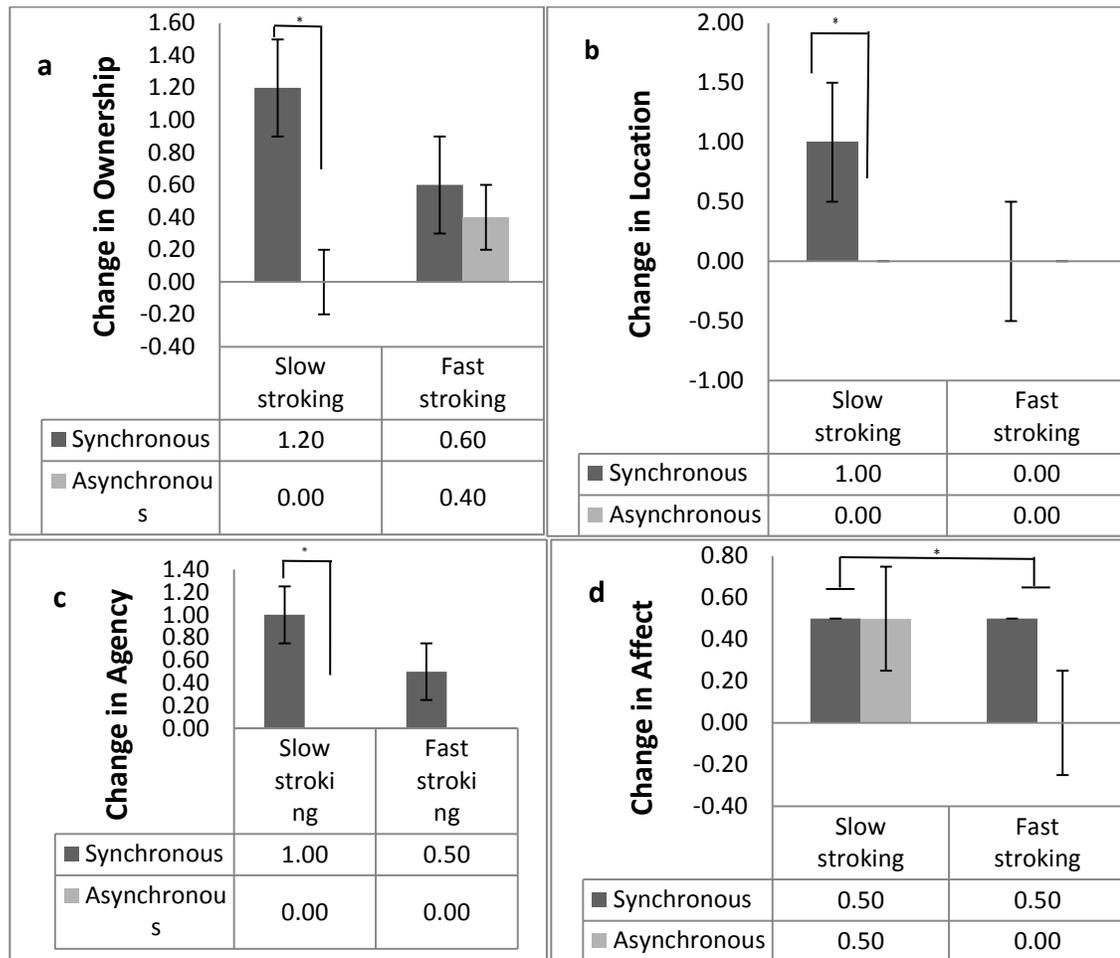


Figure 2.3. (a) Median and interquartile range (error bars) of change in ownership scores for synchronous (dark grey bars) and asynchronous (light grey bars) stroking. (b) Median and interquartile range (error bars) of change in location scores for synchronous (dark grey bars) and asynchronous (light grey bars) stroking. (c) Median and interquartile range (error bars) of change in agency scores for synchronous (dark grey bars) and asynchronous (light grey bars) stroking. (d) Median and interquartile range (error bars) of change in affect scores for synchronous (dark grey bars) and asynchronous (light grey bars) stroking.

2.3.2.2. Two-way effects

The interaction between Stroking Mode and Stroking Velocity was analysed by calculating the difference between synchronous and asynchronous scores in the slow and in the fast stroking conditions separately and subsequently using a Wilcoxon signed rank test to compare these two differential scores. This analysis revealed a significant interaction ($Z = -3.47$, $p < 0.001$, $r = -0.5$). Bonferroni-corrected post-hoc analyses ($\alpha = 0.025$) revealed that, when slow velocity was applied, synchronous stroking resulted in significantly higher embodiment scores compared with asynchronous stroking ($Z = -4.48$, $p < 0.001$, $r = -0.64$, Fig. 2b). This comparison was not significant when fast velocity was applied ($Z = -0.6$, $p = 0.55$, $r = -0.009$, Figure 3.2.b). The interaction between Seen Hand and Stroking Mode, as well as the interaction between Seen Hand and Stroking Velocity were likewise analysed by calculating the relevant differentials and comparing these between groups (real vs. rubber hand) using Mann-Whitney U tests. Both interactions were non-significant ($Z = -0.74$, $p = 0.47$, $r = -0.11$ and $Z = -0.71$, $p = 0.48$, $r = -0.1$, respectively).

2.3.2.3. Three-way effects

The interaction between Seen Hand, Stroking Velocity and Stroking Mode was analysed by averaging synchronous and asynchronous scores in the slow and the fast stroking conditions separately, calculating their difference, and then analysing the effect of Seen Hand on this difference using a Mann-Whitney U test. This interaction was not significant ($Z = -0.57$, $p = 0.58$, $r = -0.08$).

2.3.3. Sub-component analysis

2.3.3.1. Main effects

The above analyses were also run on the four subcomponents of the embodiment questionnaire. The pattern of results was identical to the one of the composite embodiment score for the ownership, location and agency subcomponents, while the results for the affect component showed some differences consistent also with the

pleasantness ratings results above. Specifically, Wilcoxon signed rank tests revealed a main effect of Stroking Mode, with synchronous stroking producing significantly higher ownership, location, agency and affective component scores than asynchronous stroking ($Z = -3.55, p < 0.001, r = -0.36$; $Z = -2.69, p = 0.006, r = -0.27$; $Z = -3.17, p = 0.001, r = -0.32$; $Z = -2.38, p = 0.02, r = -0.24$, respectively; Figure 2.3.). However, not surprisingly, there was also a main effect of Stroking Velocity in the affective sub-component, with participants giving significantly higher ratings when slow (median= 0.50) versus fast (median = 0.25) stroking was applied ($Z = -2.33, p = 0.02, r = -0.33$, Figure 2.3.d).

2.3.3.2. Two-way effects

The interaction between Stroking Mode and Stroking Velocity was analysed by calculating the difference between synchronous and asynchronous scores in the slow and in the fast stroking conditions separately and subsequently using a Wilcoxon signed rank test to compare these two differential scores. This analysis conducted separately for the four subcomponents revealed significant interactions for ownership, location and agency ($Z = -3.27, p = 0.001, r = -0.33$; $Z = -2.69, p = 0.006, r = -0.27$; $Z = -2.98, p = 0.002, r = -0.30$, respectively); there was no significant interaction for the affective component ($Z = -0.098, p > 0.9, r = -0.01$). Bonferroni-corrected post-hoc analyses ($\alpha = 0.025$) revealed that, when slow velocity was applied, synchronous stroking resulted in significantly higher ownership scores ($Z = -4.43, p < 0.001, r = -0.45$, Fig. 3a), location scores ($Z = -3.43, p < 0.001, r = -0.35$, Fig. 3b) and agency scores ($Z = -3.93, p < 0.001, r = -0.39$, Fig. 2.3.c) compared with asynchronous stroking. None of these comparisons was significant when fast velocity was applied (all $p > 0.12$). The interaction between Seen Hand and Stroking Mode, as well as the interaction between Seen Hand and Stroking Velocity were likewise analysed by calculating the relevant differentials and comparing these between groups (real vs. rubber hand) using Mann-Whitney U tests. All interactions were non-significant (all $p > 0.05$).

2.3.3.3. Three-way effects

The interaction between Seen Hand, Stroking Velocity and Stroking Mode was analyzed by averaging synchronous and asynchronous scores in the slow and the fast stroking conditions separately, calculating their difference, and then analyzing the effect of Seen Hand on this difference using a Mann-Whitney U test. This interaction was not significant for any of the subcomponents (*ownership*: $Z = -0.74$, $p = 0.46$, $r = -0.07$; *location*: $Z = -0.20$, $p = 0.85$, $r = -0.02$; *agency*: $Z = -1.05$, $p = 0.30$, $r = -0.11$; *affective component*: $Z = -1.50$, $p = 0.13$, $r = -0.15$).

2.3.4. Proprioceptive drift

Proprioceptive drift was analysed following the same plan of analyses as detailed above. These analyses revealed no significant main effects, two-way effects or three-way effects (all $ps > 0.10$).

2.4. Discussion

The results of this study confirmed previous findings that slow velocity, light touch on hairy skin is perceived as more pleasant than fast touch (Löken et al., 2009). Importantly, this study demonstrated for the first time that when such tactile stimulation is congruent to corresponding visual stimuli it produces higher levels of subjective embodiment during the RHI compared with fast, neutral touch. This result has been replicated in another recent study, confirming the influence of affective touch on the subjective experience of the rubber hand illusion only (Lloyd, Gillis, Lewis, Farrell & Morrison, 2013; but see van Stralen et al., 2014 for similar effect on proprioceptive drift only). Existing research has examined the effect of various multisensory, exteroceptive signals on embodiment by manipulating factors such as visual-tactile congruency (Botvinick & Cohen, 1998), limb position (Preston, 2013), and physical properties of the materials used to deliver tactile stimulation during the RHI (Schütz-Bosbach et al. 2009). However, to the author's knowledge, at the time when this experiment was run no study had specifically examined the effect of engaging the specialised, interoceptive modality of pleasant touch during the RHI. Thus, these data provided the first, direct

evidence that the perception of specialised interoceptive signals from the skin play an important role in both feelings and judgments of body ownership, as revealed by the different components of the embodiment questionnaire used in the current study. To the extent that the sense of body ownership is considered a fundamental aspect of self-consciousness (Gallagher, 2000), these findings provide support for the idea that interoception lies at the basis of the embodied psychological “self” (Craig, 2009; Damasio, 1999).

The results further showed that slow, synchronous stroking did not affect the perceived location of the participants’ own hand during the illusion. Although classic RHI studies have found that a reliable behavioural measure of the illusion is the degree to which one’s arm is felt to be closer in space to the rubber hand (proprioceptive drift, Botvinick and Cohen, 1998; Tsakiris and Haggard, 2005), this finding was consistent with recent studies that showed a dissociation between introspective (embodiment questionnaire) and behavioural (proprioceptive drift) measures of body ownership (Rohde, Di Luca & Ernst, 2011; Abdulkarim & Ehrsson, 2016). The results further specifically suggested that pleasant touch had a greater effect on introspective than behavioural measures of body ownership. This finding thus implied that an interoceptively-mediated embodiment of an external body part does not necessarily involve a spatial update of one’s own hand location. This conclusion may also relate to the more general observation that interoceptive pathways mainly convey homeostatic information that are relatively poor in spatial and discriminatory properties in relation to exteroceptive signals (Craig, 2002).

Lastly, these findings showed that participants generally embodied a confederate’s hand to a greater extent than a rubber hand, but this difference was unrelated to visuotactile congruency or stroke velocity. Contrary to the prediction, these findings suggest that the top-down knowledge and corresponding visual evidence that one is observing another person’s arm, are not sufficient to influence the effect of multisensory integration of congruent visual and tactile signals on body ownership (see also Longo, Schüür, Kammers, Tsakiris & Haggard, 2009), even if the tactile stimulation carries interoceptive information.

In conclusion, this study showed that dynamic, slow-velocity affective touch can have a fundamental role in the malleability of our sense of body ownership and highlights the central role of interoception and embodied affectivity in self-consciousness.

2.5. Limitations and future directions

Future studies could determine the precise tactile velocities most likely to maximise the effects of multisensory integration on body ownership, perhaps also in relation to individual differences in pleasant touch perception, as well as more generally interoceptive sensitivity. Furthermore, CT fibres have been reported to innervate only hairy skin (Vallbo et al., 1999) and the majority of RHI studies have applied tactile stroking to hairy skin sites. On this note, van Stralen and colleagues (2014) explored the effects of CT optimal and CT-non optimal stimulation during the rubber hand illusion separately on hairy (dorsal hand) and non-hairy (ventral hand) skin sites. It has been shown that slow, CT optimal touch enhanced the embodiment of the rubber hand illusion only for stimulation on the hairy skin, but not glabrous skin (van Stralen, van Zandvoort, Hoppenbrouwers, Vissers, Kappelle et al., 2014). Therefore, the role of affective touch in the sense of body ownership seemed to specifically relate to the involvement of additionally interoceptive information mediated by slow, caress-like touch.

In this study only female participants have been tested and the RHI paradigm has been applied only to the left hand, because of the previously reported link of the right insula with interoceptive awareness (Critchley et al., 2004), body ownership and awareness of action (Fotopoulou, Pernigo, Maeda, Rudd & Kopelman, 2010; Karnath et al., 2005; Tsakiris et al., 2007). Thus, future similar studies should explore the role of gender and right hand stimulation in the observed effect. Moreover, to the extent that pleasant touch (Bermudez, 2005; Björnsdotter, Löken, Olausson, Vallbo & Wessberg, 2009) and other interoceptive modalities such as pain (Krahé, Sringer, Weinman & Fotopoulou, 2013) are thought to play an essential role in affiliation and social interaction, these findings call for future studies that can investigate the potential role of

social, affiliative signals on the sense of body ownership and more generally, the malleability of the bodily self.

Integration of interoceptive and exteroceptive modalities during the Rubber Hand Illusion: An experimental study on the sense of body ownership

3.1. Introduction

Chapters 1 and 2 have already highlighted the importance of the sense of body ownership to bodily self-consciousness. We usually take the ability to identify our body as our own for granted, but in order to identify our limbs as our own and as part of our body, information coming from outside our body (exteroceptive stimuli) needs to be integrated with information from inside our body (interoceptive stimuli). Recent research has shown how important it is to successfully integrate these two aspects in order to develop a coherent sense of self (Aspell et al., 2013). More generally, the integration of different sensory modalities (multisensory integration, see Maravita, Spence & Driver, 2003 for a review) is a key component of the sense of body ownership (Tsakiris & Haggard, 2005).

As described in Chapter 2, the Rubber Hand Illusion (RHI, Botvinick & Cohen, 1998) is a widely-used experimental paradigm which allows us to investigate how multisensory integration takes place and affects body ownership. In its classic version, the illusion focuses on the interplay between vision, touch and proprioception. After a few minutes of synchronous (but not asynchronous) tactile stimulation, most of the participants experience a greater feeling of ownership for the rubber hand, in the sense that they agree with statements such as “it feels like the rubber hand is my own hand”. In particular, the traditional outcome measures of the illusion are: a subjective *embodiment questionnaire*, which includes questions such as “I felt like the rubber hand was my own hand”, and a *proprioceptive drift* which is the extent to which participants perceive the position of their own hand as shifted towards the rubber hand (Botvinick & Cohen, 1998). Both these outcome measures are considered evidence of the occurrence of the illusion, even though recent studies and the finding of Chapter 2 suggest that they might

highlight two dissociated aspects of the multisensory integration process, one being more introspective and one more behavioural (Rohde et al., 2011; Abdulkarim & Ehrsson, 2016).

Traditionally studies using the RHI manipulate only exteroceptive sources of information, such as vision and touch. Thus, the RHI sheds some light on the role of exteroception in the sense of body ownership, but the role of interoception and most importantly the relation between interoception, exteroception and body ownership has received less attention. Recent studies have, therefore, attempted to address this outstanding issue specifically. For example, it was originally found that the experience of owning a rubber hand can cause a drop in temperature of the participants own hand (Moseley et al., 2008). This finding seems to suggest that exteroceptive, multisensory integration can have an effect on the physiological regulation of the body during the illusion; however, subsequent studies have failed to replicate these findings (Guterstam et al., 2011; Rohde, Wold, Karnath & Ernst, 2013).

Tsakiris and colleagues (2011) showed that interoception sensitivity, in the sense of how good or bad participants perform in a Heartbeat Counting Task (Schandry, 1981), can predict the malleability of the sense of body ownership. In particular, participants with low interoceptive sensitivity seem to acquire ownership of the rubber hand to a greater extent compared to people with high interoceptive sensitivity. This effect seems to be due to a much more malleable sense of bodily self in the low compared to high interoceptive sensitivity participants (Tsakiris et al., 2011). According to this finding, interoceptive sensitivity could be considered a trait that is a rather fixed characteristic of each individual. Moreover, interoceptive sensitivity seems to correlate and predict behavioural and autonomic measures of temporary change in body-ownership, namely proprioceptive drifts and drop in skin temperature. This finding has been partially replicated and extended also in the context of the virtual body illusion (Aspell et al., 2013) and virtual RHI (Suzuki et al., 2013). In both studies, cardio-visual feedback was provided in synchrony or out-of-synchrony with the participants' own heartbeats, with only the synchronous condition increasing self-identification with the virtual body (Aspell et al., 2013) and embodiment of the rubber hand (Suzuki et al.,

2013). Furthermore, although Suzuki and colleagues (2013) found that this effect was modulated by the participants own interoceptive sensitivity, the direction of this finding seems to partially contradict the previous ones (Tsakiris et al., 2011). That is, Suzuki and colleagues observed a positive correlation between interoceptive sensitivity and proprioceptive drift in their virtual rubber hand study, indicating that better interoceptive awareness produced greater embodiment of the rubber hand; however one possible reason for this discrepancy with previous findings could be more methodological (due to differences in the procedures used and measures taken) rather than conceptual.

Although many studies on interoception focus on cardiac awareness and particularly the Heartbeat Counting Task to establish participants' levels of interoceptive sensitivity (Schandry, 1981), there are many other modalities of interoception, including some whose stimuli do not actually originate from within the skin. Specifically, according to Craig (2002; 2009), other modalities originating peripherally in the skin, such as pain and affective touch can be re-defined as interoceptive modalities, since they provide information about the internal states of the body at any given time and they may be associated with specialised neuroanatomical systems. In particular, as described in Chapter 1 and 2, affective touch is coded by specialised, unmyelinated CT afferents, which take a distinct ascending pathway from the periphery to the posterior insula (Olausson et al., 2002; Morrison et al., 2011). The posterior insular cortex is understood to support an early convergence of sensory and affective signals about the body that are then re-represented in the mid and anterior insula; the proposed sites of interoceptive awareness (Critchley et al., 2004; Craig, 2009).

Importantly, as described in Chapter 2, recent studies show that affective touch can modulate the sense of body ownership in the RHI. In particular, slow, caress-like touch that activates CT afferents can enhance the experience of owning a rubber hand more than fast, emotionally-neutral touch that does not cause CT activation (see Chapter 2; Lloyd et al., 2013; van Stralen et al., 2014). These findings support the idea that affective touch, and more generally interoception, may play a key role in the sense of body ownership, and by implication to our embodied psychological "self".

Taken together, the above studies suggest that interoception and particularly its integration with exteroception may be central for the sense of body ownership. However, to the author's knowledge no study has thus far addressed the role of interoceptive sensitivity as a trait (off-line) in paradigms that study the on-line, integration of interoceptive with exteroceptive modalities. Specifically, it is unclear whether the perception of interoceptive signals such as affective touch during the RHI, and their integration with exteroceptive signals will influence the sense of body ownership differently depending on individual differences in interoceptive sensitivity, as measured by a heartbeat counting task. Accordingly, this study aimed to observe for the first time whether interoceptive sensitivity would modulate the extent to which affective touch influences the multisensory process taking place during the rubber hand illusion, as measured using 1) subjective self-reports (i.e. an embodiment questionnaire), 2) an objective, behavioural measure (i.e. proprioceptive drift), and 3) physiological changes in the body (i.e. the temperature drop previously observed as a consequence of acquiring ownership of the rubber hand). To address this research question this study measured participants' interoceptive sensitivity with the standard heartbeat detection task (Schandry, 1981) and ran a RHI manipulating the velocity of touch, with stroking applied at slow, borderline and fast speeds.

3.2. Methods

3.2.1. Participants

Seventy-five, right handed females (mean age = 22.8 years; SD = 3.95) participated in the study in exchange for University credit or a £6 financial compensation. Six participants were later excluded from the data analysis due to technical issues (e.g. equipment failure) during data collection. Institutional ethical approval was obtained and the experiment was conducted in accordance with the Declaration of Helsinki. After giving their informed consent, participants reported their age, weight and height in order to calculate the Body Mass Index (BMI).

3.2.2. Design and Statistical analysis

The experiment used a 2 (Interoceptive Sensitivity (IS): High vs. Low) x 3 (Stroking Velocity: Slow vs. Borderline within the optimal range vs. Fast) mixed factorial design, with repeated measures on the latter factor. All these conditions were completed applying Synchronous stroking. An asynchronous control condition was also included using only the borderline velocity of touch in order to establish that the RHI was taking place during only synchronous trials, and to address the issue of synchronicity in the context of multisensory integration. The order of conditions was randomised across participants. Dependent variables comprised: (1) A subjective *pleasantness rating* (100 points rating scale; 0 = not at all pleasant, 100 = extremely pleasant) of stroking per condition, used to test whether slow touch was perceived as more pleasant than fast touch. (2) An *embodiment questionnaire* (Longo et al., 2008) was used to capture the subjective experience of the illusion (13 statements rated on a 7-point Likert-type scale; -3 = strongly disagree, +3 = strongly agree). In each condition, the questionnaire was administered pre- (i.e. to measure embodiment purely due to the visual capture effect; see Pavani, Spence and Driver, 2000; see Appendix 1) and post-stroking (see Appendix 2), and their difference was calculated to obtain a measure of subjective embodiment due to visuo-tactile integration. This questionnaire is composed of 4 sub-components: ownership, location, agency and affect. Also recorded was (3) the *proprioceptive drift*, defined as the degree to which the hand is perceived to be closer to the rubber hand after the stroking. In each condition the value corresponding to the *actual* position of the participant's index finger was subtracted from the value corresponding to the *felt* position (see Experimental Procedures and Materials below and Figure 3.1.c). This procedure was repeated before ('pre' value) and after ('post' value) stroking and their difference was calculated to obtain a measure of proprioceptive drift due to multisensory integration. Lastly, a (4) *temperature change* was measured, defined as the difference in skin temperature of the hand before and after the occurrence of the illusion. Following the procedure of Moseley et al. (2008), this study checked the temperature in three different locations on the hand (Figure 3.1.b). An average of these three measurements was considered as the final hand skin temperature and used for the

calculation temperature change. Correlational analyses including BMI, visual capture and proprioception were run to investigate their potential relationships with the primary outcome measures above. The data were tested for normality by means of the Shapiro-Wilk test and found to be non-normal ($p < .05$). Subsequent Log, Square Root and Reciprocal transformations did not correct for the normality violations, therefore appropriate non-parametric tests were used to analyse the data.

3.2.3. Apparatus and Materials

Participants' heart rate (HR) was measured using a Biopac MP150 Heart Rate oximeter, connected to a PC with AcqKnowledge software (version 3.9.2). To obtain a HR reading the oximeter was attached to the distal phalanx of the participant's non-dominant index finger (Figure 3.1.a): this was later transformed using the 'count peaks' function to give the number of recorded heartbeats. The Biopac was set up to begin recording when the experimenter selected 'Start' on the AcqKnowledge program and to stop recording after a pre-set time interval (25, 45 and 65 seconds). A baseline reading was obtained over a three minute period during which HR was recorded continuously.

The RHI was performed using a black, wooden box measuring 34 cm x 65 cm x 44 cm to control visual feedback of the participants' arm and the rubber hand during the experiment (see Figure 3.1.d). The box was placed approximately 15 cm in front of the participant's torso, with the centre of the box in alignment with the participant's left shoulder. The box was divided into two equal parts by a perpendicularly placed piece of opaque glass. Two circular holes (14 cm in diameter) on either side of the box allowed the participant and experimenter to place their arms inside; the left half of the box accommodated the participant's left forearm and hand, and the right half the rubber. A wooden lid prevented visual feedback of the participant's own arm. The top side of the box on the right was uncovered, allowing direct vision of the rubber forearm and hand. The participant also wore a black cape to occlude vision of the proximal end of the rubber arm and participant's left arm. Tactile stimulation (i.e. stroking) was applied using two, identical, cosmetic make-up brushes (Natural hair Blush Brush, N°7, The

Boots Company). Before and after each condition skin temperature was measured using an infrared thermometer with dual laser targeting (Precision Gold, N85FR).

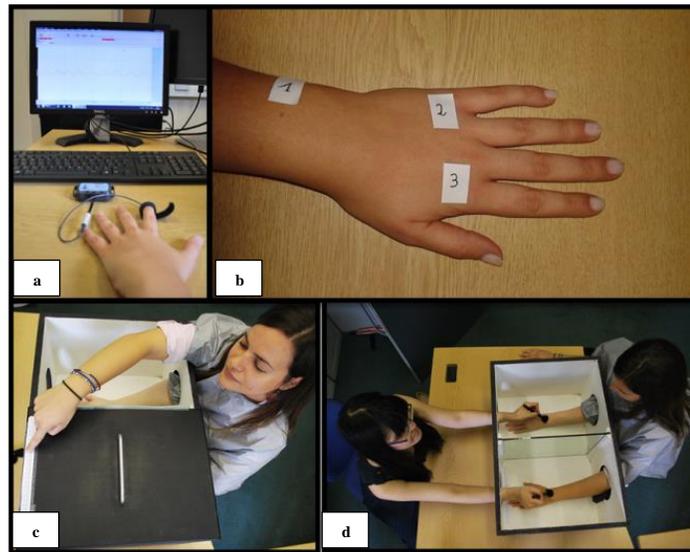


Figure 3.1. Materials and experimental procedure. **(a)** The Biopac pulse oximeter was attached to the participant's non-dominant index finger. **(b)** Sites at which the skin temperature was recorded on the participant's left hand, pre and post the stroking. **(c)** Procedure to record the Proprioceptive Drift. Participants were asked to close their eyes and indicate with the right hand using the ruler the position where they felt their left index finger was inside the box. This procedure was repeated before and after each condition of the RHI. **(d)** To induce the RHI the participant's left hand (usually hidden inside the box) is synchronously brushed with a rubber hand placed in front of the participant's view.

3.2.4. Experimental procedure

Participants sat at a table, with one experimenter seated on her left hand site, and the other one seated opposite to them. Upon arrival, a heartbeat baseline reading was obtained over a three minute period before the beginning of the counting task. Then, participants completed the heartbeat counting task (Schandry, 1981). Upon hearing an audio start cue participants were instructed to begin counting their heartbeat until they heard an audio stop cue. They were advised not to take their pulse and/or feel their chest; they were only allowed to “feel” the sensation of their heart beating. They did not receive any feedback regarding their performance. Following the audio stop cue participants verbally reported the number of heartbeats counted and a rest period of 30

seconds was given before the next interval began. Participants received no information about the interval lengths (25, 45 and 65 seconds), and these were presented in a randomised order across conditions.

The RHI procedure was conducted following completion of the heartbeat counting task. Prior to the RHI, participants were familiarised with the general procedures (e.g. they will be touched on their forearms) and all rating scales (see section Design and Statistical Analysis above). Two adjacent stroking areas, each measuring 9cm long x 4cm wide were identified and marked with a washable marker on the hairy skin of participants' left forearm (wrist crease to elbow, McGlone et al., 2012). Tactile stimulation was alternated between these two areas to minimise habituation (see Chapter 2), and because CT fibers are easily fatigued (Vallbo et al., 1999). The same stroking area was touched on the rubber hand in all the instances.

The RHI was conducted following the procedure fully described in Chapter 2. In this study only, skin temperature at the three sites on the participants' left hand was measured (Moseley et al. 2008) before obtaining a pre-stroking estimate of finger position (for the measurement of proprioceptive drift; see section Design and Statistical Analysis above) using a tailor's tape-measure placed on top of the box lid. Participants were asked to close their eyes and to indicate on the ruler with their right hand the position where they felt that their own left index finger was inside the box (Figure 3.1.c). The experimenter then measured and recorded the actual position of the participant's left index finger. Subsequently, the rubber arm was positioned and participant completed the pre-stroking *embodiment questionnaire*, as described in Chapter 2. The experimenter then sat opposite the participant and stroked the previously identified stroking areas (McGlone et al., 2012) for three minutes using a speed of either 3cm/s (slow/pleasant); 9 cm/s (borderline) or 18cm/s (fast/neutral). After the stimulation period, temperature and the felt and actual location of the participant's left index finger was again measured following the pre-induction procedure. Participants then completed the post-stroking *embodiment questionnaire*. Prior to commencing the next condition, they were given a 60s rest period, during which they were instructed to freely move their left hand.

3.3. Results

3.3.1. Interoceptive sensitivity

Interoceptive Sensitivity was calculated considering the three heartbeats perception intervals and using the following formula (Schandry, 1981; Pollatos, Kurz, Albrecht, Schreder, Kleemann et al., 2008):

$$\frac{1}{3} \sum (1 - (| \text{recorded heartbeats} - \text{counted heartbeats} |) / \text{recorded heartbeats})$$

The Interoceptive Sensitivity scores obtained following this transformation can vary between 0 and 1, with higher scores indicating a better estimation of the heartbeats (i.e. smaller differences between estimated and actual heartbeats). The median value of Interoceptive Sensitivity was 0.697 (SD = 0.233). As in previous studies (Ainley, Tajadura-Jimenez, Fotopoulou & Tsakiris, 2012; Maister & Tsakiris, 2014), following the median split method, the group of 69 participants was split into two groups of high Interoceptive Sensitivity (HIGH group, mean heartbeat perception = 0.836; SD = 0.08; n = 34) and low Interoceptive Sensitivity (LOW group, mean heartbeat perception = 0.479; SD = 0.19; n = 35).

3.3.2. BMI and pre-RHI measures

An analysis of the baseline measures (i.e. pre-RHI procedure) was conducted to ensure that there were no differences between the high and low groups in BMI, heartbeat baseline, skin temperature, proprioception and visual capture which could affect: 1) the performance on the Heartbeat Detection Task itself, and 2) any potential differences between groups following the RHI. The absence of any differences between groups before the RHI would suggest that any potential differences between groups following the RHI phase would be uniquely due to the online multisensory integration processes taking place during the illusion (Tsakiris et al., 2011). Table 3.1. summarises the pre-RHI measures for high versus low IS participants, and demonstrates that there were no significant differences between groups at baseline.

Table 3.1. Means and standard deviations are reported for illustrative purposes only

Baseline measures		Low IS group	High IS group	Mann-Whitney U	
		Mean (SD)	Mean (SD)		
BMI (Kg/m ²)		21.77 (2.49)	21.66 (3.06)	Z = -0.60	p = 0.55
Heartbeat baseline (3 mins)		229.24 (26.09)	228.89 (37.06)	Z = -0.16	p = 0.88
Pre-RHI measures	Baseline Skin Temperature	31.73 (2.55)	31.19 (2.39)	Z = -1.22	p = 0.23
	Visual Capture - Pre-Embodiment Questionnaire	-0.52 (1.37)	-0.68 (1.75)	Z = -0.64	p = 0.53
	Pre-Proprioceptive Drift	0.41 (3.59)	0.58 (4.53)	Z = -0.19	p = 0.85

3.3.3. Rubber Hand Illusion

3.3.3.1. Pleasantness ratings

As a preliminary check to establish whether slow stroking was generally perceived by participants as more pleasant than fast stroking, the main effect of Stroking Velocity on pleasantness ratings was examined. A Friedman test confirmed a main effect of Stroking Velocity ($\chi^2(2) = 37.9; p < 0.001$). Bonferroni-corrected post-hoc analyses ($\alpha = 0.017$ for 3 comparisons) revealed that participants rated slow stroking ($Z = -4.75; p < 0.001$; median = 85; Interquartile Range (IQR) = 25) and borderline stroking ($Z = -3.71; p < 0.001$; median = 80; IQR = 25.5) as significantly more pleasant than fast stroking (median = 75; IQR = 27.5). No significant differences were found between slow and borderline stroking ($Z = -2.14, p = 0.032$).

Subsequently, the analysis investigated the main effect of Group on pleasantness ratings regardless of velocity. Mann-Whitney *U* Test showed no significant differences between the high and low IS groups in the rating of pleasantness ($Z = -0.57; p = 0.57$; median high = 250; IQR = 100; median low = 235; IQR = 60). The interaction between Stroking Velocity and Group was analysed by calculating the difference between the CT optimal velocity (slow) and the no-CT optimal velocity (fast) in each group separately

and applying a Mann-Whitney U to test this differential between groups. The result was not significant ($Z = -0.024$, $p = 0.98$; median high = 5; IQR = 15; median low = 7; IQR = 15). Thus, although velocity influences the perceived pleasantness of the touch, IS group did not have an effect on pleasantness overall, nor during any particular velocity of stroking.

3.3.3.2. Embodiment Questionnaire

First, to confirm whether the procedure was able to elicit the classic RHI, synchronous and asynchronous stroking conditions were compared using a Wilcoxon signed rank. This revealed a main effect of Stroking Mode, with synchronous stroking (median = 1.11; IQR = 1.69) producing significantly higher embodiment scores than asynchronous stroking (median = 0.00; IQR = 1.06; $Z = -5.54$, $p < 0.001$), confirming the classic RHI effect. In order to investigate the main effect of Group on embodiment regardless of synchronicity, a Mann-Whitney U test was run comparing High and Low IS groups; the result was not significant ($Z = -0.71$; $p = 0.48$; median high = 0.67; IQR = 1.83; median low = 1.31; IQR = 2.13). The interaction between Stroking Mode and Group was analysed by calculating the difference between synchronous and asynchronous stroking for each group separately and applying a Mann-Whitney U test to compare these differential scores between groups. The result was not significant ($Z = -0.53$, $p = 0.60$; median high = 0.89; IQR = 2.22; median low = 1.22; IQR = 2.19). Thus, IS Group did not have an effect on embodiment scores overall, nor on the synchronous condition in particular.

Next, to investigate whether slow (pleasant) stroking leads to greater embodiment of the rubber hand overall, the effect of Stroking Velocity was analysed using a Friedman ANOVA, which showed a significant main effect ($\chi^2(2) = 9.36$; $p = 0.009$). Bonferroni-corrected post-hoc analysis revealed that slow touch (median = 1.00; IQR = 1.47; $Z = -2.05$, $p = 0.02$) and borderline touch (median = 1.11; IQR = 1.69; $Z = -2.57$, $p = 0.005$; Figure 3.2.) resulted in significantly greater embodiment of the rubber hand compared with fast touch (median = 0.56; IQR = 1.58). No significant difference was found between slow and borderline touch ($Z = -0.33$; $p = 0.37$).

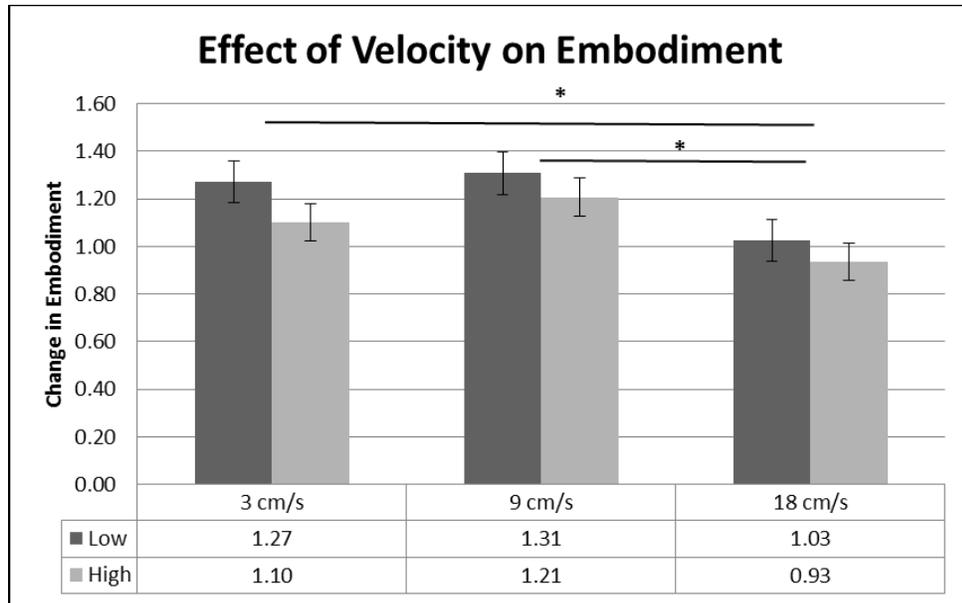


Figure 3.2. Main effect of Stroking Velocity on embodiment. The High and Low interoceptive sensitivity groups are represented separately.

Subsequently, the analysis investigated the main effect of Group on embodiment regardless of velocity and on synchronous conditions only. The Mann-Whitney *U* Test showed no significant differences between the high and low groups on embodiment ($Z = -0.74$; $p = 0.46$; median high = 2.22; IQR = 1; median low = 3.25; IQR = 3.97). The interaction between Stroking Velocity and Group was analysed by calculating the difference between the CT optimal velocity (slow) and the CT non-optimal velocity (fast) in each group separately and applying a Mann-Whitney *U* test to examine this differential between groups. The result was not significant ($Z = -0.18$, $p = 0.86$; median high = 0.22; IQR = 4.56; median low = 0.28; IQR = 1.25). Thus, although velocity influences embodiment overall during the RHI, IS group did not have an effect on embodiment overall, nor during any particular velocity of stroking.

Given the analysis conducted in Chapter 2, showing that the pattern of results was identical between the composite embodiment score for the ownership, location and

agency subcomponents and the subcomponents separately; in this study only the composite score for embodiment was analysed.

3.3.3.3. Proprioceptive Drift

The same plan of analysis described above for the embodiment scores were run for proprioceptive drift, with all analyses being non-significant (minimum $p = .35$). The summary statistics and test results are in Table 3.2.

Table 3.2. Summary statistics and test results for Proprioceptive Drift

		Results	Medians (Interquartile Ranges)		
Main effects	<i>Stroking Mode</i>	Z = -0.78; p = 0.44	Synch = -1.00 (2.50)	Asynch = -0.50 (3.50)	
	Group	Z = -0.60; p = 0.56	Low = -1.25 (6.75)	High = -1.50 (5.00)	
Interaction	Stroking Mode x Group	Z = -0.55, p = 0.59	Low = -0.75 (6.38)	High = 0.00 (5.50)	
Main effects	<i>Stroking Velocity</i>	$\chi^2 (2) = 1.59$; p = 0.46	Slow = -1.00 (4.00)	Borderline = -1.00 (2.50)	Fast = -0.5 (4.00)
	Group	Z = -0.08; p = 0.94	Low = -1.25 (8.25)	High = -2.00 (4.50)	
Interaction	Stroking Velocity x Group	Z = -0.94; p = 0.35	Low = 1.25 (4.00)	High = -0.50 (7.00)	

Note: Stroking mode = Synchronous vs. Asynchronous; Group = High vs. Low IS; Stroking Velocity = Fast vs. Slow.

3.3.3.4. Temperature Change

The same plan of analysis described above for the embodiment scores were run for temperature change, with all analyses being non-significant (minimum $p = .30$). The summary statistics and test results are in Table 3.3.

Table 3.3. Summary statistics and test results for Temperature Change

		Results	Medians (Interquartile Ranges)		
Main Effects	<i>Stroking Mode</i>	Z = -0.80; p = 0.43	Synch = -0.07 (0.55)	Asynch = -0.17 (0.48)	
	Group	Z = -0.88; p = 0.38	Low = -0.24 (0.98)	High = -0.23 (1.23)	
Interaction	Stroking Mode x Group	Z = -1.04; p = 0.30	Low = 0.20 (0.57)	High = 0.00 (0.56)	
Main effects	<i>Stroking Velocity</i>	χ^2 (2) = 0.36; p = 0.83	Slow = -0.03 (0.59)	Borderline = -0.07 (0.55)	Fast = -0.07 (0.59)
	Group	Z = -0.35; p = 0.73	Low = -0.25 (1.11)	High = -0.31 (1.60)	
Interaction	Stroking Velocity x Group	Z = -0.20; p = 0.84	Low = 0.07 (0.78)	High = 0.00 (0.70)	

Note: Stroking mode = Synchronous vs. Asynchronous; Group = High vs. Low IS; Stroking Velocity = Fast vs. Slow.

3.3.4. Correlational analysis

Exploratory (Spearman's) correlations were run to investigate whether the interoceptive modalities (interoceptive sensitivity and affective touch) were associated with BMI and the outcome measures of the RHI, namely embodiment questionnaires, proprioceptive drift and temperature drop. Neither interoceptive sensitivity nor the ratings of slow and fast touch correlated with (i) embodiment scores in the slow, borderline and fast conditions (all r between -0.125 and 0.12; all p between 0.31 and 0.99), nor (ii) the proprioceptive drifts in the slow, borderline and fast conditions (all r between -0.15 and 0.11; all p between 0.11 and 0.99). No correlations were found between the aforementioned modalities and the temperature drops in the slow, borderline and fast conditions (all r between -0.12 and 0.08; all p between 0.08 and 0.90).

3.4. Discussion

The aim of this study was to investigate for the first time the interplay between different interoceptive modalities, namely cardiac awareness and affective touch, in body representation. In particular, the study sought to explore whether interoceptive sensitivity would modulate the extent to which affective touch influences the multisensory process taking place during the rubber hand illusion, as measured using 1) subjective self-reports (i.e. an embodiment questionnaire), 2) an objective, behavioural measure (i.e. proprioceptive drift), and 3) physiological changes in the body (i.e. the temperature drop previously observed as a consequence of acquiring ownership of the rubber hand).

The results confirmed previous findings showing that the subjective (i.e. embodiment questionnaire) but not the objective (i.e. proprioceptive drift) component of the illusion can be enhanced by slow, affective touch (Chapter 2; Lloyd et al., 2013; but see van Stralen et al., 2014), resulting in a stronger conscious experience of acquiring ownership over the rubber hand. The dissociation between embodiment questionnaire and proprioceptive drift is widely accepted since these outcome measures seem to reflect two different aspects of the multisensory process taking place during the rubber hand illusion (Rohde et al., 2011). Even though the experience of owning a rubber hand is the result of multisensory integration processes, Rohde and colleagues (2011) proposed that the embodiment questionnaire is the most reliable measure to capture the phenomenological illusory experience. This aspect which gives rise to the subjective experience of owning the rubber hand might not be sufficient to result also in a re-location of the participant's own hand, which is responsible for the proprioceptive drift. Importantly, a recent study found no correlation between an experimentally induced proprioceptive drift and the sense of body ownership, supporting the idea that a spatial update of the hand position does not play a fundamental causal role in the experience of the rubber hand illusion (Abdulkarim & Ehrsson, 2016). Therefore, the mechanisms underlying the subjective and behavioral experience of the illusion seem to be independent, which explains why the effect of affective touch on body ownership may

be primarily captured by responses to embodiment questionnaires (Chapter 2; Lloyd et al., 2013, but see van Streelen et al., 2014).

In contrast, the findings reported here fail to support previous studies suggesting that interoceptive sensitivity, considered as a trait, can modulate the experience of the rubber hand illusion (Tsakiris et al., 2011; Aspell et al., 2013; Suzuki et al., 2013). That is, no difference was found between the low and high interoceptive sensitivity group in either the subjective/explicit or objective/implicit outcome measures of the rubber hand illusion.

Finally, in line with recent studies (e.g. Rohde et al., 2013), this study failed to replicate previous findings arguing for a physiological change (i.e. temperature change) in the hand as a consequence of the illusion induction (Moseley et al., 2008). As in the case of embodiment questionnaire and proprioceptive drift, this study did not find any modulation of interoceptive sensitivity and/or affective touch on this temperature effect. One potential explanation of this inconsistency between the original findings and the ones of this Chapter could be the implementation of a different methodology. In fact, the present study explored whether there was a change in temperature before and after the induction of the illusion in the stimulated hand only (as in Tsakiris et al., 2011 and Rohde et al., 2013). In contrast, Mosley and colleagues (2008) observed the difference in temperature between the two hands; therefore their results argue for a difference in temperature between the stimulated and the non-stimulated hand after the induction of the rubber hand illusion rather than focusing on the stimulated hand only. Taken together this evidence supports the idea proposed by Rohde and colleagues (2013) that the drop in temperature is observed only when following a specific experimental procedure (i.e. hand stroking and comparison between the two hands). Therefore this phenomenon cannot be considered a reliable indicator of the subjective experience of owning the rubber hand/ disowning the real hand.

Recent studies investigated the multisensory integration across interoceptive (i.e. cardiac awareness) and exteroceptive modalities in the rubber hand illusion, and they argue for a modulation of interoceptive sensitivity on the illusory experience (Tsakiris et al., 2011; Aspell et al., 2013; Suzuki et al., 2013). However, this research has provided

inconsistent results so far, potentially due to the involvement of different methodologies, such as the implementation of different tasks to assess interoceptive sensitivity, the difference in sample size (21 vs. 46 participants) and the use of a virtual rubber hand paradigm rather than the classic one in Suzuki et al. (2013). If on the one hand there is evidence supporting a greater tendency to acquire ownership of the rubber hand in people with lower interoceptive sensitivity (Tsakiris et al., 2011), on the other hand recent evidence argues for an opposite tendency (Suzuki et al., 2013). In this scenario, the results of this study might suggest a potential dissociation between off-line interoception (i.e. cardiac awareness as a trait) and exteroceptive interplay taking place between vision and touch during the rubber hand illusion. On the contrary, the relationship between on-line interoception (i.e. affective touch as part of a multisensory integration paradigm) and exteroception (vision in the same multisensory integration paradigm) is supported by the data presented in this study, confirming previous findings in this direction (see Chapter 2; Lloyd et al., 2013; van Stralen et al., 2014).

Given the recent evidence arguing for a role of affective touch as an interoceptive modality for the sense of body ownership, it was expected to find a relationship between the bodily pleasure raised by affective touch and the extent to which participants were aware of their body from within (i.e. interoceptive sensitivity). However, as tested in the present study, this prediction could not be confirmed, suggesting a potential dissociation between these two interoceptive modalities.

Interoception, by definition, is the physiological condition of the body (Craig, 2002; 2009). It includes several, different modalities, such as visceral sensation, cardiac awareness, pain, affective touch, and bladder distention, which all ultimately contribute to the awareness of the body from within. A study has attempted to investigate the relationship between two interoceptive modalities, namely cardiac awareness and sensibility for gastric functions (Herbert et al., 2012). These results show that there is a negative correlation between the performance on the heartbeat counting task and the water load test (i.e. amount of water drunk until reaching the point of individually perceived fullness), supporting the idea of a general sensitivity for interoceptive perception. However, to the author's knowledge, this is the only attempt to investigate

the relationship between two interoceptive modalities. Therefore, future research should extend these findings to include further modalities, as this study attempted to do.

On the basis of these findings, it is not possible to confirm a relationship between cardiac awareness and bodily pleasure resulting from affective touch. It could, alternatively, be speculated that these interoceptive modalities considered in the present study both contribute, but to a different extent, to the process of becoming aware of our body.

3.5. Limitations and future directions

In this study interoceptive sensitivity was considered as a trait, which means a stable measure of the way we perceive the body from within. Given this operational definition, the possibility could be considered that interoceptive sensitivity may be linked to specific personality traits, such as neuroticism-related traits (Ehlers & Breuer, 1992) and anxiety sensitivity (Stewart, Buffett-Jerrott & Kokaram, 2001) which have been associated with different levels of interoceptive awareness. However, information about personality traits has not been collected in this study; therefore future studies could extend this investigation including psychometric measures. Furthermore, given the interpersonal nature of affective touch, future studies should investigate the possibility that social presence and proximity might play a role in the performance on this task and therefore in the rating of perceived pleasantness. Additionally, it would be interesting to observe whether the same social modulation would apply to the performance on the heartbeat detection task (see Krahé et al., 2013 for similar investigation in the context of pain perception).

The heartbeat counting task has been used to measure interoceptive sensitivity, which is a well-established technique and widely used method (Schandry, 1981). However, recent evidence challenges the validity of the heartbeat detection task as measuring a trait since the performance on this task seems to be sensitive to changes such as beliefs (Ring & Brener, 1996), contingent feedback and physical exercise (Ring et al., 2015). Furthermore, heartbeat baseline measurements have been collected for a time window of 3 minutes. The author came to the knowledge that a 5 minutes baseline

is more informative of the heart rate variability after data collection had been performed. Therefore, this should be acknowledged as a limitation of this study.

It should also be noted that the temperature change has been measured only on the hidden hand and not in both hands as reported in other studies (Tsakiris et al., 2011; Rohde et al., 2013). A comparison between the temperature in both stroked and not stroked hand could provide further strength to the findings here reported.

In conclusion, this study further clarifies the relation between interoception and exteroception in the context of the rubber hand illusion. In particular, it is the first study to investigate the relation between trait cardiac awareness and the perception of affective touch, providing support for the idea that they might have independent roles in the sense of body ownership.

The effect of oxytocin on the perception of affective touch and body awareness

4.1. Introduction

The physical and mental wellbeing of humans seems to be connected to the quality of social interactions (Eisenberger & Cole, 2012). An active social network has been associated with reduced morbidity and mortality (Berkman, 1995). Individuals who report to have strong social relationships have fewer hospital admissions and health-care visits (Bosworth & Schaie, 1997; Rodríguez-Artalejo, Guallar-Castillón, Herrera, Otero, Chiva et al., 2006), and the quantity and quality of social relationships seems to have a protective role for the development of disorders such as depression and dementia (Russell & Cutrona, 1991; Fratiglioni, Wang, Ericsson, Maytan & Winblad, 2000).

Recent research has started to explore whether some of the above benefits can be explained by tactile aspects of social interactions (see Walker & McGlone, 2013 for a review). Although the physiological and neurobiological effects of touch are not fully understood, in humans as well as in others animals, touch appears to have a fundamental importance in promoting social relationships and physical and psychological wellbeing (Gallace & Spence, 2010). Animal research has firstly suggested the importance of “contact comfort” early in life for the developing monkey (Harlow & Zimmermann, 1958), as well as in rats (Sullivan, Wilson & Leon, 1989). Subsequently, in humans, a range of studies provided support for the importance of somatosensory stimulation early in life in reducing distress and crying response (Stack & Muir, 1990; Vannorsdall, Dahlquist, Shroff Pendley & Power, 2004). Tactile interactions have also been found to reduce the association between maternal depression and negative outcome in infancy (Sharp et al., 2012), and to promote a healthy development in the case of premature infants (Feldman & Eidelman, 2003). More generally, the positive effect of touch for physical and psychological wellbeing has been supported by a wide range of clinical studies, which also stress the positive impact of the so called ‘massage therapy’ (Field,

2010; 2014 for a review). However, there is a lack of experimental research supporting this idea, and there is a need for more specificity regarding which mechanisms mediate the positive influence of touch, and what the neurobiological basis is of the aforementioned effect.

A neurobiological mechanism involving oxytocinergic systems has been hypothesised to provide the motivation to initiate and maintain affiliative and tactile behaviours. By implication, this mechanism might promote social interactions and wellbeing (Ellingsen et al., 2015 for a review; Uvnäs-Moberg, Handlin & Petersson, 2015, for a review). Oxytocin is a neuropeptide consisting of nine amino acids, mostly synthesised in the hypothalamus. This neuropeptide acts both peripherally as a hormone and centrally as a neurotransmitter within the brain (Viero, Shibuya, Kitamura, Verkhatsky, Fujihara et al., 2010; MacDonald & MacDonald, 2010; Uvnäs-Moberg et al., 2015, for reviews). The most well-known situations which are related to oxytocin release are labor and breastfeeding, when oxytocin acts peripherally as a hormone to stimulate uterine contractions and milk ejection, respectively (Burbach, Young & Russell, 2006). On the other hand, oxytocin seems to act centrally, to regulate social behaviors and stress regulation. In fact, oxytocin is also associated with the onset of maternal behavior; however, it is not only released during interaction between mothers and infants, but also during positive interaction between adults or between humans and animals (see Insel, 2000; Light et al., 2005; Dunbar, 2010). Furthermore, oxytocin may have an important role in promoting general wellbeing by means of its interaction with both the dopaminergic system in the nucleus accumbens (Insel, 2003) and the opioid systems, by reducing the perceived stress and sensitivity to pain, respectively (Lund, Yu, Uvnäs-Moberg, Wang, Yu et al., 2002; McCall & Singer, 2012). Animal studies have also shown that oxytocin is released in response to various types of sensory stimulation, such as painful and light pressure massage-like somatosensory stimulation (Uvnäs-Moberg et al., 2015 for a review). In humans, fifteen minutes of slow massage is associated with plasma oxytocin release (Morhenn, Beavin & Zak, 2012, but see also Wikström, Gunnarsson & Nordin, 2003) and the experience of 'warm touch' between married partners enhanced salivary but not plasma oxytocin concentrations in both males

and females (Holt-Lunstad, Birmingham & Light, 2008). Importantly, one study showed that light touch, but not deep tissue massage, increases the peripheral release of oxytocin (Rapaport, Schettler & Bresee, 2010).

Oxytocin has the capacity to stimulate its own release. Non-noxious sensory stimulation have been found to increase the release of oxytocin from the oxytocinergic neurons, which project from the paraventricular nucleus to the locus coeruleus and the nucleus tractus solitaries. This activation might result in decreased stress levels and decreased reactivity to stress (Uvnäs-Moberg & Petersson, 2005). However, the precise physiological nature of these sensory nerves, which mediate the effects of non-noxious stimulation, is still unknown. The unmyelinated, CT fiber afferents may be involved in mediating this effect of hedonic tactile stimulation (McGlone et al., 2014; see Chapter 1, section 1.2.). Slow, CT optimal touch has been found to play a role in promoting affiliative behaviours, social bonds and the communication of emotions (Morrison et al., 2010 for a review). Hence, the affective dimension of touch could have a specific role in mediating the positive effect of touch on wellbeing via oxytocin release; however, there is no direct evidence for this relationship.

The development of a nasal spray which allows safe, non-invasive, central administration of oxytocin to the human brain (MacDonald, Dadds, Brennan, Williams, Levy et al., 2011) has recently made it possible to study directly the effect of oxytocin administration on human behavior. Over the last two decades, intranasal oxytocin has been widely administered in doses between 18 to 40 International Units (IU), without observing any adverse or specific side effects (MacDonald et al., 2011). Intranasal administration seems to be an effective way for oxytocin to penetrate the blood-brain barrier compared to blood injection methods. In fact, Mens and colleagues showed that just a minimum part (0.002%) of oxytocin injected in the blood reached the central nervous system (Mens, Laczi, Tonnaer, de Kloet & van Wimersma-Greidanus, 1983). In contrast, when oxytocin is delivered as nasal spray, it might enter the central nervous system directly via olfactory or trigeminal neurons, or it might act peripherally to affect behaviours indirectly, via oxytocin receptors which are activated at high concentrations of oxytocin (MacDonald & MacDonald, 2010; Striepens, Kendrick, Hanking, Landgraf,

Wüllner et al., 2013). Research involving intranasal oxytocin has uniquely contributed to our understanding of human social brain and showed that this delivery method provides a direct pathway to the brain (for a review, MacDonald & McDonald, 2010). However, studies investigating the relationship between the central and peripheral effects of intranasal administered oxytocin are mostly correlational and still controversial. Intranasal oxytocin may facilitate the function of these neurons and therefore increase oxytocin release, via the activation of oxytocin receptors located on sensory neurons (Burbach et al., 2006). Several studies have demonstrated the effect of intranasal oxytocin on human behavior by comparing this with an identical placebo spray condition containing all the ingredients except the active oxytocin (Bartz, Zaki, Bolger & Ochsner, 2011).

Several accounts have been proposed to explain the mechanisms by which oxytocin might produce its effects on human behaviour. These include: (1) the *prosocial hypothesis*, which argues that oxytocin has mainly the positive effect to enhance affiliative prosocial behaviours, such as trust and generosity (Kosfeld, Heinrichs, Zak, Fischbacher & Fehr, 2005; Zak, Stanton & Ahmadi, 2007), and it helps understanding others' affective mental states and emotions (Domes, Heinrichs, Michel, Berger & Herpertz, 2007); (2) the *fear/stress hypothesis*, which suggests that oxytocin affects social performance by attenuating stress (McCarthy, McDonald, Brooks & Goldman, 1996); (3) the *in-group/out-group hypothesis*, which proposes that oxytocin regulates cooperation within a group, but enhances conflict among individuals of different groups (De Dreu, Greer, Handgraaf, Shalvi, van Kleef et al., 2010). Since oxytocin has been traditionally associated with an improvement in social cognition and promotion of prosocial behavior, this hypothesis seems to suggest that the effects of oxytocin are not always positive and may be context-dependent. In addition, (4) the *social salience hypothesis* argues that oxytocin increases sensitivity to social cues depending on contextual variables and individual traits (Averbeck, 2010; Shamay-Tsoory, 2010; Bartz et al., 2011; Olf, Frijling, Kubzansky, Bradley, Ellenbogen et al., 2013). For example, traits such as aggression or introversion have been argued to influence the behaviour in

specific contexts, and should be taken into account when observing the potential modulation of intranasal oxytocin (Bartz et al., 2011 for a review).

Finally, (5) consistently with the framework of the social salience hypothesis, it has been proposed that oxytocin might increase the precision (i.e. the difference between top-down expectations and bottom-up experiences) of interoceptive signals. This account, developed in a predictive coding framework, argues that oxytocin might sharpen the salience of signals conveying homeostasis and socially relevant information, facilitating the development of the emotional and social self (Quattrochi & Friston, 2014). Here the focus will be mainly on the social salience theoretical framework, which attempts to integrate the prosocial account, the stress hypothesis, and the intergroup effect in one unique account, by focusing on the role of oxytocin in increasing the salience of social cues. In this context, it has been proposed that oxytocin might interact with the dopaminergic system in order to increase the attention orientation towards social cues (Shamay-Tsoory & Abu-Akel, 2016).

As reviewed in Chapter 1, affective touch has been redefined as an interoceptive modality, since it provides information about the internal states of the body. Interoceptive signals, such as cardiac awareness and bodily pleasure, contribute to maintain homeostasis, to infer emotional states, and ultimately to provide a sense of the embodied self (Craig, 2002). Additionally, the study described in Chapter 2 supported the important role played by interoceptive sensations elicited by CT optimal touch to the sense of body ownership, which is a fundamental aspect of bodily self-consciousness. To date, only a handful of studies have attempted to specifically investigate the effect of oxytocin on the perception of social, affective touch. These studies offer novel avenues to further explore the reciprocal relationship between oxytocin and affective touch, also in relation to interoceptive sensitivity and bodily self-consciousness.

A recent behavioral study did not find any effect of intranasal oxytocin on the perception of touch pleasantness (Ellingsen, Wessberg, Chelnokova, Olausson, Laeng et al., 2014). Specifically, following the self-administration of 40 IU of oxytocin or placebo, participants were asked to rate the pleasantness of the tactile stroking delivered at a CT optimal velocity only on their left forearms, while looking at human faces

displaying different emotional expressions. The results showed no effect of intranasal oxytocin on the perception of affective touch; however an increase of perceived attractiveness and friendliness of the faces was found. It should be pointed out that the study did not control for contextual effects that could have played a role in the experimental setting, such as the gender of the person delivering the touch. Furthermore, the sample was mixed gender and the female participants were recruited in different phases of the menstrual cycle and without considering the use of contraceptive pills (see Salonia, Nappi, Pontillo, Daverio, Smeraldi et al., 2005, for evidence that plasma oxytocin varies across the menstrual phase and effect of contraceptive pill on hormonal levels). Also, the experimenter was delivering the human touch with his/her hand covered with a silk glove, rather than by means of the traditional brush used in studies investigating the perception of CT optimal touch (Björnsdotter et al., 2009; Löken et al., 2009) and at a CT optimal velocity only. These aspects of the experimental design might have played a role in the perceived pleasantness of the touch, and they do not allow for conclusions to be made regarding the specific involvement of the CT afferents system, since a non-CT optimal control condition was not included. Therefore, the potential effect of intranasal oxytocin on tactile pleasantness remains an open question, and it should be compared to the potential modulation of emotionally neutral touch using standard procedures whilst controlling for velocity of touch, gender of the toucher, and testing time within the menstrual cycle.

Top-down expectations about the physical characteristics of the touch, manipulated by means of words labels, have been found to positively modulate the perceived pleasantness of the touch (McCabe, Rolls, Bilderbeck & McGlone, 2008). In line with this finding, a recent study provided further support to the modulation of top-down expectations on the perception of touch, by investigating the effect of positive expectations on an inactive nasal spray (i.e. placebo). Participants were given a nasal spray which was verbally associated to analgesic properties and they were asked to rate the pleasantness of the touch. The results showed that the placebo enhanced the perceived pleasantness of touch, and reduced the unpleasantness of painful touch, confirming previous data on the so-called placebo analgesia effect. This study might

support the hypothesis that similar circuits seem to regulate the placebo analgesia and placebo hyperhedonia effect (Ellingsen, Wessberg, Eikemo, Liljencrants, Endstad et al., 2013). This evidence supporting the influence of top-down factors on tactile pleasantness is particularly informative in the context of oxytocin research and provides important suggestions for the optimal methodology to be used. Specifically, the above data suggested the importance of adding a placebo condition to the active one to control for the expectations that participants might have. Furthermore, it highlighted the necessity to apply a double-blind methodology in order to avoid any potential influence, even if unwanted, coming from both the participant and/or the experimenter.

The modulation of the context and top-down information on the perception of tactile pleasantness and on the effect of intranasal oxytocin was further explored in another recent study. Scheele and colleagues (2014) investigated whether the effect of intranasal oxytocin on the perception of interpersonal touch was dependent on the person delivering the touch, and the extent to which this effect was correlated with autistic traits. In the randomised, placebo-controlled study they tested the effect of a single intranasal dose (24IU) of oxytocin in response to CT optimal touch on a male only sample. Participants were made to believe that the experimenter was either gender matched or not, although the same touch pattern (and female experimenter) was actually used in all the experimental sessions. The results showed that oxytocin increased the perceived pleasantness of female, but not male, touch and this effect was negatively correlated with autistic-like traits. This study provides evidence for the importance of the context in which touch is delivered, particularly in terms of the gender of the person delivering the touch.

Accordingly, this study explored (1) how the pleasantness of affective, CT-optimal touch and emotionally neutral, non-CT optimal, touch was modulated by intranasal oxytocin vs. placebo; (2) the extent to which interoceptive sensitivity - in the sense of cardiac awareness - was influenced by oxytocin vs. placebo; and (3) whether oxytocin vs. placebo has an effect on the sense of body ownership, as tested by means of the rubber hand illusion (see Chapter 2 and 3).

To the extent that affective touch reflects a unique mechanism for social affiliation and based on the theory suggesting a sharpened effect of oxytocin for social stimuli and interoceptive signals, intranasal oxytocin was expected to increase the perceived pleasantness of CT optimal touch compared to non-CT optimal touch. Additionally, given the role of affective touch to the sense of body ownership, as investigated by means of the rubber hand illusion (see Chapter 2), it was hypothesised that embodiment of the rubber hand would be enhanced following administration of oxytocin only, and specifically in the condition where touch was delivered at slow/CT optimal velocity. In contrast, intranasal oxytocin was not expected to influence the rubber hand illusion when touch was applied at fast/non-CT optimal velocity. That is, intranasal oxytocin was expected to enhance the embodiment of the rubber hand to a greater extent when interoceptive signals were involved (i.e. affective touch) compared to the emotionally neutral condition (i.e. fast touch). Quattrocki and Friston's (2014) theory would suggest an increase in interoceptive sensitivity following the administration of intranasal oxytocin but not placebo. However, given the evidence suggesting that contextual and individual factors might play a role in the effect of intranasal oxytocin (see above), interoceptive sensitivity was here included as a trait measurement and therefore no increasing effect of intranasal oxytocin vs. placebo on cardiac awareness was expected. Furthermore, only heterosexual females were tested, and all of the experimenters involved in the study were gender matched, to avoid any additional meaning that could be attributed to the touch as the study of Scheele and colleagues (2014) seems to suggest (Scheele et al., 2014).

4.2. Methods

4.2.1. Participants

Forty-one healthy females were recruited through the University College London subject pool system. They were aged between 18 and 40 years ($M = 24.73$, $SD = 3.84$). Participants were recruited in the follicular phase of their menstrual cycle (between the 5th and 14th day) to control for hormonal levels (Salonia et al., 2005). All participants

were heterosexual and were not taking any medication (including the contraceptive pills; see Salonia et al., 2005). Exclusion criteria included being left handed, being pregnant or breastfeeding (see MacDonald et al., 2011), a history of any medical, neurological or psychiatric illness, BMI out of the normal range (18.5 – 25; M = 21.31; SD = 2.84), use of any drugs within the last six months, and consumption of more than five cigarettes per day. Participants were asked to refrain from consuming any alcohol the day before testing and any alcohol or coffee on the day of testing. All participants provided informed consent to take part and received a compensation of £40 for travelling expenses and time. Ethical approval was obtained by the National Research Ethics Service NRES Committee London - Queen Square, as this study was part of a wider investigation involving also patients recruited in NHS sites. Ten participants were later excluded due to an error in the experimental protocol (in which CT optimal touch was administered following an incorrect procedure) and five participants were excluded from the analysis as they were found to be extreme outliers in their pleasantness scores at baseline (difference from the sample mean greater than two standard deviations). Therefore, the total sample used for the analyses reported below is of 26 participants.

4.2.2. Experimental design and statistical analysis

The study employed a double-blind, placebo-controlled, randomised, cross-over design, with treatment (oxytocin vs. placebo) as the within-subjects factor. Each subject participated in two identical sessions lasting 1.5 hours each and between 1 to 3 days apart; this was to ensure that they were tested in the same phase of the menstrual cycle. In one session participants were asked to self-administer 40 IU of oxytocin and in the other session 40 IU of placebo (see Materials section below for details and Figure 4.1.) in a counter-balanced and double-blinded manner. Participants were randomly allocated to the nasal spray sequence (AB/BA); twelve participants received placebo on the first visit and intranasal oxytocin on the second visit, whereas fourteen participants received intranasal oxytocin on the first visit and placebo on the second visit.

All data were analysed using SPSS, and by means of parametric tests as the data were normally distributed. The data were analysed using a linear mixed models design

which allowed the use of both fixed and random effects in the same analysis. Fixed effects have levels that are of primary interest and would be used again if the experiment were repeated. Random effects have levels that are not of primary interest, but rather are thought of as a random selection from a much larger set of levels. For example, subject effects are almost always random effects, while treatment levels are almost always fixed effects. An advantage offered by mixed-effects models is that hypotheses about the structure of the variance-covariance matrix can be tested by means of maximum likelihood methods that are now in common use in many areas of science, medicine, and psychophysiology (Seltman, 2009).

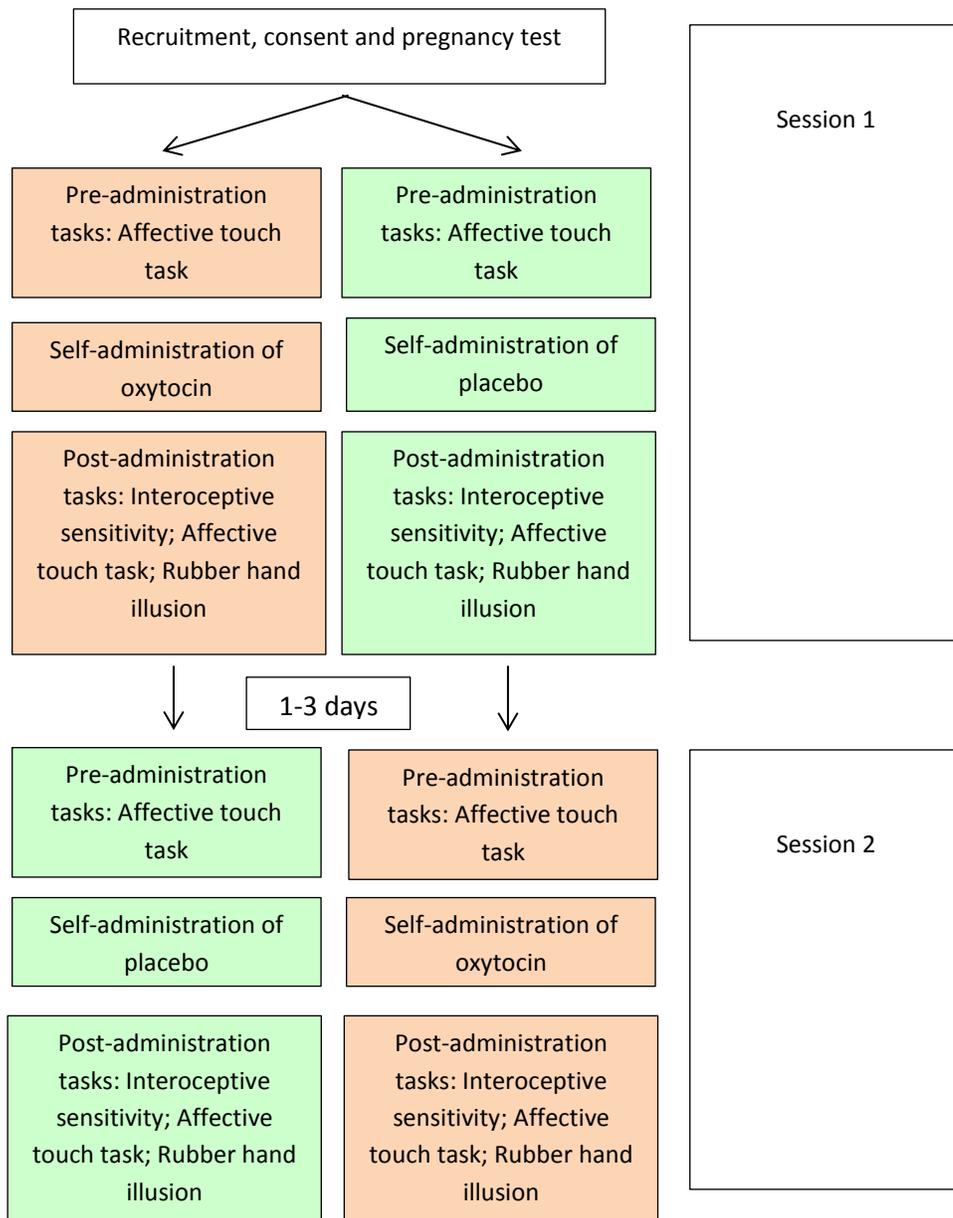
In this study, separate linear mixed model (LMM) analyses were run for the heart rate variability, interoceptive sensitivity, affective touch task, and rubber hand illusion (these being different dependent variables, as detailed below). In these analyses, participants were treated as random variables, since the interest is on the effects present in the general population rather than specifically for the individuals who participated to the experiment; order of nasal spray administration (oxytocin-placebo or placebo-oxytocin) was included as a covariate in all the analyses.

For the LMM analysis of heart rate variability, five minutes heart rates were recorded for three times throughout the testing session in order to control for any change due to the effect of nasal spray based on different time effects. Previous research suggests that oxytocin might increase heart rate variability (Kemp, Quintana, Kuhnert, Griffiths, Hickie et al., 2012) and therefore the three measurements taken at different stages of the testing procedure allowed a critical observation of any change in resting heartbeat activity during the entire study. The primary outcome measures were the heart rates and observation were made of the effect of time of recording and nasal spray. The interoceptive (cardiac awareness) scores were obtained only after the nasal spray administration and, therefore, a separate Linear Mixed Model analysis was run with interoceptive sensitivity post nasal spray administration as the dependent variable, and nasal spray as the independent variable. Interoceptive sensitivity has been used as a trait measure in this study and therefore, no change was expected between oxytocin and placebo.

In the analysis of the affective touch task, the primary outcome dependent variable was the pleasantness of the touch following nasal spray administration. The pre-administration baselines measurements of pleasantness from both the experimental sessions were then entered as covariates in the linear mixed model analysis. The independent variables were the nasal spray and the velocity of touch. The treatment effects (oxytocin versus placebo) was tested using the ANCOVA approach (Senn, 2002; Metcalfe, 2010; Paloyelis, Krahé, Maltezos, Williams, Howard et al., 2015) for the analysis of AB/BA cross-over designs with baseline measurements before each treatment treated as covariates.

The rubber hand illusion data were collected only after nasal spray administration. As in Chapters 2 and 3, outcome measures were the proprioceptive drift and embodiment questionnaire. Pleasantness ratings were also collected and analysed as a manipulation check that slow touch was perceived and rated as more pleasant than fast touch. The rubber hand illusion was repeated under three different conditions (see below); these were analysed by means of two separate LMM analyses. One analysis was run to test the effect of synchronicity only on the occurrence of the illusion (i.e. comparison between synchronous and asynchronous touch condition, see Chapter 2) and the subsequent interaction between synchronicity and nasal spray. The other analysis in the context of the rubber hand illusion was run to test the effect of velocity in synchronous conditions only on the occurrence of the illusion (i.e. comparison between slow and fast touch in synchronous conditions only) and the subsequent interaction between velocity of touch and nasal spray.

Figure 4.1. Study design and flowchart.



4.2.3. Materials

4.2.3.1. Oxytocin and placebo spray

Oxytocin nasal sprays have been developed and widely used in research (see e.g., Guastella & MacLeod, 2012, for a review). In the present study, participants received 40 IU of oxytocin (Syntocinon-Spray, Novartis, Basel, Switzerland) and 40IU of placebo (containing the same ingredients as Syntocinon except without the active ingredient oxytocin, Victoria Apotheke Zuerich, Switzerland) by means of a nasal spray. Two practice bottles containing water were used for the participants to familiarise themselves with the procedure; one for the experimenter to demonstrate and one for the participant to practice. Participants self-administered a puff containing 4IU every 30 seconds alternating between nostrils (five for each nostril) for a total of ten puffs. Half of the sample started the administration on the right nostril, and half on the left nostril. The self-administration procedure took about nine minutes, including three minutes of rest at the end (Paloyelis et al., 2015).

4.2.3.2. Heartbeat baseline and interoceptive sensitivity

The participant's actual heartbeat was recorded using a Biopac MP150 Heart Rate oximeter, and data were analysed using AcqKnowledge software (version 3.9.2). In the present study, a heartbeat baseline of five minutes was recorded three times throughout the experiment; immediately after the end of the administration nasal spray (non-active post administration, HB1), at the beginning of the nasal spray active window (post administration, HB2) and at the end of the experiment (non-active post administration, HB3).

A full account of the methods used to assess interoceptive sensitivity can be found in Chapter 3. Briefly, interoceptive sensitivity was assessed by means of the heartbeat detection task (Schandry, 1981), where participants are asked to count their own heartbeat without feeling their chest or taking their pulse. As in Chapter 3, the counting procedure was repeated for three different lengths time intervals (25, 45 and 65 seconds), presented in a randomised order and separated by a resting time of 30 seconds.

Participants did not receive any feedback regarding their performance and the interval length.

4.2.3.3. Affective touch task

For the affective touch procedure, two rectangles were drawn on the hairy skin of the participants left forearm, each measuring 4cm x 9cm (as in Chapter 2 and 3). Participants placed their left arm on the table with palm facing down and they were asked to wear a blindfold to avoid visual feedback of the tactile stimuli. Tactile stimulation (i.e. stroking) was administered for three seconds using a soft cosmetic make-up brush (Natural hair Blush Brush, N°7, The Boots Company) at two different velocities: one CT-optimal (3 cm/s: one stroke in 3 seconds) and one not CT-optimal (18 cm/s: six strokes in 3 seconds). In the present study a total of sixteen tactile stimuli were delivered, eight at slow velocity (3 cm/s) and eight at fast velocity (18 cm/s). The order of velocity was randomised and tactile stimulation was alternated between the rectangles drawn on the skin, to minimise habituation (see Chapter 2 and 3). After each brush stroke participants verbally rated the pleasantness of the touch using a scale from 0 (not at all pleasant), to 100 (extremely pleasant). A copy of the scale was placed on the table for reference. The affective touch task was performed twice at each testing session: before and after nasal spray administration.

4.2.3.4. Rubber hand illusion

The rubber hand illusion was performed following the procedure fully described in Chapters 2 and 3. In each condition, the experimenter placed the participant's left hand (palm facing down; fingers pointing forwards) at a fixed point inside a wooden box. A pre-stroking estimate of finger position was then obtained (for the measurement of proprioceptive drift; see section Design and Statistical Analysis of Chapter 2 and 3) using a tailor's tape-measure placed on top of the box lid. Participants were asked to close their eyes and to indicate on the ruler with their right hand the position where they felt that their own left index finger was inside the box. The experimenter then measured

and recorded the actual position of the participant's left index finger. Subsequently, the rubber arm was positioned in the right half of the box, in front of the participant's body midline, and in the same direction as the participant's actual left arm. The distance between the participants' left arm and the visible arm (on the sagittal plane) was approximately 25 cm. The participant was then instructed to look at the visible arm continuously for 15 seconds, before completing the pre-stroking *embodiment questionnaire* (i.e. visual capture measurement; see Appendix 1). In this study, the experimenter then sat opposite the participant and stroked the previously identified stroking areas (McGlone et al., 2012) for one minute using a speed of 3 cm/s (slow/pleasant) or 18cm/s (fast/neutral). In the synchronous conditions, the participant's left forearm and the rubber forearm were stroked such that visual and tactile feedback were congruent, whereas in the asynchronous conditions, visual and tactile stimulation were temporally incongruent. The asynchronous condition was run only at slow velocity to control for the occurrence of the illusion, while the synchronous condition was repeated twice; one at slow velocity and one at fast velocity to control for the effect of velocity on the embodiment process. The order of the three conditions (slow/synchronous, slow/asynchronous and fast/synchronous) was randomised between participants, but it was kept constant within participants. After the stimulation period, the felt and actual location of the participant's left index finger was again measured following the pre-induction procedure. Participants then completed the post-stroking *embodiment questionnaire* (see Appendix 2). Prior to commencing the next condition, they were given a 60s rest period, during which they were instructed to freely move their left hand.

4.2.4. Procedure

The experiment was run by two female experimenters. After signing the consent form and in the first session only, participants were asked to provide a urine sample and a pregnancy test (Pregnancy test device, SureScreen Diagnostics) was carried out by one experimenter to exclude the possibility of any ongoing, unknown pregnancy. This was done for security reasons given the role of oxytocin on labor (see section 4.1. of the

present Chapter). After confirmation of the negative result of the pregnancy test the experimental procedure started. Participants were familiarised with the pleasantness ratings scale and with the experimental procedure (above). They were asked to place their left arm resting on the table, palm down, and the two rectangular areas on the forearm were marked. Participants then wore the blindfold and were asked to rate the pleasantness of the touch.

Subsequently, participants self-administered, under both experimenters' supervision, either intranasal oxytocin or the placebo. The order of the treatment was counterbalanced across participants, and both experimenters and participants were blind to the treatment order. Experimental instruction about the aim of the nasal administration, the position of the head and of the nasal spray inside the nasal cavity, and breathing technique were given to the participants. Participants were familiarised to the administration procedure by means of a practice nasal spray as described above. Before the beginning of the self-administration procedure, all the participants were asked to blow their nose. Thirty-seconds breaks were given between puffs and participants were specifically instructed to not blow their nose during the administration procedure.

At the end of the last puff, participants were given three minutes of resting time in which they were instructed to rest. After that, the first heartbeat baseline reading was recorded for 5 minutes (HB1). During the 25 minutes time post-spray administration (see MacDonald et al., 2011; Paloyelis, Doyle, Zelaya, Maltezos, Williams et al., 2014 for optimal temporal window) no social contact between the participant and the experimenters took place beyond necessary experimental instructions. Participants were asked to refrain from checking their phones or doing any personal reading. During the waiting time of oxytocin activation, a weight estimation task was completed (as part of an experiment not reported in this Chapter). In the remaining time, participants were offered the opportunity to complete a Sudoku. At the beginning of the active oxytocin window (25 minutes after the end of the administration procedure, see Paloyelis et al., 2014 for optimal temporal window), the second heartbeat baseline was recorded for five minutes (HB2). Participants then completed the heartbeat detection task for the

assessment of interoceptive awareness (see section 4.2.3. above). Following this, the affective touch task (section 4.2.3.) and the rubber hand illusion (section 4.2.3.) tasks were completed in a counterbalanced order (half of the sample followed the post administration order of affective touch task-rubber hand illusion and half of the sample followed the post administration order of rubber hand illusion-affective touch task). After completion of the full experimental procedure, the heartbeat baseline was recorded for the last time (HB3). Participants were fully debriefed and reimbursed £40 for their time at the end of the second study visit.

4.3. Results

4.3.1. Heartbeat baseline and interoceptive sensitivity

In order to investigate the effect of nasal spray on heart rate, a LMM analysis was run as described above. Participants' heart rates were the dependent variables, the order of administration of the compound was the covariate, and nasal spray (oxytocin, placebo) and time of recordings of the baselines (HB1, HB2 and HB3) were the two independent variables. No significant main effects of nasal spray or time of recording were found on heart rate ($F(1, 25.28) = 1.29, p = 0.266$; $F(2, 26.04) = 0.41, p = 0.668$; respectively). No significant interaction of nasal spray and time was found ($F(2, 26.84) = 0.56, p = 0.576$). Contrary to previous studies (Kemp et al., 2012), this analysis failed to highlight a specific effect of intranasal oxytocin on participants' heart rates.

A separate LMM analysis was run to investigate the effect of nasal spray (independent variable) on interoceptive sensitivity (dependent variable), taking into account the order of administration (covariate). As expected, no significant main effect of nasal spray was found on interoceptive sensitivity ($F(1, 25) = 3.29, p = 0.08$); therefore, intranasal oxytocin did not seem to specifically affect the ability to detect internal cardiac signals.

4.3.2. Affective touch task

A separate LMM analysis was run following an ANCOVA approach (see above). The dependent variable was the post administration pleasantness scores, whereas the independent variables were the nasal spray (oxytocin vs. placebo) and the velocity of touch (slow vs. fast). The order of administration (AB/BA) and the baseline measures were considered in the model as covariates. As expected there was a significant main effect of velocity of touch ($F(1, 31.60)$; $p = 0.012$), with slow touch (Mean = 69.31, Standard Error = 1.56) being rated as significantly more pleasant than fast touch (M = 65.95, SE = 1.36). Nasal spray did not have a significant main effect on pleasantness ratings ($F(1, 29.28) = 1.17$; $p = 0.289$). Contrary to the predictions, there was no significant interaction between nasal spray and velocity of touch ($F(1, 34.63) = 0.62$, $p = 0.438$). Oxytocin was not found to affect the perception of pleasantness of either affective or neutral touch.

4.3.3. Rubber hand illusion

4.3.3.1. Pleasantness ratings

To establish whether slow stroking was generally perceived by participants as more pleasant than fast stroking, this study examined the effect of velocity of touch and nasal spray (independent variables) on pleasantness ratings during the rubber hand illusion procedure (dependent variable) by means of a linear mixed model analysis. The order of administration was considered in the analysis as a covariate. Contrary to the predictions, the effect of velocity did not have a main effect on pleasantness ratings ($F(1, 26) = 3.33$; $p = 0.079$); however there was a non-significant tendency ($p < .10$) for slow touch (M = 77.22; SE = 3.07) to be rated as more pleasant than fast touch (M = 73.15; SE = 3.49). Also, nasal spray did not have a significant main effect on pleasantness ratings ($F(1, 26) = 3.809$; $p = 0.062$). However, there was again a non-significant tendency ($p < .10$) for higher pleasantness ratings following intranasal oxytocin (M = 77.40; SE = 2.94) administration compared to placebo (M = 72.97; SE =

3.62). The interaction between velocity of touch and nasal spray was not significant ($F(1, 26) = 1.285; p = 0.267$).

4.3.3.2. Embodiment questionnaire

As specified in section 4.2.2., a linear mixed model analysis was run to explore the effect of synchronicity and nasal spray (independent variables) on the change in embodiment. The order of administration was considered in the analysis as a covariate. This analysis revealed a main effect of synchronicity ($F(1, 26) = 11.45; p = 0.002$), with synchronous touch ($M = 0.817, SE = 0.196$) leading to greater embodiment compared to asynchronous touch ($M = 0.140; SE = 0.163$). This result confirmed the occurrence of the illusion from a subjective point of view. Nasal spray did not have a significant main effect of the change in embodiment ($F(1, 26) = 0.369; p = 0.549$). Additionally, the interaction between synchronicity and nasal spray was not significant ($F(1, 26) = 1.952; p = 0.174$), suggesting that oxytocin did not seem to affect the subjective experience of embodiment of the rubber hand.

A separate linear mixed model analysis was run to investigate the effect of velocity of touch and nasal spray (independent variable) on the change in embodiment (dependent variable) in synchronous conditions only (i.e. slow/synchronous vs. fast/synchronous) and with order of nasal spray administration considered as a covariate. This analysis showed a main effect of nasal spray ($F(1, 26) = 11.71; p = 0.002$), with oxytocin leading to a greater embodiment (embodiment oxytocin, $M = 0.896, SE = 0.169$) compared to placebo (embodiment placebo, $M = 0.793; SE = 0.194$). However, velocity of touch did not have a significant main effect on the change in embodiment ($F(1, 26) = 3.16, p = 0.087$). The interaction between nasal spray and velocity of touch was non significant ($F(1, 26) = 0.735; p = 0.399$). This analysis seemed to suggest that oxytocin, but not the velocity of touch, enhanced the subjective experience of the illusion. That is, the effect of oxytocin on embodiment seemed to be independent of whether the touch was delivered at slow/CT optimal or fast/non-CT optimal velocities.

4.3.3.3. Proprioceptive drift

As specified in section 4.2.2., a LMM analysis was run to explore the effect of synchronicity and nasal spray (independent variables) on proprioceptive drift (dependent variable). The order of administration was considered in the analysis as a covariate. This analysis showed that neither synchronicity ($F(1, 26) = 0.03$; $p = 0.956$) nor nasal spray ($F(1, 26) = 1.183$; $p = 0.287$) had a significant main effect on proprioceptive drift. The interaction between synchronicity and nasal spray was found to be non-significant ($F(1, 26) = 2.434$; $p = 0.131$). These results showed that the participants did not experience the illusion at a behavioural/objective level, in line with previous findings suggesting a dissociation between the subjective and objective experience of the rubber hand illusion (see Chapter 2 and 3; Rohde et al., 2011; Abdulkarim & Ehrsson, 2016). Additionally, oxytocin did not have an effect on the multisensory mechanisms that underlie the illusion objective experience of the illusion.

Finally, a separate LMM analysis was run to investigate the effect of velocity of touch and nasal spray (independent variable) on proprioceptive drift (dependent variable) in synchronous conditions only (i.e. slow/synchronous vs. fast/synchronous) and with order of nasal spray administration considered as a covariate. This analysis showed that neither velocity of touch ($F(1, 26) = 0.106$; $p = 0.748$) nor nasal spray ($F(1, 26) = 1.175$; $p = 0.288$) had a significant main effect on proprioceptive drift. Additionally, the interaction between velocity of touch and nasal spray was non-significant ($F(1, 26) = 0.708$; $p = 0.408$). These results showed that velocity of touch did not affect the objective experience of the illusion.

4.4. Discussion

This study aimed to explore (1) how the pleasantness of affective, CT-optimal touch and emotionally neutral, non-CT optimal, touch was modulated by intranasal oxytocin vs. placebo; (2) the extent to which interoceptive sensitivity - in the sense of cardiac awareness - was influenced by oxytocin vs. placebo; and (3) whether oxytocin

vs. placebo had an effect on the sense of body ownership, as tested by means of the rubber hand illusion.

To the extent that affective touch reflects a unique mechanism for social affiliation and based on the theory suggesting a sharpened effect of oxytocin for social stimuli and interoceptive signals, intranasal oxytocin was expected to increase the perceived pleasantness of CT optimal touch compared to non-CT optimal touch. The results confirmed that slow touch was perceived as more pleasant compared to fast touch; however, contrary to the prediction, intranasal oxytocin did not affect the perceived pleasantness of the touch differently for CT optimal and non-CT optimal touch. This result was in line with previous findings showing that oxytocin did not affect the perception of slow touch (Ellingsen et al., 2014). However, the results of pleasantness ratings' analysis in the context of the rubber hand illusion showed a significant trend of oxytocin to increase the pleasantness of touch regardless of velocity. In the present study, the non-CT optimal touch condition was included to investigate a potential different modulation of tactile pleasantness perception between slow vs. fast touch conditions. Additionally, in this study participants were asked to wear a blindfold to control for the effect of visual feedback and all the experimenters were gender matched. When controlling for these factors, intranasal oxytocin did not affect the perception of tactile pleasantness differently compared to placebo. To the author's knowledge only one study found an increasing effect of intranasal oxytocin in the hedonic experience of touch (Scheele et al., 2014). However, Scheele et al. tested only heterosexual males, and an increase in pleasantness rating by means of intranasal oxytocin was found only when participants believed they were being touched by a female experimenter, rather than a male experimenter. In the study presented here, the participants were heterosexual females and all the experimenters were females. Therefore, the previously reported increase in pleasantness of touch by means of intranasal oxytocin may not be related to the velocity of touch. Instead, the observed modulation of pleasantness by Scheele et al. (2014) might have been strongly context dependent and associated with factors that go beyond the tactile stimulation *per se* (i.e. gender of the person delivering the touch).

Given the role of affective touch to the sense of body ownership (as investigated by means of the rubber hand illusion; see Chapter 2), it had been hypothesised that embodiment of the rubber hand would be enhanced following administration of oxytocin only, and specifically in the condition where touch was delivered at slow/CT optimal velocity. In contrast, intranasal oxytocin was not expected to influence the rubber hand illusion when touch was applied at a fast/non-CT optimal velocity. That is, intranasal oxytocin was expected to enhance the embodiment of the rubber hand to a greater extent when interoceptive signals are involved (i.e. affective touch) compared to the emotionally neutral condition (i.e. fast touch). The results showed that intranasal oxytocin, but not affective touch, might lead to a greater embodiment compared to placebo. That is the effect of oxytocin on embodiment seemed to be independent of whether the touch was delivered at slow/CT optimal or fast/non-CT optimal velocities. In contrast, oxytocin did not seem to affect the objective experience of the illusion; that is, proprioceptive drift was not affected by oxytocin or placebo in a different way.

As discussed in previous Chapters (Chapters 2 and 3) and in line with previous findings, this study showed a dissociation between the subjective experience of the illusion, as assessed by means of the embodiment questionnaire, and the objective measure of the illusion, in the sense of proprioceptive drift toward the rubber hand. In fact, the results showed that participants experienced the rubber hand illusion (i.e. difference between the synchronous and asynchronous condition) only when measured by means of the change in embodiment, but not by means of the spatial update of their felt hand position (proprioceptive drift) (Rohde et al., 2011; Abdulkarim & Ehrsson, 2016; Chapters 2 and 3). Therefore, intranasal oxytocin did not affect the experience of the illusion differently when CT optimal touch was involved. This finding seems to be in line with recent findings suggesting a role of oxytocin in differentiating and sharpening the distinction between self and other (Colonello, Chen, Panksepp & Heinrichs, 2013). If this were the case, the oxytocin might actually have diminished the illusion, enhancing the awareness of the distinction between the participants' and the rubber hands. However, it should be acknowledged that more early studies conducted in animals suggested that oxytocin might “soften” the boundaries between self and others,

particularly in bodily terms, promoting social bonds and affiliation, as well as patterns of relating (Insel, 1992; 2000).

Given the evidence suggesting that contextual and individual factors might play a role in the effect of intranasal oxytocin (see above), interoceptive sensitivity was included in this study to control for this. In fact, interoceptive sensitivity could be potentially used as a trait measurement and therefore no increasing effect of intranasal oxytocin vs. placebo on cardiac awareness was expected. As predicted, interoceptive sensitivity did not change following the administration of intranasal oxytocin, supporting the idea that it could be considered as a rather fixed trait. Also, it should be noted that, although both affective touch and cardiac awareness can be considered as interoceptive modalities; the first has a social component that the latter one does not. However, in this study, data relative to a baseline measure of interoceptive sensitivity (i.e. pre administration of oxytocin or placebo) had not been collected; therefore it had not been possible to include this as a trait measure in the analysis.

In conclusion, this study showed a non-significant effect of intranasal oxytocin on social touch regardless of velocity of touch, since the same pattern of results has been found for both slow and fast touch. Additionally, interoceptive sensitivity, as measured by means of the heartbeat detection task, was not affected by intranasal oxytocin. Taken together, the findings of the present study might suggest that intranasal oxytocin did not influence the detection of interoceptive signals, regardless of their internal (i.e. cardiac awareness) or external (i.e. tactile pleasantness) nature. This could also relate to the fact that oxytocin did not influence the embodiment of the rubber hand to a greater extent when touch was delivered at CT optimal velocity. This finding was not surprising given the evidence suggesting that an integration of exteroceptive and interoceptive signals is necessary in order to construct the sense of body ownership (see Chapter 1). To the extent that the sense body ownership is a constitutive aspect of bodily self-consciousness, together with the perceived location and the first-person perspective (Dijkerman, 2015), this study showed that oxytocin might only partially affect the bodily self. In fact, the integration of three components of bodily self-consciousness is fundamental in order to build a coherent sense of bodily self. This study seemed to

suggest that oxytocin might enhance the subjective experience of body ownership during the illusion, regardless of the involvement of interoceptive signals from the body.

4.5. Other Limitations

In line with evidence showing the importance of top down factors and expectation on the effect of the nasal spray (e.g. Scheele et al., 2014), it should be acknowledged that in this study individual differences (i.e. psychometric measures) have not been taken into account. Although the findings above highlighted the possibility to use interoceptive sensitivity as a trait measure given the fact that oxytocin did not seem to affect it, in this study a baseline of interoceptive sensitivity measured before nasal spray administration was missing. Therefore, future research should take individual traits measured both by means of questionnaires and interoceptive awareness task. In the same context, the experimenter was always a gender-matched unfamiliar person. Given the role of oxytocin on social and affective bonding, it could be argued that the effect of oxytocin might be stronger when the touch is delivered by a loved one.

The results reported above showed significant trends, especially in the context of the rubber hand illusion. Therefore, given the complexity of the study, it should be acknowledged that a bigger sample would increase the power and maybe highlight some significant effects that the current study failed to show.

Finally, the intranasal administration of oxytocin has its own limitations that should be pointed out and, as highlighted in the Introduction of this Chapter, the debate around this methodology is still ongoing.

The perception of affective touch in anorexia nervosa

5.1. Introduction

Anorexia nervosa (AN) is a psychiatric disorder characterised by: (a) the persistent restriction of energy intake leading to significantly low body weight relative to healthy norms, (b) fear of gaining weight and related behaviors, and (c) a disturbance in body weight or shape perception, including unawareness of such perceptual disturbances (DSM-V, American Psychiatric Association, 2013). In addition, patients with AN may show other deficits, such as hyperactivity (Kron, Katz, Gorzynski & Weiner, 1978), repetitive and stereotypic behaviors (Anderluh, Tchanturia, Rabe-Hesketh & Treasure, 2003, Cassin & von Ranson, 2005), disturbances in mood (Blinder, Cumella & Sanathara, 2006) as well as social cognition and attachment difficulties (see Caglar-Nazali, Corfield, Cardi, Abwani, Leppanen et al., 2014 for a systematic review).

The aetiology of AN remains unknown. One proposal is that decreased serotonin neurotransmission as a consequence of malnutrition is thought to play a role in the hyperactivity, depression and behavioral impulsivity observed in this population (Haleem, 2012; Kaye, Fudge & Paulus, 2009). Another line of research including animal models and human neuroimaging studies suggests that a dysfunctional dopamine-based reward system is associated with the disorder (Avena & Bocarsly, 2012; Kaye, Wierenga, Bailer, Simmons & Bischoff-Grethe, 2013). It is unclear whether these abnormalities are the cause or the result of chronic dysfunctions in eating behavior; nevertheless, AN patients show low novelty seeking and seem to be more anhedonic than those with bulimia nervosa (Davis & Woodside, 2002) and other eating disorders (Tchanturia, Davies, Harrison, Fox, Treasure et al., 2012). Some researchers propose that restricting food intake and exercising have become aberrantly rewarding in AN patients, in a fashion similar to the pathological processes seen in addiction (Scheurink, Boersma, Nergardh & Södersten, 2010). Other theorists claim that AN is associated with

a reduced experience of pleasure associated with food (food anhedonia) and a hyporesponsive striatal dopamine system (Zink and Weinberger, 2010). The present study mainly focuses on the latter aspects of the disorder.

More generally, it has been proposed that impaired social cognition and interpersonal relating play a key role in the onset and maintenance of anorexia nervosa (Zucker, Losh, Bulik, LaBar, Piven et al., 2007; Castro, Davies, Hale, Surguladze & Tchanturia, 2010; Arcelus, Haslam, Farrow & Meyer, 2013). Individuals with AN are typically reserved, have limited social networks, and self-report poorer quality and quantity of relationships (Tchanturia, Smith, Weineck, Fidanboyly, Kern, et al., 2013; Tiller, Sloane, Schmidt, Troop, Power et al., 1997). Furthermore, experimental studies have shown that patients with AN have impairments in emotion recognition, as well as cognitive and affective ‘theory of mind’ (i.e. inferring other people’s mental states; see Zucker, Merwin, Bulik, Moskovich, Wildes et al., 2013; Caglar-Nazali et al., 2014, for reviews). For example, people with AN may show attentional biases when processing social stimuli, paying more attention to angry, negative (Harrison, Tchanturia & Treasure, 2010), or ‘rejecting’ human faces (Cardi, di Matteo, Corfield & Treasure, 2012). Moreover, some of these attentional biases are correlated with early adverse social experiences (e.g. early separation from parents, unwanted sexual experiences) (Cardi et al., 2012).

Despite the above evidence and theories, few studies have attempted to understand the possible relationship between social cognition and reward abnormalities in AN. One possibility is that some of the social difficulties patients with AN show may be associated with the lack of pleasant feelings coming from social interactions; a disturbance termed social anhedonia (Tchanturia et al., 2012). To examine this further, this study focused on the perception of interpersonal, ‘affective touch’ and its social modulation. As described in Chapter 1, affective touch is associated with a distinct class of slow-conducting, unmyelinated CT afferents, present only in the hairy skin of mammals and responding specifically to gentle stroking delivered at slow speeds (between 1-10 cm/s) (Löken et al., 2009). Neuroimaging evidence suggests that CT afferents take a distinct ascending pathway from the periphery to the posterior insular

cortex (Morrison et al., 2011; Olausson et al., 2002), which is thought to serve the convergence of interoceptive signals from the body, i.e. signals that monitor the homeostatic state of the organism (Craig, 2009). Further re-mappings of such signals in anterior cortical areas are thought to allow integration of such signals with other information about the body, as well as with other cognitive and social factors, ultimately serving body awareness and its modulation by dispositional and contextual factors (Craig, 2009; Critchley et al., 2004). Given the aforementioned role of the anterior insula in bodily self-awareness, and the altered neural activity in this area in individuals with AN as shown by a functional neuroimaging study (Kerr, Moseman, Avery, Bodurka, Zucker et al., 2015), it has been argued that this population might suffer from a physiologically distorted sense of self (Pollatos et al., 2008; Kaye et al., 2009).

Interoceptive perception in individuals with AN has been associated with altered activity in the insular cortex (Strigo, Matthews, Simmons, Oberndorfer, Klabunde et al., 2013; Wagner, Aizenstein, Mazurkewicz, Fudge, Frank et al., 2008; Vocks, Herpertz, Rosenberger, Senf & Gizewski, 2011; Kerr et al., 2015). Indeed many of the symptoms observed in AN could be related to deficits in interoceptive perception, such as altered subjective responses to food (Bruch, 1962), pain and heart beat awareness (Raymond, Faris, Thuras, Eiken, Howard et al., 1999; Pollatos et al., 2008; Strigo et al., 2013). There is also a more general, increasing interest in somatosensory disturbances in AN, and their potential role in body image distortions (Zucker et al., 2013; Keizer, Smeets, Dijkerman, van den Hout, Klugkist et al., 2011). Keizer and colleagues (2014) reported that patients with AN do not differ from healthy controls in the amount of pleasantness they report from interpersonal, ‘neutral’ touch, delivered as part of a body perception task (Keizer, Smeets, Postma, van Elburg & Dijkerman, 2014). However, in order to specifically assess the perception of CT-based, ‘affective touch’ in patients with AN, the perceived pleasantness of gentle, dynamic touch applied at CT-optimal versus non-optimal speeds must be tested, as in the present study.

Given the aforementioned social difficulties in AN, studying the CT afferent system in AN is important, not only because affective touch is a distinct interoceptive modality, but also because the CT afferent system is considered specialised for detecting

the velocities of interpersonal touch that may have social relevance (Olausson et al., 2008), and for promoting social bonding and affiliation between individuals (Morrison et al., 2010). Indeed, more recent neuroimaging studies (e.g. Gordon, Martin, Feldman & Leckman, 2011; Voos, Pelphrey & Kaiser, 2013), have shown that in addition to the insular cortex, the processing of affective, CT-based touch involves several key nodes of a neural network previously implicated in social perception and social cognition (for reviews see Gallagher & Firth, 2003; Koster-Hale & Saxe, 2013). These regions involve the posterior superior temporal sulcus, medial prefrontal cortex, the orbitofrontal cortex and the amygdala (Gordon et al., 2011; Voos et al., 2013). Thus, it would be of interest to investigate how this socio-affective modality can be influenced by both bottom-up factors (sensory properties of the tactile stimulation) and top-down factors (concomitant manipulations of social context) in individuals with AN.

Accordingly, this study aimed to examine 1) whether the perception of affective touch (as operationalised by responses to a pleasantness rating scale) was reduced in patients with AN compared to healthy controls, 2) whether this effect could be linked to the CT fibers system, and 3) whether the perception of tactile stimulation was differentially affected in AN and healthy controls by the concomitant presentation of emotional facial expressions. The perception of touch pleasantness was predicted to be reduced in people with AN, given their general anhedonia. However, this effect was expected to be specific to the CT afferent system, in the sense that it would be driven by the perception of tactile stimulation at CT-optimal speeds. Furthermore, it was predicted that simultaneously presenting socially accepting vs. neutral faces would increase the perception of touch pleasantness, while rejecting vs. neutral faces should have the opposite results. Finally, this effect was expected to be stronger in patients with AN compared to controls, given the selective biases of the former towards rejecting faces (Cardi et al., 2012).

5.2. Methods

5.2.1. Participants

Twenty-five female participants with AN were recruited from clinics associated with the Maudsley NHS Trust in London over a one year period. All patients met the Diagnostic and Statistical Manual of Mental Disorders, 4th Edition (DSM-IV; American Psychiatric Association, 2013) criteria for AN, as assessed using the Structured Clinical Interview for DSM-IV Axis I Disorders (SCID). Thirty, gender and age matched healthy controls (HC) were also recruited from University College London. Exclusion criteria for both groups included being left handed, any skin condition (e.g. psoriasis, eczema, etc.) and any substance abuse (i.e. drug and alcohol). Exclusion criteria specific for the HC group included a known history of any other axis I clinical disorder, a body mass index (BMI) out of the normal range (18.5 – 25) and any indications on psychometric assessments of clinical depression, or anxiety disorders. A total of one AN and five HC participants were later excluded from the data analysis; one AN patient and one HC did not comply with the experimenter instructions, two HC had a body mass index below the normal range, and two HC showed a depression score outside the normal range as assessed using the Depression Anxiety Stress Scale (DASS, Lovibond & Lovibond, 1995; a 21-item, three-scale self-reported measure of depression, anxiety and stress, where higher scores are related to a higher level of depression, anxiety and stress; see Appendix 3).

5.2.2. Design and data analysis

The experiment used a 2 (Group: AN vs. HC) x 2 (Stroking Velocity: slow vs. fast) x 3 (Facial Expression: accepting vs. rejecting vs. neutral) mixed factorial design, with repeated measures on the latter two factors. The dependent variable was the perceived pleasantness of touch, measured using a pleasantness rating scale ranging from 0 (not at all pleasant) to 100 (extremely pleasant), presented visually, to which participants responded verbally by choosing a number between the two specified anchors.

Statistical analyses were conducted with SPSS version 21.0. The data were tested for normality by means of the Shapiro-Wilk test and found to be non-normal ($p < .05$). Subsequent Log, Square Root and Reciprocal transformations did not correct for the normality violations, therefore appropriate non-parametric tests were used to analyze the data (described below). Bonferroni-corrected planned contrasts ($\alpha = 0.025$) were used to follow up significant interactions between group and the two within-subject factors. Thus, to assess whether reduced pleasantness in AN related specifically to impairment in the CT afferents system the responses to CT optimal speeds, and separately the non-optimal speeds, were compared between groups. To assess whether affective touch perception was modulated by social feedback the perception of accepting vs. neutral faces between groups, and the perception of rejecting vs. neutral faces between groups were contrasted. Given the directional nature of these predictions one-tailed tests were used for all analyses.

This study also controlled whether differences in somatic and psychological characteristics of the two samples could influence the perception of pleasantness. Therefore, non-parametric correlational analysis was run to investigate possible association of pleasantness ratings with BMI, mood ratings (DASS-21) and duration of illness.

5.2.3. Stimuli and apparatus

Participants sat at a table in front of a 15-inch laptop computer screen positioned ~60 cm from their eyes. The visual stimuli were 45 gray-scale photos (8cm x 13cm) of young female (age matched with the sample of this study) faces displaying accepting/smiling ($n=15$), rejecting/critical ($n=15$) or neutral ($n=15$) expressions (Dandeneau & Baldwin, 2004; Cardi et al., 2012). Pre-testing conducted before the first use of the stimuli confirmed that the faces showing a smile were judged as more accepting than a neutral point on a 7-point scale. Using the same rating scale, participants judged the frowning faces as being significantly more rejecting (Dandeneau & Baldwin, 2004). Photos of age-matched females have been chosen based on evidence

supporting the importance of peer influence in this clinical sample (Marcos, Sebastián, Aubalat, Ausina, & Treasure, 2013; Keel & Forney, 2013). Stimuli were presented for 3 seconds on a black background in a random order using Microsoft PowerPoint 2010 (Microsoft Corporation). A blank (black) screen was displayed for 3 seconds between each face (i.e. inter-stimulus-interval = 3 seconds).

Simultaneous tactile stimulation of the left forearm (i.e. stroking) was administered during the 3 seconds when each face was presented, using a soft cosmetic make-up brush (Natural hair Blush Brush, N°7, The Boots Company) at two different velocities: one CT-optimal (3 cm/s) and one not CT-optimal (18 cm/s), for a total of 45 trials including 3 buffer trials. Each speed was paired with seven faces of each of the categories in random order. Three buffer trials were delivered in these velocities at random pairings for familiarisation purposes. Previous research showed that stroking movements at 3 cm/s velocity are optimal for CT afferent activation, while touch faster than 10 cm/s (e.g. 18 cm/s) and slower touch (below 1 cm/s) are not related to CT activity (Löken et al., 2009). To avoid visual feedback of the tactile stimuli, participants were asked to place their left arm inside a white plastic box (25 x 40 x 25 cm), open on two, opposite sides to allow the experimenter to deliver the touch (Figure 5.1.).

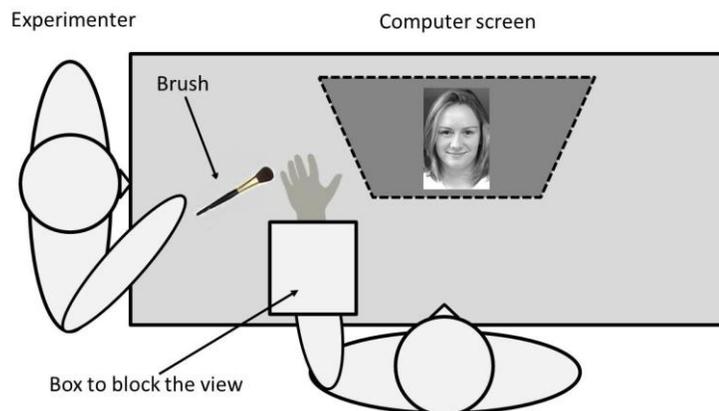


Figure 5.1. Experimental set-up. Participants were asked to sit in front of a computer screen with their left arm rested on the table. The experimenter was sitting on the left hand side of the table, delivering the touch with a soft brush. A plastic box was used to block the visual feedback of the touch.

5.2.4. Procedure

Institutional ethical approval was obtained and all participants gave written informed consent. The study was carried out in accordance with the provisions of the Helsinki Declaration of 1975, as revised in 2008.

Prior to the main experimental phase, participants were familiarised with the experimental procedure and the rating scale. Participants placed their left hand with the palm facing down on a table and two adjacent stroking areas, each measuring 9cm long × 4cm wide were identified and marked with a washable marker on the hairy skin of participants' left forearm (wrist crease to elbow, McGlone et al., 2012). Stimulation was alternated between these two areas to minimise habituation (Chapter 2), and because CT fibers are easily fatigued (Vallbo et al., 1999). Additionally, delivering the touch inside the delineated rectangular spaces allowed the experimenter to be constant not only in space, but also in force/pressure by controlling the lateral spreading of the brush bristles. Subsequently, participants were instructed to place their left arm inside the box and to watch the computer screen showing the pictures, while simultaneously receiving the tactile stimulation delivered at one of the two velocities (i.e. fast, slow) as described above. The experimenter was trained to deliver the touch at the exact speed by counting the number of strokes within the tactile stimulation window of 3 seconds (i.e. 1 stroke, 3-seconds-long for the 3 cm/s velocity and 6 strokes, each 0.5-seconds-long for the 18 cm/s velocity). The order of conditions was randomised across participants.

After each trial participants used the rating scale ranging from 0 (not at all pleasant) to 100 (extremely pleasant) to judge the tactile sensation.

5.3. Results

5.3.1. Demographics and mood

Demographic and clinical measures are summarised in Table 5.1. As expected the BMI was significantly higher in the HC group compared to the AN group. In addition, the DASS-21 questionnaire indicated significantly greater depression, anxiety

and stress in AN patients compared to HCs, in line with previous research (Kaye et al., 2009). No significant differences in age were found.

Table 5.1. Summary of demographic and clinical measures.

<i>Demographic / Clinical measures</i>	Anorexia Nervosa (n=20) ^a	Healthy Controls (n=25)	Z	P
Age	24 (12.75)	26 (7.25)	-0.32	0.75
BMI	14.38 (1.68)	21.03(3.04)	- 6.041	<0.001***
Years of illness	9.50(21.50)	NA		
Depression (DASS 21)	12.00 (10)	3.00 (5.25)***	-4.71	< 0.001***
Anxiety (DASS 21)	8.00 (7.75)	3.00 (4.50)***	-4.26	< 0.001***
Stress (DASS 21)	15.00 (6)	6.00 (6.50)***	-4.68	< 0.001***

Values provided are medians and interquartile ranges (in parentheses) for both Anorexia Nervosa (AN) and Healthy Control (HC) groups.

*** $p < .001$ difference between AN and HC groups

^aDemographic data were not available for four AN patients due to an administrative error

5.3.2. Pleasantness ratings

5.3.2.1. Main effects

A Mann-Whitney *U* Test revealed a main effect of Group on pleasantness ratings, with HCs rating touch as significantly more pleasant overall compared to patients with AN (see Table 5.2.). A Wilcoxon signed rank test also showed a main effect of Stroking Velocity ($Z = -4.30, p < 0.001$), with slow touch (median = 57.50, Interquartile Range, IQR = 26.22) producing significantly higher pleasantness ratings compared to fast touch (median = 44.73, IQR = 24.78). Finally, a Friedman's ANOVA revealed a main effect of Facial Expression ($\chi^2 (2) = 16.52, p < 0.001$; median accepting = 57.00, IQR = 15.38; median rejecting = 46.75, IQR = 19.69; median neutral = 50.00, IQR = 22.23). Bonferroni-corrected post hoc analyses ($\alpha = 0.017$) revealed that touch was rated as significantly more pleasant when it was delivered simultaneously with accepting faces compared to neutral faces ($Z = -3.32, p = 0.001$) and rejecting faces ($Z =$

-4.65, $p < 0.001$). No significant differences were found between rejecting and neutral faces ($Z = -2.08$, $p = 0.037$).

5.3.2.2. *Two-ways effect*

The interaction between Group and Stroking Velocity was analysed by calculating the difference between fast and slow stroking in each group separately, and comparing these differential scores between groups using a Mann-Whitney U Test. This analysis revealed a significant interaction ($Z = -1.78$, $p = 0.038$). Subsequent Bonferroni-corrected planned contrasts ($\alpha = 0.025$; see section 2.2. above) using Mann-Whitney U tests showed a significant difference between the groups in the slow ($Z = -1.99$, $p = 0.023$; median AN = 50.33, IQR = 37.40; median HC = 59.57, IQR = 59.57) but not the fast condition ($Z = -1.03$, $p = 0.16$; median AN = 35.20, IQR = 29.78; median HC = 47.00, IQR = 16.32; see Table 5.2.).

The interaction between Group and Facial Expression, Velocity and facial Expressions, and Group, Stroking Velocity and Facial Expressions were similarly analysed by calculating and comparing relevant difference scores, revealing no additional, significant interactions (all $ps > 0.10$).

Table 5.2. Summary of experimental measures. Ratings of pleasantness of slow and fast touch reported during vision of Accepting, Neutral and Rejecting facial expressions. The Total rating refers to the rating of pleasantness regardless of facial expressions and it has been obtained by averaging the pleasantness scores obtained during the Accepting, Neutral and Rejecting conditions.

Velocity of touch	Facial Expression	Group		Z	p
		Anorexia Nervosa	Healthy Controls		
Slow touch	Accepting	51.59 (22.74)	63.09 (11.05)	-1.49	0.14
	Neutral	46.68 (21.86)	59.95 (13.16)	-1.93	0.053
	Rejecting	44.51 (21.26)	57.88 (17.27)	-2.29	0.021
	Total	47.62(21.45)	60.31(12.85)	-1.99	0.023*
Fast touch	Accepting	43.98 (19.53)	47.28 (16.89)	-0.88	0.38
	Neutral	39.17 (18.93)	44.78 (17.06)	-1.15	0.26
	Rejecting	36.85 (20.94)	43.08 (17.75)	-1.20	0.23
	Total	40.00(19.12)	45.05(16.91)	-1.03	0.16

For illustration purposes only, values provided are means and standard deviations for both anorexia nervosa (AN) and healthy controls (HC) groups. The analyses were conducted using non-parametric tests; medians and interquartile ranges of significant analysis are reported in Section 3.2.2.

** Significant difference between AN and HC groups, based on Bonferroni corrected analysis.*

5.3.3. Correlations

Spearman's correlations were run to investigate whether the aforementioned experimental effects on pleasantness ratings were associated with the groups' ratings on mood questionnaires (DASS-21), BMI, and duration of illness. Neither the total DASS score nor the depression, anxiety and stress subscales correlated with (i) pleasantness scores in each group, nor (ii) the difference between slow and fast touch in each group (all r between -0.34 and -0.08; all p between 0.14 and 0.71). No correlations were found between the BMI and the pleasantness scores in each group, nor the difference between slow and fast touch in each group (all r between -0.32 and 0.21; all p between 0.13 and 0.36). Finally, no relationship was found between the duration of illness (in participants

with AN) and pleasantness scores during slow touch, nor the difference between slow and fast touch (all r between -0.27 and -0.06 ; all p between 0.28 and 0.81).

5.4. Discussion

The aim of the present study was to investigate (1) whether the perception of affective touch would be reduced in AN compared to healthy controls; (2) whether the bodily pleasure reduction would relate specifically to the CT-afferent system, and (3) whether these effects would be modulated by social stimuli differentially between the two groups. The results confirmed the first prediction, showing that individuals with AN perceived affective touch as less pleasant compared to healthy controls. Furthermore, this difference between groups was specific to CT-optimal (i.e. slow) stroking velocities; although patients with AN rated CT-optimal touch as more pleasant than non-CT optimal touch, there was no significant difference between groups when touch was delivered at a non-CT optimal speed (i.e. a fast velocity). These findings confirm the second prediction of this study, suggesting that the reduced pleasantness of interpersonal touch may at least in part relate to a dysfunctional CT afferent system. However, contrary to the third prediction of this study, the perception of affective touch was not differently affected by social stimuli in healthy controls and AN patients. The simultaneous display of accepting faces enhanced the perceived pleasantness of touch, irrespective of group, while there were no statistically significant differences between rejecting and neutral faces.

It has long been established that individuals with AN show reduced subjective perception of pleasure (anhedonia) and several interoceptive deficits, possibly related to abnormalities in various dopamine-based brain systems (see Kaye et al., 2013, for a recent review). These findings suggest that patients with AN show anhedonia also in the perception of tactile stimuli, replicating previous findings (Keizer et al., 2014). However, the present study is the first to demonstrate that this reduction in tactile pleasure in individuals with AN could relate, at least in part, to a dysfunctional CT afferent system. Moreover, this ‘bottom-up’ explanation of the observed tactile

anhedonia is supported by the secondary finding that ‘top-down’ socio-affective modulation of tactile stimuli (i.e. synchronous viewing of human faces) did not seem to affect the perception of tactile pleasure differently between the groups. This suggests that tactile perception in people with AN can be positively influenced by top-down, cognitive mechanisms of social feedback, which do not differ from those of healthy controls. Lastly, ratings of tactile pleasantness did not correlate with depressive symptoms in either group, providing further support for a potential abnormality that is specific to CT-based, tactile perception rather than generally related to the observed anhedonia.

A possible alternative explanation for this finding might be that the observed reduction in pleasantness perception reflects an attempt to control (i.e. reduce) anxiogenic experiences. Research in AN has shown that there is a high prevalence of anxiety, and increased activation of cognitive control as an attempt to counteract the reduced limbic function (i.e. more strategic choices can compensate for the impaired ability to perceive interoceptive information; Connan, Campbell, Katzman, Lightman & Treasure, 2003). Thus, the reduced bodily pleasantness observed in this study could be an attempt to cognitively control for an “unwanted” arousing experience (i.e. pleasant interpersonal touch). However, this explanation would need to be investigated in further studies, as we did not find any correlation between anxiety and pleasantness ratings in individuals with AN or healthy controls in the present study.

The finding that individuals with AN have a disordered, CT-based affective touch system may have implications for their distorted body representation. Affective touch has been shown to contribute uniquely to the multisensory integration processes that underlie the subjective sense of body ownership (Chapter 2 and 3; van Stralen et al., 2014; see also Lloyd et al., 2013 for top-down contributions to such effects). Moreover patients with AN have been found to be more susceptible to the influence of visual, exteroceptive signals about the body rather than proprioceptive information (Eshkevari, Rieger, Longo, Haggard & Treasure, 2012; Keizer et al., 2014). Individuals with strong interoceptive signals seem to possess a body representation that is more resilient to visual changes (Tsakiris et al., 2011) and vice versa (Mosley et al., 2008, but see Rohde

et al., 2013). The findings of the present study raise the possibility that an enhanced susceptibility to visual signals about the body, and related body distortions in AN, may in part be linked to their weakened interoceptive perception. However, these conclusions remain tentative, serving as hypotheses for future studies.

Furthermore, given the social aspects of CT-based touch, these findings suggest future avenues for the investigation of a potential link between tactile anhedonia, social anhedonia, and other social disturbances observed in individuals with AN. As the present study focused on adults with AN, it is not possible to know the developmental time course of the CT-afferent system in this population, nor whether this sensory disturbance is secondary to other pathological factors in AN, such as a primary disturbance in appetite and motivational systems. Recent studies have formulated similar hypotheses for the role of an abnormal CT afferent system in autistic spectrum disorders, in both healthy population (Voos et al., 2013) and in individuals with autistic spectrum disorders (Cascio, McGlone, Folger, Tannan, Baranek et al., 2008; Cascio et al., 2012). Thus, the results of the present study justify further investigations of the developmental time course of disturbances in the CT-afferent system, and its implication for social relating and cognition in individuals with AN.

The unique role played by the CT afferent system in social interaction is supported and further specified in recent studies. Croy and colleagues (2015) showed that slow, CT optimal touch seems to be the spontaneously preferred one in human social interaction, specifically when stroking partners and babies, compared to the situation in which participants were asked to stroke a rubber arm (Croy, Luong, Triscoli, Hofmann, Olausson et al., 2015). Furthermore, the activation of the CT afferent system seems to be maximised at human skin-like temperature, rather than at cooler or warmer temperatures (Ackerley et al., 2014). Additionally, the affective but also motivational role of the CTs system is supported by a recent study showing that participants constantly rated others' skin as being softer than their own, giving rise to the so-called social softness illusion (Gentsh, Panagiotopolou & Fotopoulou, 2015). Taken together this evidence is in line with the findings here reported. However in the present study the touch was always delivered by a stranger/experimenter and the social modulation has

been investigated by mean of pictures showing different facial expression (offline social interaction). Therefore, the results of this study could be extended and further clarified by investigating affective touch and the potential modulation of facial expressions in an experimental setting involving participants' loved ones and online social interaction (see Krahé et al., 2013; Krahé, Paloyelis, Condon, Jenkinson, Williams et al., 2015 for a similar approach in the domain of pain).

5.5. Limitations and future directions

Future studies need to replicate the present findings, ideally with a larger sample of individuals, including both males and females, different types of eating disorders, weight-restored participants, medicated and non-medicated individuals, and possibly also testing tactile perception on body parts that do not contain CT-afferents, such as the glabrous skin of the palm (Olausson et al., 2002). In addition, neural and physiological responses to affective versus neutral touch could provide additional specificity regarding the involvement of the CT-afferent system in the observed tactile anhedonia. It is possible that the social modulation task used in this study had a limited effect in AN because of their more general social cognition difficulties and their specific face recognition and attentional biases (see section 5.1.). However, this interpretation is unlikely, given the fact that AN patients were influenced by the current social stimuli in the same way as healthy controls, and also contrary to their own attentional biases in previous studies (Cardi et al., 2012). However, future studies could control for gaze and attention on such tasks, and social cognition difficulties could be tested in the same sample to determine the precise relation between the CT afferent system and social cognition. Furthermore, future studies could explore other facets of rewarding tactile perception, such as its anticipation and desirability, which were not explored in the current study. In addition, given that the majority of the experimental sample were outpatients at the time of the research, it was not possible to have reliable or comprehensive information on medication that may have affected their symptoms, and particularly reward circuits. Only sixteen patients self-reported being on medication and

only a small proportion of those were able to specify the type of medication. However, these included Selective Serotonin Reuptake Inhibitors (SSRIs) that have been shown to reduce the processing of both rewarding and aversive stimuli (e.g. McCabe, Mishor, Cowen, & Harmer, 2010). Future studies should therefore examine the effect of SSRIs and other medications on affective touch perception, although these results were selective in the sense that positive social stimuli (i.e. accepting/smiling faces) had a comparable ‘top-down’ effect of increasing the perceived pleasantness of the touch in healthy controls and anorexia nervosa participants, and tactile pleasantness ratings did not correlate with other psychometric measures of mood. Lastly, it would be of interest to test the role of affective touch in multisensory integration paradigms targeting the formation of body representations in AN, in both developmental and cross-section studies.

In conclusion, the present findings suggest a disturbance of the CT-afferent system in AN, and open novel avenues for integrative research on some of the core facets of AN, such as reward processing, somatosensory perception and social cognition.

Look into the mirror: The effect of self vs. other-mirror observation on interoception

6.1. Introduction

As introduced in Chapter 1, interoceptive signals are believed to play a fundamental role in self-awareness, by providing information about the internal states of the body at any given time (Damasio, 2010; Craig, 2010). A renewed interest in this modality has guided extensive research, which highlights the importance of the ability to feel visceral and homeostatic sensations, in order to become aware of our body and, by implication, of our psychological self (see Chapter 1). Interoceptive stimuli include pain, heartbeat, hunger, distention of the bladder and affective touch (Craig, 2002); all of these modalities have been shown to activate the right anterior insula, which seems to underpin the sense of the material self as a feeling entity (Craig, 2003). As explained in detail in Chapter 3, the heartbeat detection counting task (Schandry, 1981) is the technique commonly adopted in research to quantify how accurate people are in feeling their body from within (Ainley et al., 2012; Ainley & Tsakiris, 2013). However, our bodies exist within an interactive world, and we perceive our body also through external signals, such as visual feedback. Therefore, in order to develop a coherent sense of self, information coming from *inside* our body (interoception) needs to be integrated with information coming from *outside* our body (exteroception). Although it is known that both internal and external signals provide important information for body awareness, the mutual interaction between the two has only recently been considered and investigated, mainly in the context of the rubber hand illusion (Botvinck & Cohen, 1998; Tsakiris et al., 2011; Aspell, Heydrich, Marillier, Lavanchy, Herbelin & Blanke, 2013; Suzuki et al., 2013; see Chapter 2 for a detailed description). In fact some recent studies support the idea of a potential modulation of the sense of body ownership by means of interoceptive sensitivity, although this evidence seems to be inconsistent. Tsakiris and

colleagues (2011) showed that performance on the heartbeat detection task can predict the extent to which participants are susceptible to the rubber hand illusion (Botvinck & Coehn, 1998). That is, the better a person is in feeling the body from *inside*, the less likely he/she is to embody the rubber hand. This evidence suggests that when the ability to feel the internal state of the body is good, the influence of external stimuli, and the malleability of the bodily self, is weak. In contrast, Suzuki and colleagues (2013) showed an opposite pattern of results, with people with high interoceptive sensitivity showing a more malleable sense of bodily self. However, these two studies have some methodological dissimilarity which could account for the discrepancy in the results, such as the implementation of different tasks to assess interoceptive sensitivity, the difference in sample size (21 vs. 46 participants), and the use of a virtual rubber hand paradigm rather than the classic one in Suzuki and colleagues' study (2013). Additionally, the data presented in Chapter 3 of the present thesis failed to replicate any of the aforementioned results in the context of a potential relationship between interoceptive sensitivity and the malleability of body ownership.

What all of the aforementioned studies have in common is the use of the heartbeat detection counting task (Schandry, 1981) in order to quantify interoceptive awareness. However, interoception comprises several other modalities originating peripherally in the skin, such as pain and pleasant touch which provide information about the internal states of the body at any given time (Craig, 2002; 2009). As aforementioned in Chapter 1, affective, pleasant touch has been re-defined as an interoceptive modality due to the involvement and activation of CT afferent fibers, which maximally fire as a consequence of slow, low-pressure touch (Löken et al., 2009). The activation of these fibers linearly correlates with the pleasant percept reported by participants. Evidence collected in the context of the rubber hand illusion, show that slow, caress-like touch enhanced the rubber hand illusion more than fast, emotionally-neutral touch (see Chapter 2 and 3; Lloyd et al, 2013; van Straleen et al., 2014). That is, pleasant touch seems to play a role in the sense of body ownership.

Additionally, studies conducted with clinical populations can help to further characterise the role played by interoceptive awareness in the construction of our bodily

self. For example, Eshkevari and colleagues (2012) exposed people with anorexia nervosa to the rubber hand illusion. This clinical population experienced the illusion to the same extent as healthy controls, that is, both groups embodied the rubber hand following synchronous stroking with their own hand in a similar fashion. However, anorexia nervosa participants showed a much stronger visual capture, which is the extent to which participants acquire ownership over the rubber hand illusion just by looking at it before experiencing any synchronous visuo-tactile stimulation. These results are in line with evidence showing an impaired interoceptive system in anorexia nervosa (Pollatos et al., 2011; see also Chapter 5), which could explain the much more malleable sense of bodily-self observed in Eshkevari and colleagues' study (2012).

Taken together this evidence supports the proposed role of interoception (as assessed by means of the heartbeat counting task and pleasant touch task) in the construction of our sense of body ownership, which represent a fundamental aspect of the psychological self (Gallagher, 2000). Additionally, these data show that interoception has an influence in multisensory, exteroceptive based illusions, such as the rubber hand illusion.

However, less attention has been paid to the opposite modulation; that is, the extent to which exteroception can influence interoception. Recent studies showed that interoception can be modulated by exteroceptive guided feedback. For example, Ainley and colleagues (2012) asked participants to complete a heartbeat detection task under two conditions: looking at a blank screen or looking at their reflection in a mirror. Participants were more accurate in judging their own heartbeat when looking at their own reflection, suggesting that exteroceptive feedback improved their cardiac (interoceptive) awareness. However, this result applied only when the participants had a poor performance at baseline (i.e. counting their heartbeat while looking at the blank screen); in contrast, no improvement was found in the group of participants who had a high performance at baseline. Unfortunately, it is not clear whether the improvement in interoceptive awareness comes from looking specifically at one's own face, or whether we could observe the same improvement also by showing any face in the mirror. In fact, research in face processing argues for two distinct brain pathways during face

perception; one subcortical pathway seems to be specific for face detection, while a cortical pathway is activated specifically for face recognition (Johnson, 2005). Therefore, it would be important to clarify whether recognising the face as belonging to the self is necessary in order to observe the improvement in interoceptive sensitivity.

In this context, Maister and Tsakiris (2014) found that in Western culture, interoceptive sensitivity (measured using the heartbeat detection task) significantly improved when the face observed in a photograph was their own. In contrast, participants did not observe any improvement when they were asked to look at the photograph of someone else's face matched for age, gender and ethnicity. These findings seem to indicate that face recognition may be necessary for improving interoception, and support the modulation of exteroceptive signals on interoceptive bodily awareness. However, this study used a photograph rather than a mirror; therefore the results are not directly comparable with the ones from Ainley and collaborators (2012).

These findings have been further extended beyond the domain of face processing, with purely conceptual or narrative information about the self leading to apparent improvements in heartbeat detection task performance. Ainley and colleagues (2013) presented participants with either self-bodily (i.e. photograph of the participant's face) or self-narrative (i.e. set of self-related words) information while they were asked to complete the heartbeat counting task. Both types of self-related stimuli successfully increased interoceptive awareness, arguing for a crucial role of self-related information in the perception of the internal states of the body, and more generally for self-awareness (Ainley, Maitser, Brokfeld, Farmer & Tsakiris, 2013). However, a recent study failed to replicate the enhancing effect of self-focus on interoceptive awareness (Durlík, Cardini & Tsakiris, 2014). Durlík and colleagues observed whether looking at a camera, which could be "on" or "off", would affect the performance on the heartbeat detection task and a touch detection task. Results showed that the condition "camera on" had an effect of enhancing the touch detection, while no effect was found on the heartbeat detection task. Therefore, the idea of being watched by a third party seemed to improve exteroceptive tactile detection but not interoceptive sensitivity. However, all the aforementioned

studies used photographs or camera to create the condition when participants were watching and/or being watched by someone else. These can be considered as *offline* manipulations compared to an *online* manipulation, which takes place when participants are asked to look at their face vs. someone else's face directly in a mirror. In fact, mirrors represent a unique tool to explore both the sense of body ownership (i.e. the sense that one's body belongs to oneself) and agency (i.e. the sense that one is the cause or author of one's actions; Jenkinson & Preston, 2015). If on the one hand mirrors offer an image that people can recognise as belonging to them, on the other hand they offer an image of the body in third person perspective in terms of visual information (Bertamini, Berselli, Bode, Lawson & Ting Wong, 2011). Additionally, and what is more relevant in the context of the study here presented, mirrors can guarantee the direct, online eye-contact with the self or the other depending on the experimental condition, in contrast with photographs or cameras.

Another line of research has investigated the extent to which eye contact, which is a form of *online* manipulation, can affect interoception. Eye contact is a strong social signal which communicates that we are the object of someone else's attention and by implication could increase self-awareness (Argyle, 1975; Baltazar, Hazem, Vilarem, Beaucousin, Picq et al., 2014). A recent study showed that the perception of a face of another person with direct gaze increases the awareness of emotional physiological reactions compared to the perception of a face with no direct gaze. Therefore, eye-contact seems to have a "self-reflective" power and enhances the ability to detect bodily states (Baltazar et al., 2014).

Given the varied and inconsistent range of evidence in the context of exteroceptive modulation of interoceptive perception, it remains unclear whether the improvement in interoceptive sensitivity is more guided by eye contact or by self-related information. Therefore, this study aimed to examine these two possible explanations by 1) replicating the original procedures of Tsakiris et al 2011, to investigate whether observation of the self (face) in a mirror would improve performance on the classic heartbeat detection task; and 2) investigate whether the same increase in interoceptive sensitivity also occurs when making eye contact with someone else in a mirror.

Furthermore, given the fact that the potential relationship between distinct interoceptive modalities is still under investigated (see Chapter 3), the secondary aim of this study was to further investigate the use of pleasant touch as a measure of interoception, by comparing the effect of the above mentioned manipulations on the perception of pleasant touch as well as the more widely used measure of interoception (i.e. the heartbeat detection task). To this end, participants were asked to complete the heartbeat detection task and a pleasant touch task under three different visual feedback conditions: blank screen, observation of the self (i.e. face) in a mirror (self-mirror condition), and observation of another face in a mirror (other-mirror condition). Based on the previous findings of Ainley and colleagues (2012), participants with high interoceptive awareness were expected to be less susceptible to exteroceptive manipulation, given the fact that they rely to a greater extent on their own internal signals. That is, it was anticipated to observe an improvement in the performance on the heartbeat detection task and pleasant touch task following mirror-observation only in people with low interoceptive sensitivity at baseline. This finding would indicate that in the absence of good interoceptive perception people rely more on exteroceptive signals, namely eye contact by means of mirror reflection, irrespective of the self or other-mirror conditions. In contrast, the high interoceptive sensitivity group was not expected to improve following either the self or other-mirror observation conditions.

6.2. Methods

6.2.1. Participants

Seventy-six females, aged 18 and over ($M = 22.07$, $SD = 2.75$), were recruited via the University of Hertfordshire research participation system. Participants received course credit or £5 for participating. Exclusion criteria included: being left handed, a personal history of neurological or psychiatric disorders and current eating disorder. Two participants were later excluded from the data analysis as they failed to follow the experimental instructions. The study was approved by the University of Hertfordshire Ethics Committee and conducted in accordance with the Declaration of Helsinki.

6.2.2. Experimental design and statistical analysis

Participants completed the heartbeat detection task (Schandry, 1981) and pleasant touch task under three separate conditions. In the 'blank' (i.e. control) condition participants looked at a blank screen (see Materials section below for details); this condition was used to establish the participant's interoceptive sensitivity (heart beat detection) baseline. In the two remaining conditions participants looked in a mirror, which was positioned at an angle to reflect either their own face (i.e. self-focus condition) or the reflection of someone else (a confederate; i.e. other-focus condition). Therefore, the interoceptive sensitivity (heartbeat detection) task followed a within-subjects design with three levels of the independent factor 'visual feedback' (blank vs. self. vs. other). Additionally, for the pleasant touch task two velocities of stroking were employed, thereby producing a 2 (Stroking velocity: slow [3cm/s] vs. fast [18cm/s]) x 3 (Visual feedback: blank vs. self. vs. other) fully-factorial, within-subjects design. The outcome measure was the pleasantness of the touch provided by means of a pleasantness rating scale ranging from 0 (not at all pleasant) to 100 (extremely pleasant), which was placed on the table, and to which participants responded verbally. Under each visual-feedback condition, participants were asked to rate the pleasantness of four touches delivered at fast (18 cm/s) velocity and four touches delivered at slow (3 cm/s) velocity, for a total of eight trials for each condition. The four scores for slow touch and the four scores for fast touch were later averaged to obtain one slow touch rating score and one fast touch rating score for each participant. Each block (i.e. blank screen, self-mirror observation, other-mirror observation) included the same number of slow and fast velocity trials presented in a randomised order. The order of task presentation (i.e. heartbeat detection task and pleasant touch task) was counterbalanced across conditions. We followed this procedure in order to control for any potential influence of the one task on the other one.

A median split procedure was used to divide the sample in two equal groups based on their performances on the heartbeat counting task; the high group (i.e. good perceivers of interoceptive sensitivity) and low group (i.e. poor perceivers of interoceptive sensitivity). Any difference between groups on the 3 minutes heart rate

baseline was investigated by means of a one way ANOVA. Consequently, a 2 (Group: high vs. low interoceptive sensitivity) by 3 (Visual feedback: blank vs. self vs. other) repeated measures ANOVA was used to explore the effect of visual conditions on interoceptive sensitivity and any differences between the two groups.

The pleasant touch task was analysed by means of a 2 (Group: high vs. low interoceptive sensitivity) by 2 (Velocity: slow vs. fast) by 3 (Visual feedback: blank vs. self vs. other) repeated measures ANOVA in order to investigate the effect of visual feedback and velocity on the perceived pleasantness of touch. Interactions between the visual conditions and velocity of touch were also of interest, as well as any difference between groups.

Correlational analyses were run to investigate the potential relationships between the performance on the heartbeat detection and affective touch tasks. The data were tested for normality by means of the Shapiro-Wilk test and found to be normal ($p > 0.05$), therefore appropriate parametric tests were used to analyse the data. Bonferroni corrected post-hoc analyses were applied when multiple comparison were conducted.

6.2.3. Materials

The exteroceptive feedback conditions were manipulated by providing participants with different visual feedback. In the control or baseline condition ('blank screen') participants were asked to look at a 40cm x 40cm white screen placed approximately 60 cm in front of them and to focus on a fixation point. The blank screen was a white piece of cardboard placed over the reflective surface of the mirror that was used for the other two conditions, for consistency. During the self-focus condition, participants focused on their own reflection, in a 40cm x 40cm mirror placed on the table, approximately 60cm in front of them. During the other-focus, an age and gender matched confederate was sitting on the right hand side of the participant, and slightly behind her. The mirror was slightly rotated (approximately 40°) so that the participant could see the confederate's face reflected in the mirror, but not her own reflection. The female confederate was the same for all the participants, and none of the participants were familiar with her face. The condition order was randomised between participants.

The participant's actual heartbeat (HR) was recorded using a Biopac MP150 Heart Rate oximeter, connected to an Apple Mac laptop with AcqKnowledge software (version 3.9.2). To obtain a HR reading the oximeter was attached to the participant's non-dominant index finger. The recorded heartbeats were later transformed using the 'count peaks' function to give the number of recorded heartbeats. The Biopac was set up to begin recording when the experimenter selected 'Start' on the AcqKnowledge program and to stop recording after a pre-set time interval. The well-established heartbeat counting task (Schandry, 1981) was employed during the heartbeat task (see Chapter 3).

For the pleasant touch task, two rectangles were drawn on the hairy skin of the participants left forearm, each measuring 4cm x 9cm. Participants placed their left arm on the table with palm facing down and to avoid visual feedback of the tactile stimuli, they were asked to place their left arm inside a white plastic box (25 x 40 x 25 cm), open on two, opposite sides to allow the experimenter to deliver the touch. Tactile stimulation (i.e. stroking) was administered during the 3 seconds using a soft cosmetic make-up brush (Natural hair Blush Brush, N°7, The Boots Company) at two different velocities: one CT-optimal (3 cm/s) and one not CT-optimal (18 cm/s). Tactile stimulation was alternated between the rectangles drawn on the skin, to minimise habituation. After each brush stroke participants verbally rated the pleasantness of the touch using a scale from 0 (not at all pleasant), to 100 (extremely pleasant). A copy of the scale was placed on the table for reference.

6.2.4. Experimental procedure

Participants sat at a table in front of the mirror. The experimenter was seated on her left hand side, and the confederate was present and seated on her right hand side from the beginning and throughout the entire duration of the experimental procedure. Upon arrival, a heartbeat baseline reading was obtained over a three minute period before the beginning of the counting task. Participants were then familiarised with the pleasantness ratings scale and with the experimental procedure.

In each visual feedback condition participants were asked to complete the heartbeat counting task following the procedure fully described on Chapter 3 (i.e. three pre-set time intervals - 25, 45 and 65 seconds- in a randomized order and separated by a 30 seconds interval).

Additionally, either before or after the interoceptive sensitivity task, participants were asked to rate the pleasantness of the touch they perceived on their left forearm, which was out of view. The order of tasks was randomised across participants.

Concurrently, they were asked to keep their eyes either on the blank screen, on the self-reflection in the mirror or on the other-reflection in the mirror (see the Materials section above for details). During the self- and other-focus, participants were instructed to make direct eye contact with herself and with the confederate, respectively. The confederate was checking that the experimental instructions were followed as accurately as possible. Therefore, her role was also to stop the trial and ask the experimenter to start again in the case that the participant was not maintaining direct eye contact with herself and/or with the confederate.

6.3. Results

6.3.1. Interoceptive sensitivity

As in Chapter 3, Interoceptive Sensitivity (IS) was calculated using the following formula (Schandry, 1981; Pollatos et al., 2008):

$$1/3 \sum (1 - (| \text{recorded heartbeats} - \text{counted heartbeats} |) / \text{recorded heartbeats})$$

The median value of Interoceptive Sensitivity was 0.663. As in previous studies (Ainley et al., 2012; Maister and Tsakiris, 2014), following the median split method, the group of 74 participants was split into two groups of high Interoceptive Sensitivity (HIGH group, mean heartbeat perception = 0.825; SD = 0.09; n = 37) and low Interoceptive Sensitivity (LOW group, mean heartbeat perception = 0.533; SD = 0.11; n

= 37). A one-way ANOVA showed no differences in the 3 minute heart rate between the LOW and HIGH group ($F(1, 69) = 0.069; p = 0.794; r = 0.001$).

A 2 (Group: high vs. low interoceptive sensitivity) by 3 (Visual feedback: blank vs. self vs. other) repeated measures ANOVA, showed a main effect of group ($F(1, 72) = 108.9; p < 0.001; r = 0.78$), with the high IS group performing significantly better on the heartbeat counting task than the low IS group, as expected. However, there was no significant main effect of Visual feedback, indicating no overall differences between performance on the heartbeat counting task under the three visual conditions (blank screen, self-focus and other-focus) ($F(1, 72) = 1.20, p = 0.30, r = 0.13$). The analysis did not find any significant interaction between Visual feedback and group ($F(1, 72) = 0.644; p = 0.53; r = 0.09$, Figure 6.1.).

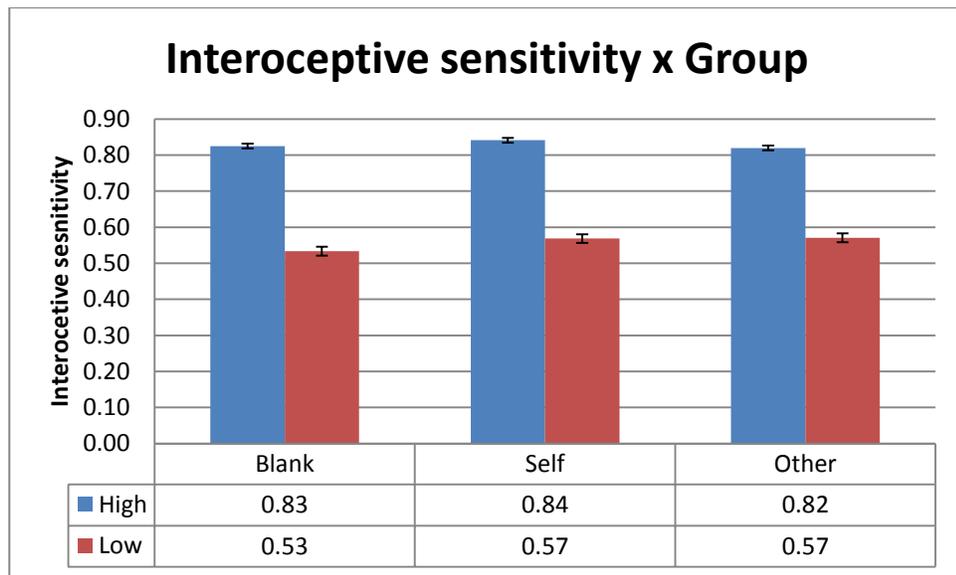


Figure 6.1. Means and standard errors of interoceptive sensitivity (High vs. Low group) in the different visual conditions.

6.3.2. Pleasant touch

A 2 (Group: high vs. low interoceptive sensitivity) by 2 (Velocity: slow vs. fast) by 3 (Visual feedback: blank vs. self vs. other) repeated measures ANOVA, showed a main effect of Stroking Velocity ($F(1, 73) = 61.35, p < 0.001, r = 0.676$), with slow

touch ($M = 61.64$; $SD = 19.35$) being rated as significantly more pleasant than fast touch ($M = 47.37$; $SD = 18.88$). The analysis also showed a main effect of Visual feedback ($F(1, 73) = 5.4$; $p = 0.005$, $r = 0.377$). Specifically, touch perceived while looking at the blank screen was rated as significantly more pleasant compared to the other-mirror condition ($t(73) = 3.47$; $p = 0.001$; $r = 0.21$). No significant differences in pleasant touch ratings were found between the blank and self-focus conditions ($t(73) = 1.85$; $p = 0.068$; $r = 0.158$) or between the self and other-focus conditions ($t(73) = 1.32$; $p = 0.19$; $r = 0.133$). Finally, the main effect of interoceptive group on the performance on the pleasant touch task was non-significant ($F(1, 72) = 1.39$; $p = 0.243$; $r = 0.137$) (Figure 6.2.). The interaction between velocity of touch and interoceptive group ($F(1, 72) = 0.252$; $p = 0.617$; $r = 0.059$), velocity of touch and visual feedback ($F(1, 72) = 0.727$; $p = 0.485$; $r = 0.10$), as well as between interoceptive group and visual feedback ($F(1, 72) = 0.958$; $p = 0.386$; $r = 0.11$) were not significant. Finally, the three-way interaction between velocity of touch, visual feedback and interoceptive group did not reach significant level ($F(1, 72) = 1.46$; $p = 0.237$; $r = 0.14$).

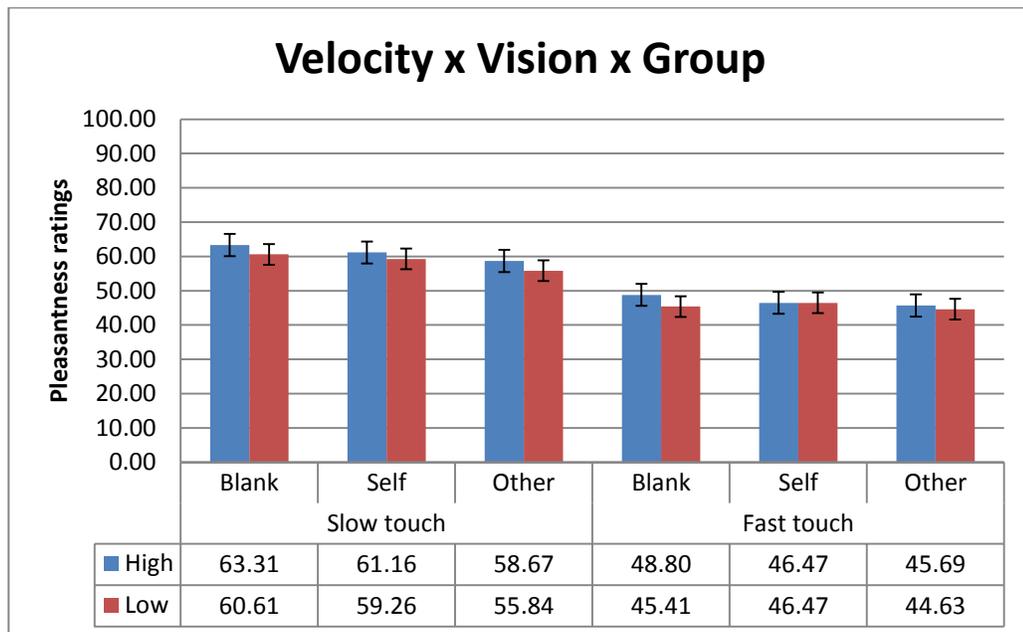


Figure 6.2. Means and standard errors of pleasantness ratings in the different visual conditions. Data from the High and Low interoceptive sensitivity groups are reported separately.

6.3.3. Correlational analysis

Correlational analyses were run in order to investigate the relationship between interoceptive sensitivity at baseline (as a trait) and the performance on the pleasant touch task at baseline (Blank-screen condition). IS did not correlate with the ratings of slow touch or fast touch separately ($r = 0.09$; $n = 74$; $p = 0.46$ and $r = 0.08$; $n = 74$; $p = 0.51$, respectively). Also, the difference of the ratings between slow and fast touch was calculated to obtain a measure of how accurate participants are in detect differences between slow and fast touch. This measure did not correlate with IS ($r = 0.003$; $n = 74$; $p = 0.98$).

6.4. Discussion

In this study, the performance on the heartbeat detection task and pleasant touch task were compared under three different visual feedback conditions: mirror self-observation, mirror other-observation and baseline. The participants were split in two groups based on whether their ability to count their own heartbeat while looking at the black screen (i.e. baseline) was above or below the median of the group. The findings show no difference in the heartbeat performances across the self- and other-mirror observation conditions. Previous studies showed that self-mirror observation can improve interoceptive sensitivity compared to a blank screen condition, but only in participants with low interoceptive sensitivity at baseline (Ainley et al., 2013). This study failed to replicate the Ainley and colleagues' finding, suggesting that visual feedback does not seem to affect the performance on the heartbeat counting task in either of the two groups. It is worth mentioning that the data of this study showed a comparable performance between the self-observation and other-observation conditions in both groups. Therefore, this finding could suggest that there is no difference in looking at one's own face or someone else's face in the mirror, arguing for a centrality of eye contact rather than face recognition in *online* mirror interaction (see Introduction of this Chapter). Hence, based on this and previous findings (Baltazar et al., 2014) it could be argued that eye-contact, regardless of the self or other nature, might have a

“self-reflective” power and enhance the ability to detect bodily states. However, in line with recent findings (Durlik et al., 2014), this study failed to detect the aforementioned enhancement.

The performance on the pleasant touch task indicated that perceiving touch whilst looking at someone else (and being looked back at) reduced the perceived pleasantness compared to looking at a blank screen or at one’s own face at the mirror. To a certain extent, this finding is in line with recent evidence showing that exteroception, but not interoception, can be affected by the awareness of being watched (Durlik et al., 2014). Durlik and colleagues observed whether looking at a camera which could be “on” or “off” would affect the performance on the heartbeat detection task and a touch detection task. Results showed that the condition “camera on” had an effect of enhancing the touch detection, while no effect was found on the heartbeat detection task. Therefore, the idea of being watched by a third party seemed to improve exteroceptive tactile detection but not interoceptive sensitivity. Similarly, the present study showed an effect of other-observation only in the touch task regardless of velocity of touch, but not in the heartbeat detection task. This could suggest that being observed by someone else (not the person performing the touch) does affect the perception of touch since the nature of tactile stimulation itself is interpersonal, and therefore probably more sensitive to social manipulation. In contrast, interoceptive sensitivity is a more intimate, inner modality and therefore it might be less susceptible to the presence of others. The selective nature of these findings, that is the fact that being watched affected tactile pleasantness but not cardiac awareness, might more generally suggest that interoception, but not exteroception, is more susceptible to social manipulation. On the one hand, in order to successfully complete the heartbeat counting task, participants needed to focus on an internally originated feeling; in contrast, when completing the pleasant touch task, participants were asked to focus on the bodily feeling derived by the tactile stimulation, which was externally originated. Therefore, this might explain why social manipulation affected the pleasant touch task to a greater extent. Additionally, the other-mirror condition did not affect slow and fast touch differently; that is, there did not seem to be a specific involvement of the interoceptive, affective facet of touch on this effect.

One could argue that the reduced pleasantness of touch observed in the other-mirror condition could be due to social distraction. However, if this was the case, the distraction effect should have affected also the performance on the heartbeat counting task and this was not the case.

Furthermore, interoceptive sensitivity does not seem to affect the performance on the pleasant touch task, suggesting that these two modalities might be independent from each other. In support of this, the secondary aim of this study was to investigate the relationship between two interoceptive modalities, by comparing the pleasant touch task to the widely used measure of interoception (i.e. the heartbeat detection task). The correlational analysis did not show any significant relation between performance on the two tasks. These results are consistent with the ones presented on Chapter 2, and they additionally strengthen the idea that there is no systematic relationship between these two interoceptive modalities, as assessed by means of the heartbeat detection task and pleasant touch task. A potential explanation might lie in the dissimilar nature of these two measures. In fact, the heartbeat detection task generates a sensitivity score, which provides us with a measure of how well or poorly participants are able to feel their body from within. In contrast, pleasant touch is measured by subjective ratings of pleasantness expressed by means of a rating scale and hence it is a different kind of measure. Cardiac awareness originates within the body, whereas the bodily pleasure derived from affective touch is triggered by tactile, and therefore, external stimulation; therefore these modalities might refer to different aspects of interoception. This fundamental difference implies the interpersonal and social nature of affective touch, which does not belong to the heartbeat counting task. Consequently, also the neurobiological mechanisms which underlie these interoceptive modalities might be different and further support the results of this study. One of the implications of the findings presented here is that interoceptive sensitivity measured by means of the heartbeat detection task seems to not be affected by visual manipulations, providing further support to the idea that it represents a rather fixed trait and it can be considered a reliable measure of one aspect of interoception.

6.5. Limitations and future directions

This study has some limitations which should be noted. First of all, in all the conditions there were two additional people present; the experimenter and the confederate. On the one hand this is an advantage because this was a variable always present; however, on the other hand, the self-observation was still within a social context of other people present in the room. What is more, in the mirror self-observation condition, the confederate was actually observing the participant to make sure that she was making eye contact with herself. Therefore, this could have played a role and it could be one of the reasons why this study failed to replicate previous findings arguing for an enhancing effect during the self-observation condition.

Additionally, there are few variables that could have affected the other-observation effect and should be taken into account in future studies, such as social embarrassment of being forced to make eye contact with a stranger, different familiarity based on similarity of facial features between the participant and the confederate, and possible attractiveness of the confederate. Most importantly, participants had a greater familiarity with their own faces compared to the confederate's face. As a consequence, looking at a face we are not familiar with probably engages the attentional resources in a stronger way compared to looking at one's own face and, therefore, it might affect the attention to the tactile stimuli to a greater extent. Although this study did not find any differences in interoceptive sensitivity between the self and other-mirror conditions, it is not possible to state that these conditions are comparable since there are various aspects that should be controlled for in future studies, such as attractiveness, similarity of facial features, race and skin tone.

Finally, future studies should control for eye contact in a more consistent way. In this study, the eye tracking methodology was not used in order to keep the experimental setting as natural and socially-plausible as possible. Therefore, even though efforts were made to carefully control for eye contact, future studies could control for this in a more systematic and rigorous manner.

The effect of shared touch on bodily pleasure

7.1. Introduction

As discussed in Chapter 1, growing behavioural and neurobiological evidence shows that touch plays a positive role in development (e.g. Sharp et al., 2012) and in social interactions among individuals (Morrison et al. 2010). In this context, recent evidence supports the distinction between two separate modalities and neural systems (McGlone et al., 2014 for a review). Firstly, a discriminative/exteroceptive modality activates the classic primary and secondary somatosensory cortices, and is mainly involved in rapidly identifying the physical characteristics of a stimulus on the skin (e.g. weight and texture). Secondly, an affective/interoceptive modality is thought to be responsible for the affective states which can be derived from tactile stimulation (see Chapter 1 for details). In particular, the rewarding aspect of the affective touch modality is hypothesised to be mediated by a group of nerve fibers, the CT afferents, which respond preferentially at slow velocities (Löken et al., 2009).

According to one view, affective touch can be reclassified as an interoceptive modality (Craig, 2003) since it provides a direct source of information regarding the internal state of the body (see Chapter 1 for details). Craig argues that in the insula interoceptive information about the internal state of the body is progressively integrated with information from the exteroceptive senses (e.g. vision, audition, olfaction; Craig 2009; 2010). Evidence shows that the exteroceptive and interoceptive modalities interact and can influence each other, contributing ultimately to the experience of a coherent self (e.g. Critchley et al., 2004). For instance, recent studies showed that “cardio-visual” signals can modulate bodily self-consciousness and tactile perception (Aspell et al., 2014) and also the experience of body ownership in the classic Rubber Hand Illusion (Suzuki et al., 2013; Botvinick & Cohen, 1998). The relationship between interoception and exteroception has been discussed in Chapter 1, and investigated in Chapters 3 and 6.

However, it remains unclear whether and to what extent exteroception (i.e. vision) influences interoception (i.e. perception of affective touch).

This study aimed to investigate the interaction between exteroception and interoception in the context of shared tactile experiences, i.e. when two individuals experience tactile cutaneous stimulation at the same time. Specifically, it sought to explore whether observing touch applied to someone else's skin in synchrony with touch applied to one's own skin can influence the perception of bodily tactile pleasure. Indeed, synchronicity could have a specific importance in modulating the pleasantness perception. Research in anthropology and social psychology argues for an involvement of synchronous activity in the development of positive emotions in social relations. Specifically, synchronous activities seem to diminish the boundaries between the self and other group's members (Wiltermuth & Heath, 2009), promote social understanding (Wheatley, Kang, Parkinson & Looser, 2012) and increase affiliation (Hove & Risen, 2009). In addition, synchronicity has an important role in development, as affect synchrony (e.g. coordination of affective expressions during face-to-face interactions) between mother and infant can promote the emergence of self-control and self-regulation which represent key aspects for later socialisation (Feldman, Greenbaum & Yirmiya, 1999).

Previous research in the context of multisensory integration has also shown how crucial synchronicity is for embodiment in paradigms such as the rubber hand illusion (Botvinick & Cohen, 1998). In fact, synchronicity is a basic property of multisensory integration, the effects of which extend beyond the embodiment of a rubber hand. Recent studies have shown that synchronous visuo-tactile stimulation can also enhance self-identification with the face ("enfacement illusion"; Sforza, Bufalari, Haggard & Aglioti, 2010; Tsakiris, 2008) and with the full body of another person or with a virtual one (Petkova & Ehrsson, 2008; Lenggenhager, Tadi, Metzinger & Blanke, 2007).

Numerous studies have tried to clarify which neural mechanisms are involved when *perceiving* touch versus *observing* someone else being touched (e.g. Keysers, Wicker, Gazzola, Anton, Fogassi et al., 2004). Functional neuroimaging studies have reported activation of partially the same neural circuitry in the somatosensory cortices

during the experience of touch and the observation of another person being touched (Blakemore, Bristow, Bird, Frith, & Ward, 2005; Keysers et al., 2004; Morrison et al., 2011). Given this evidence supporting a partially overlapping neural activation during the perception of touch and the observation of others being touched, it has been hypothesised that this could reflect an automatic tendency to activate brain areas involved in the processing of our own experience of touch during the mere observation of touch applied to someone else (Ebisch, Perrucci, Ferretti, Del Gratta, Romani et al., 2008). This mechanism is considered similar to the activation of the so-called Mirror Neuron System during the observation of actions and emotions. According to this hypothesis, actions performed by others can be understood by activating the own representation of the same actions at the neural level (Rizzolatti & Craighero, 2004; for a review).

The more recent idea of a somatosensory mirror system in the brain (e.g. Blakemore et al., 2005) is supported, for example, by findings in the context of the visual remapping of touch (VRT; Serino, Pizzoferrato & Ladavas, 2008; Cardini, Costantini, Galati, Romani, Ladavas et al., 2011). During this phenomenon, tactile sensitivity on our face is enhanced when viewing another person being touched synchronously on the face at the same time. More generally, the hypothesis that a shared representation exists in the context of body perception has recently acquired more interest. Thomas and colleagues (2005) introduced the term Interpersonal Body Representations to refer to the self/other relation based on visual remapping of touch. It has been hypothesised that we might experience events that we observe occurring to other people's bodies by matching them to mental representations of corresponding events on our own body (Thomas, Press & Haggard, 2005). Furthermore, feeling touch and seeing another person being touched seem to increase our accuracy to detect tactile stimuli (Cardini, Haggard & Ladavas, 2013). Interestingly, this effect seems to increase when touch occurs in the congruent anatomical locations in both the experienced and observed body parts.

Recent fMRI evidence supports the existence of similar vicarious mechanisms in the specific domain of CT-based affective touch (Morrison et al., 2011). Observing

another's arm being stroked at CT optimal velocities activates posterior insular regions that partially overlap with those activated during felt pleasant/CT optimal touch (Morrison et al., 2011). Remarkably the insula activation seems to be modulated by velocity only when the observed touch is of social nature (i.e. observing hand stroking skin), in contrast such modulation is not observed in the case of a nonsocial touch scenario (i.e. observing hand stroking water).

Furthermore, the perception of affective touch can be influenced by top-down factors. In a study by McCabe and colleagues (2008), participants' forearms were rubbed with a cream, which was accompanied by a word label that indicated the cream was a "rich moisturising cream" (pleasant to most people) or a "basic cream". The authors showed that the perceived pleasantness of tactile stimulation can be influenced by top-down factors; namely, participants rated the touch as more pleasant and richer when the cream was labeled as rich moisturising compared to a basic one. However, in this study the authors manipulated the word label but not the velocity of touch, since the stimuli were always applied at CT optimal speeds.

On the other hand, evidence from Schütz-Bosbach, Tausche and Weiss (2009) suggests that the integration of visual information arising from another's body with tactile information originating from one's own body is not sufficient to alter the perception of tactile experiences. Specifically, Schütz-Bosbach and colleagues used a rubber hand illusion paradigm (Botvinick & Cohen, 1998) to investigate whether participants' perception of tactile stimulation on their own hidden arm was modulated by simultaneously watching the rubber hand being touched by either the same or a different material (i.e. soft or rough fabric). The results showed that participants' interpretation of the perceived roughness of the fabric on their own arm was not modulated by the perceived visual stimulation of the rubber hand, and therefore touch perception seems to be resistant to top-down manipulation (Schütz-Bosbach et al., 2009). However, the authors did not specify the velocity of touch so it is not possible to know whether an involvement of the CT afferents would have played a role in the modulation of different tactile materials.

On the basis of this inconsistent evidence, it remains unclear what the specific role of CT-based touch is in the context of perceiving and observing cutaneous stimulation together with someone else. To investigate the effect of concurrently observing and perceiving touch on the subjective experience of pleasantness, this study measured the perceived pleasantness of low-pressure, soft, dynamic (moving in slow, CT-optimal versus faster, not CT-optimal velocities) tactile stimuli applied to participants' forearms while a confederate's arm was stroked simultaneously either synchronously or asynchronously. Specifically, this study explored the following questions: 1) how is the perception of affective touch influenced by simultaneous observation of touch applied either synchronously or asynchronously to a confederate's arm? 2) In the context of such synchronous, shared touch, what is the effect of 'self' versus 'other' visual focus (i.e. observing one's own arm vs. someone else's arm being stroked while knowing that both receive the touch in synchrony) in the perceived pleasantness of tactile stimuli? And 3) how does the velocity of touch (CT optimal vs. CT non-optimal speeds) interact with these two effects?

It was predicted that synchronous touch would enhance the perceived pleasantness of touch more than asynchronous touch, given its facilitating role in inducing visual and tactile integration and the fundamental role of interpersonal synchrony (see above). Also, in the context of synchronous shared tactile experience, visual focus, and therefore visual attention, was not expected to play a role in the perceived pleasantness of touch, since the mere knowledge of sharing synchronous touch with someone else should be enough to enhance the perceived pleasantness of touch. That is, it was hypothesised that the increased pleasantness of the tactile experience would not be affected by a simple visual enhancement of touch. In fact, the manipulation of the visual focus was added to control for the effect of looking directly at the arm rather than looking at another hand. Finally, the enhancement of perceived pleasantness in the synchronous shared touch condition was expected to be stronger when touch was delivered at CT-optimal velocities, given the proposed role that the CT affective touch system plays in social affiliation (Morrison et al., 2010). In contrast when touch was delivered at CT-non-optimal speeds the shared touch experience was

not expected to increase the perceived pleasantness of touch. It was also predicted that the modulation of perceived pleasantness of tactile stimulation would have not been observed in the context of asynchronous touch, regardless of velocity of touch.

7.2. Materials and methods

7.2.1. Participants

Participants were recruited at King's College London, through email circulars and advertisements. Institutional ethical approval was obtained from King's College London and all participants gave written informed consent prior to data collection. Thirty-five healthy females (mean age = 23.14; SD = 3.82) participated in a 45-minute experiment in exchange of £5. One participant was later excluded from the analysis, since she failed to comply with experimental instructions (i.e. she did not use the rating scale correctly).

7.2.2. Experimental design and statistical analysis

The aim of this study was to investigate how velocity of tactile stimulation and the synchronicity of visual feedback of shared touch would affect perceived tactile pleasantness of touch on the self. The experiment employed a 2 (Velocity: CT-optimal vs. CT-non-optimal) x 3 (Visual Condition: *self synchronous*, *other synchronous*, *other asynchronous*) within-subjects factorial design (Table 7.1.). In the *other* conditions the participant's own arm and the confederate arm were stroked simultaneously, while participants watched the 'other' (i.e. a confederate's) arm. A *synchronous* and an *asynchronous other* conditions were included to determine to what extent synchronicity of touch on the self and visual observation of touch on another modulates tactile pleasantness. In the *self synchronous* condition, the participant watched her own left arm being stroked, while at the same time, the experimenter stroked the confederate's unseen arm, which remained hidden behind a curtain (Figure 7.2.a), in order for participants to

still be aware of the shared touch scenario even without having direct view of the confederate's arm.

Table 7.1. Summary of the experimental design.

Table 7.1.		<i>Within-subjects factors</i>		
		Self	Other synchronous	Other asynchronous
Velocity	CT optimal	Slow/Self	Slow/Synchronous	Slow/Asynchronous
	CT-non-optimal	Fast/Self	Fast/Synchronous	Fast/Asynchronous

The touch was delivered at two CT optimal speeds (3 and 6 cm/s) and at two CT non-optimal speeds (18 and 27 cm/s) (Löken et al., 2009). The main outcome measure was a subjective pleasantness rating of the touch using a scale ranging from 0 (not at all pleasant) to 10 (extremely pleasant). Since the aim of the study was to investigate any potential difference in the modulation of tactile pleasantness when CT fibers were involved, all the analyses were conducted by averaging the 3 and 6 cm/s conditions (i.e. CT-optimal), and 18 and 27 cm/s conditions (i.e. not CT-optimal).

Data were analysed by means of SPSS version 21.0. Kolmogorov-Smirnov tests and visual exploration of the data show that the pleasantness data were normally distributed ($p > 0.05$) and therefore suitable for analysis using parametric statistics. The embodiment data were analysed using non-parametric statistics, as the Kolmogorov-Smirnov tests were significant ($p < 0.05$) and therefore data were not normally distributed.

To investigate the effect of Velocity and Visual Condition on tactile pleasantness, and any potential interactions between the two within-subjects factors a 2 (Velocity: CT-optimal vs. CT non-optimal) x 3 (Visual Condition: *self synchronous*, *other synchronous*, *other asynchronous*) ANOVA was conducted. Bonferroni-corrected planned contrasts were used to follow up any significant main effects or, interaction of Velocity and Visual Condition. Specifically, the study aimed to assess whether synchronicity of touch had an effect on tactile pleasantness, as would be revealed from the comparison *other synchronous* versus *other asynchronous* conditions. The analysis also compared *self synchronous* and *other synchronous* to observe the effect of visual

focus on tactile pleasantness, in the sense of looking at your arm vs. someone else arm during the same tactile condition. Significant main effects and interaction were followed up considering CT optimal and CT non-optimal velocities separately, to observe any potential involvement of the CT fiber system.

7.2.3. Control procedure

Since the purpose of this study was to investigate the effect of *shared touch* on tactile pleasantness, it was important that the distinction between self and other was maintained throughout the stroking in all visual conditions. Therefore, the experimental procedure aimed to reduce the possibility of other arm embodiment feelings that could arise as a result of the simultaneous stroking of the participant's unseen hand and the observed confederate's hand, by placing the confederate hand at 90 degrees with respect to the participant's own hand. Previous research using the Rubber Hand Illusion (RHI; Botvinick & Coehn, 1998) shows that placing the hand at 90 degrees with respect to the participant's own hand blocks embodiment of the other hand, even when both hands are stroked simultaneously (Tsakiris & Haggard, 2005). As a check of this manipulation, a shortened version of an embodiment questionnaire (see Table 7.2.) was used to measure any changes in the subjective experience of body ownership during our tactile stimulation (Botvinick & Cohen, 1998). Participants reported to what extent they agreed with the statements using a rating scale ranging from 0 (strongly disagree) to 7 (strongly agree). In line with previous RHI studies, a score below 4 indicated a disagreement with the embodiment scores (see Ehrsson, Spence & Passingham, 2004; Petkova & Ehrsson, 2009; Kalckert & Ehrsson, 2012), whereas a score above 4 provides an a-priori criterion for the occurrence of embodiment. Participants completed the questionnaire before (pre) and after (post) the *other synchronous* and *other asynchronous* conditions only (see Procedure). For these two conditions, the post-stroking embodiment score was subtracted from the pre-stroking score, in order to obtain a measure of subjective embodiment due to visuo-tactile integration.

Table 7.2: The embodiment questionnaire (Botvinick & Cohen, 1998).

Table 7.2: Embodiment questionnaire
It seemed as if I were feeling the touch of the brush in the location where I saw the other's hand touched
It seemed as though the touch I felt was caused by the brush touching the other's hand
I felt as if the other hand were my hand

7.2.4. Materials and set-up

Participants sat at a table opposite the experimenter, and next to a female confederate sitting behind a 130 x 130 cm black curtain positioned to the right of the participant (see Figure 7.1.). Prior to data acquisition the experimenter marked two adjacent 9cm × 4cm brushing areas on the skin between the wrist crease and the elbow, on both the participant's and the confederate's left forearm. As described in Chapter 2, this was done to ensure brush strokes were consistent in space and pressure throughout the experiment. Tactile stimulation was applied using two, identical, cosmetic make-up brushes (Natural hair Blush Brush, N°7, The Boots Company). In order to block vision of the left hand in the two '*other*' conditions, participants placed their hand inside a white plastic box measuring 25 x 40 x 25 cm. The box was open on the experimenter side to allow delivery of the tactile stimulation, and had a hole on the opposite side to allow the participant to insert her left arm (see also Chapter 5)

In the *other* condition the confederate placed her left arm (through the curtain) in view of the participant on the table, at a 90-degree-angle with respect to the participant's own hand (see above). The rest of the confederate's body remained behind the curtains so that only her arm was visible (Figure 7.2.b). The participant's own left forearm was placed inside a box to block it from view, and the participant was instructed to watch the other person's arm being stroked synchronously (Figure 7.1. and 7.2.b).

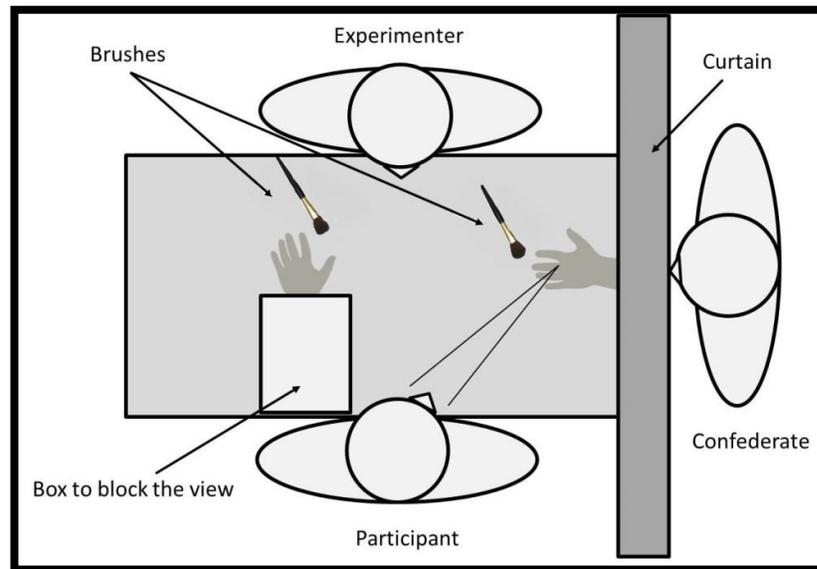


Figure 7.1: Plan view of the experimental setup. Participants were asked to sit in front of the experimenter with their left arm rested on the table. The confederate was sitting on the right hand side of the table, hidden behind the curtains with her left arm on the table visible to the participant (condition *other*). Touch was delivered by the experimenter with two identical soft brushes. A plastic box was used to block the visual feedback of the touch.

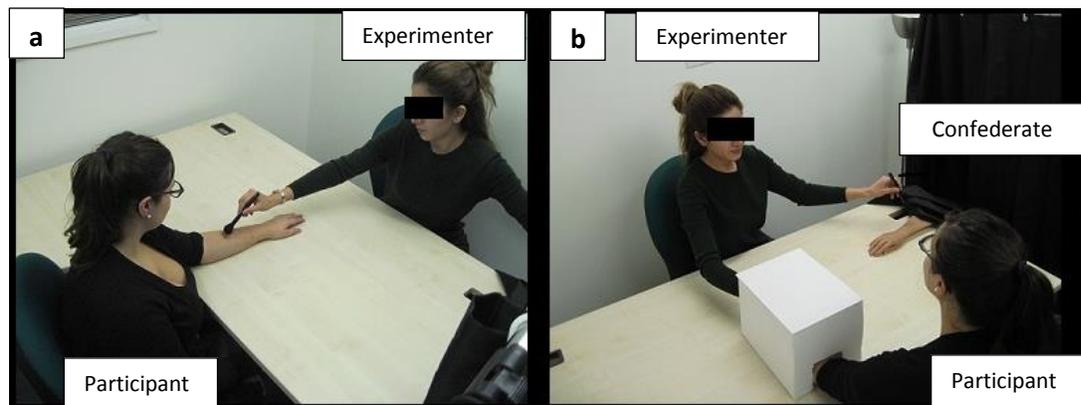


Figure 7.2: The experimental set-up. a) Condition *self*, and b) Condition *other synchronous* and *asynchronous*

7.2.5. Procedure

At the start of the every experimental session only the experimenter and participant were present in the lab, in their respective positions (described above). Then, in order to ensure that participants were aware that the arm they would see on the table

was that of another person, the experimenter invited the experimental confederate to enter the lab and take her position behind the curtain. There was no verbal interaction between the participant and the confederate in any condition. The experimental stimuli were then delivered with the participant instructed to focus on the tactile sensation on her own arm, irrespective of visual input. Prior to the perception of tactile stimulation, the participant was asked to look at the confederate's arm for 15 seconds, after which she completed the pre-embodiment questionnaire in order to have a measure of the pure visual capture. Participants were asked to complete the post-embodiment questionnaire following each *other* condition. The *other asynchronous* condition differed from the synchronous one only in terms of having the participant's and confederate's left forearms stroked asynchronously; that is, visual and tactile stimulation were temporally incongruent.

Each condition comprised 16 trials lasting 3 seconds each; 8 trials per condition were delivered at CT optimal velocities (3 and 6 cm/s) and 8 trials were delivered at CT non-optimal velocities (18 and 27 cm/s) (Löken et al., 2009). The inter-stimulus interval was approximately 2 seconds, as in previous studies (McGlone et al., 2012). The order of the above conditions, as well as the velocities of touch, was randomised across participants.

7.3. Results

7.3.1. Pleasantness ratings

The effects of Velocity and Visual Condition were investigated by conducting a 2 (Velocity: CT-optimal vs. CT-non-optimal) x 3 (Visual Condition: Self, Other Synchronous, Other Asynchronous) repeated measures ANOVA. Results confirmed a significant main effect of Velocity ($F(1, 33) = 121.99; p < 0.001; r = 0.89$), with CT optimal velocity (mean = 6.98; SD = 1.38) being rated as significantly more pleasant compared to CT non-optimal velocities (mean = 4.89; SD = 1.68) overall. The main effect of Visual Condition was not significant ($F(1, 33) = 2.10; p = 0.13, r = 0.24$); however, there was Velocity x Visual Condition interaction ($F(1, 33) = 3.26; p = 0.04; r = 0.30$), as predicted.

Subsequent analysis of this interaction with Bonferroni-corrected planned contrasts ($\alpha = 0.025$; see above) revealed that when touch was delivered at CT optimal velocities pleasantness ratings did not significantly vary between *self synchronous* and *other synchronous* conditions ($t(33) = 0.66, p = 0.52, r = 0.11$). Thus, looking at one's own arm vs. someone else's arm elicited equivalent feelings of tactile pleasantness during slow, CT-optimal touch. However, a significant difference was found between *other synchronous* and *other asynchronous* conditions at CT-optimal velocities ($t(33) = 2.4; p = 0.02, r = 0.39$), with synchronous stroking eliciting higher pleasantness scores than asynchronous stroking (synchronous mean = 7.07; SD = 1.44; asynchronous mean = 6.67; SD = 1.62).

Analysis of the non-CT optimal conditions revealed neither a significant difference between *self* and *other synchronous* conditions ($t(33) = 0.26, p = 0.80, r = 0.045$), nor between the *other synchronous* and *other asynchronous* conditions ($t(33) = 0.60; p = 0.56, r = 0.10$) (Figure 7.3.).

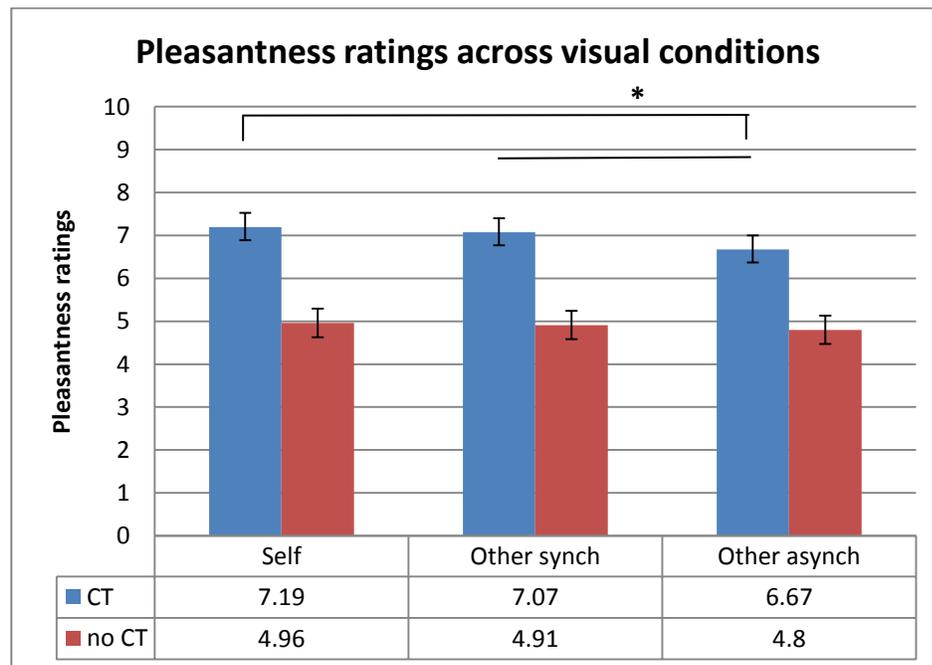


Figure 7.3. Means and standard errors of the pleasantness ratings across Visual Conditions. $*p < 0.025$

7.3.2. Control Embodiment questionnaire

The study checked for the predicted absence of embodiment during tactile stimulation of the other person's arm. Using the a-priori criteria (i.e. an average score $\geq +4$; see above), neither the synchronous nor asynchronous condition resulted in scores that indicated embodiment of the observed *other* arm. However, a Wilcoxon Signed Ranks Test did reveal a main effect of synchronicity, with synchronous touch (median= 1.15) leading to greater embodiment scores compared to asynchronous touch (median = 0.24; $Z= -2.69$; $p = 0.006$) despite the incongruent position of the observed limb. Spearman's correlations were run to explore the relationship between embodiment and pleasantness ratings in the synchronous touch condition. A positive correlation was found between embodiment and pleasantness rating at: slow/CT optimal velocities ($r_s = 0.46$, $n = 34$, $p = 0.006$) and pleasantness rating at fast/CT non-optimal velocity ($r_s = 0.45$, $n = 34$, $p = 0.007$; Figure 7.4.). The same correlational analysis was performed for asynchronous touch, revealing no significant results (all r_s between 0.18 and 0.26; all p s between 0.14 and 0.31).

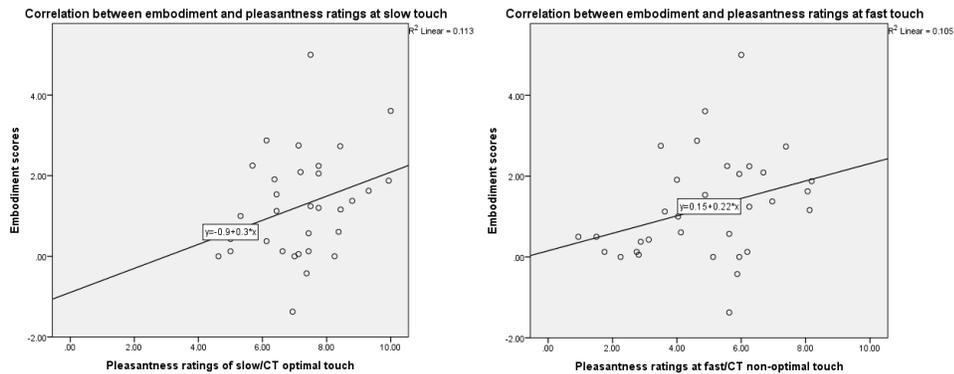


Figure 7.4. Correlations between embodiment and pleasantness ratings of slow/CT optimal and fast/CT non-optimal touch

7.4. Discussion

This study aimed to explore the interaction between interoception (i.e. affective touch) and exteroception (e.g. visual feedback) in the context of shared tactile experiences. Specifically, it aimed to investigate whether observing another person's arm being stroked in synchrony with one's own would modulate one's own pleasantness perception more than asynchronous touch. The main finding confirmed the first hypothesis, showing that visual feedback of synchronous tactile stimulation on another person's arm increases the perceived pleasantness of the touch more than asynchronous touch. Moreover, it was found that this effect applies only when the touch is delivered at CT optimal velocities, with no effect of synchronicity found when touch was applied at fast, CT-non-optimal velocities. Finally, no effect of visual feedback was found, in the sense that there were no differences in pleasantness ratings reported after looking at the subject's own arm or the confederate's arm being stroked in synchrony, for both CT- and CT-non-optimal velocities.

The findings of this study are in line with recent evidence suggesting that the observation of touch affects the perception of touch. Specifically, it has been shown that perceiving touch while observing another person being touched in a similar way increased accuracy of tactile detection (Cardini et al., 2013) in the sense of improvement of spatial tactile discrimination of experimental stimuli (i.e. tactile ratings). This finding has also been extended in the context of perceived tactile intensity of touch (i.e. forced choice task between two mostly equally intensive touches; Gillmseteir, 2014), but only when felt and observed touch were concurrent.

The present study showed for the first time that the interaction between observed and perceived touch could be extended also to the affective experience of touch; in fact a small but statistically significant increase in perceived bodily pleasure was observed when the experience of touch was shared with someone else. Most importantly, this effect seems to be dependent on a direct involvement of the CT affective touch system, providing further evidence to the importance of the affective touch system in human

interactions (see Morrison et al., 2010). The CT fibers system seems to play a key role in our development and mental health from very early stages of our life (e.g. Sharp et al., 2012). In fact, the first form of communication that the external world uses with a newborn and vice versa is a tactile one; in particular a slow, caress-like touch. As shown in previous studies (Chapter 2; see also Lloyd et al., 2013; and van Stralen et al., 2014), this touch is not only of great importance to become aware of our body, and by implication of the self-other distinction, but it also lies at the foundation of social bonding and emotional communications (Hertenstein, Keltner, App, Bulleit & Jaskolka, 2006; Hertenstein, Verkamp, Kerestes & Holmes, 2009).

The results presented here also showed that the increase in the perceived pleasantness was caused by the knowledge that participants were sharing the same, affective, tactile experience with another individual, over and above any visual effects and related vicarious touch interpretations. No significant differences were found between the condition *self* and *other synchronous*; these two conditions differ only in the visual focus. If in the *self synchronous* condition the participant is looking at her own arm but she is aware that the other person perceives the same, synchronous touch as herself, in the *other synchronous* condition, participants are instructed to look at the other's arm while receiving identical touch. On the basis of these results it could be speculated that the mere knowledge rather than the direct view that someone else perceives pleasant touch in synchrony with us is enough to result in a "shared touch effect". Therefore, when affective touch is shared an increase in pleasantness can be observed irrespective of where the visual focus, and therefore attention, is placed. When a pleasant, affective stimulation is perceived on the skin at CT-optimal velocities and there is knowledge that someone else perceives the same positive sensation simultaneously with us, perhaps there is a top-down amplification effect on one's own pleasantness. Therefore, the concurrency between felt and observed touch seems to be a key feature of this enhancement, in line with previous findings highlighting the importance of synchronicity in the context of "mirror touch" (Gillmestier, 2014).

7.5. Limitations and future directions

It could be argued that the increased pleasantness that is observed during synchronous touch of another is explained simply by differences in the level of distraction or cognitive load between these two conditions. Although asynchronous touch of another might require greater attention and processing resources, the fact that the finding is selective to CT-optimal velocities (and does not occur under the same conditions during CT non-optimal stroking), indicate that these factors cannot fully explain the observed effect.

There is also the possibility that the enhancement of perceived pleasantness in the synchronous condition might be due to the embodiment process that is observed in the classic rubber hand illusion. Consistent with the results presented in Chapter 2 and 3, it was found that increased tactile pleasantness enhanced embodiment of the other hand. Nevertheless, overt embodiment of the other hand was successfully blocked during the current experiment, by placing the hand in an incongruent position (at 90 degrees relative to the participant's own hand; see Tsakiris & Haggard, 2005). Although the synchronous and asynchronous conditions' embodiment ratings were significantly different, both conditions produced ratings that indicated no embodiment of the other hand.

A replication of these findings with a larger sample size, that also includes male participants, would also allow for greater confidence and generalisability of these results. Despite the relatively small sample size, a significant enhancement of perceived pleasantness was found in the synchronous affective touch condition; however, the magnitude of the effect is relatively small ($d = 0.03$, Cohen, 1988) and needs to be replicated in future studies. Given the social nature of the task, the effect of confederate and experimenter gender should be matched or examined as an independent variable, to establish the possible role of social factors (such as attractiveness) in the modulation of perceived pleasantness.

Finally, it is possible that early social experiences and individual differences in the way of relating to others (i.e. attachment style) can influence the perception of tactile stimulation and the meaning that is attributed to affective touch. A study showed that vicarious somatosensory responses for simple touch are influenced by observer's personality traits, such as emphatic traits (Schaefer, Heinze & Rotte, 2012). Since personality traits seem to play a role in a putative mirror neuron system, future studies could help to clarify the role of individual traits in the way we experience and observe affective touch.

Remarkably, a recent neuroimaging study investigated whether empathy for pleasant and unpleasant affective touch is underpinned by different neural networks (Lamm, Silani & Singer, 2015). The results from this fMRI study showed that empathy is subserved by distinct neural networks, in the sense that experiencing and observing pleasant touch commonly recruited medial orbitofrontal cortex (OFC), while unpleasant touch was associated with shared activation in the right fronto-insular cortex. Lamm and colleagues showed that specific neural systems are activated in the shared experience of pleasant and unpleasant touch with others; this provided support to the idea that we engaged different aspects of our affective and emotional experience in order to understand the emotions and mental states of others (Lamm et al., 2015). On the basis of this recent study and the data presented in this Chapter it would be interesting to investigate the role played by congruency between the seen and experienced touch (in the sense of pleasant/unpleasant touch) rather than synchronicity on the perception of touch pleasantness.

In conclusion, these findings provide an important contribution to better understand how others can influence and enhance our own bodily feelings. This study paves the way for future investigations in the context of "affective mirror touch", and by implication in the wider context of understanding others people feelings and states of mind.

General discussion

8.1. Introduction

The main aim of the present thesis was to explore the role of affective touch, as an interoceptive modality, to the sense of body ownership, which is a fundamental aspect of bodily self-consciousness. In order to do so, experimental, pharmacological and clinical methodologies were used. Specifically, as outlined on Chapter 1, this work aimed to advance the current state of knowledge by investigating: 1) the effect of affective touch on the sense of body ownership, which is a fundamental aspect of bodily self-consciousness; 2) the relation between interoceptive modalities and exteroception in body representation; 3) the effect of intranasal oxytocin on the perception of affective touch and bodily awareness; 4) the perception of affective touch in Anorexia Nervosa and its social modulation, and 5) the modulating role of self-other distinction and relation in the perception of affective touch and body awareness. A common thread running through the experimental chapters of this thesis (Chapter 2-7) was the investigation of affective touch as a modality providing information about the internal feeling of the body (i.e. bodily pleasure) and which contributes ultimately to a coherent sense of self that involved a balance between interoceptive and exteroceptive components.

In this final Chapter, the main findings are reviewed collectively and then discussed in the context of the accumulated knowledge about affective touch covered in Chapter 1. Specifically, the main findings are critically analysed in order to highlight their contribution to the general debate about the affective facet of touch. Strengths and limitations of all the methods applied in the experimental studies are then discussed in the Methodological discussion section. The clinical implications of the main findings from this thesis are highlighted, and novel avenues for future research are discussed.

8.2. Summary of the main findings

In **Chapter 2** the rubber hand illusion paradigm (Botvinck & Cohen, 1998) was used to investigate the role played by affective touch in the sense of body ownership. Specifically, the velocity of touch during the illusion was manipulated in order to observe the effect of affective/slow vs. neutral/fast touch on the multisensory integration process taking place during the illusion. The results confirmed previous findings that slow velocity, light touch on hairy skin is perceived as more pleasant than fast touch (Löken et al., 2009). Importantly, the experiment reported in Chapter 2 demonstrated for the first time that using slow, pleasant touch during the rubber hand illusion produces higher levels of subjective embodiment compared to fast, neutral touch. The results further showed that slow, synchronous stroking did not affect the perceived location of the participants' own hand during the illusion (i.e. proprioceptive drift). This study seemed to suggest that affective touch had a greater effect on subjective than behavioural measures of body ownership.

To better understand the role of affective touch in bodily self-consciousness, the relation between affective touch and another interoceptive modality (i.e. cardiac awareness) was examined in **Chapter 3**. The heartbeat counting task (Schandry, 1981) and the affective touch task were combined in the context of the rubber hand illusion, in order to explore the relationship between interoception and exteroception in the sense of body ownership. The aim of this study was to investigate for the first time the interplay between different interoceptive modalities, namely cardiac awareness and affective touch, in body representation. In particular, this Chapter explored whether interoceptive sensitivity would modulate the extent to which affective touch influences the multisensory process taking place during the rubber hand illusion, as measured using 1) subjective self-reports (i.e. an embodiment questionnaire), 2) an objective, behavioural measure (i.e. proprioceptive drift), and 3) physiological changes in the body (i.e. the temperature drop previously observed as a consequence of acquiring ownership of the rubber hand). In line with the findings of Chapter 2, the results confirmed that the subjective (i.e. embodiment questionnaire) but not the objective (i.e. proprioceptive

drift) component of the illusion can be enhanced by slow, affective touch (see also Chapter 2; Lloyd et al., 2013; but see van Stralen et al., 2014 for an opposing result), resulting in a stronger conscious experience of acquiring ownership over the rubber hand. Given the recent evidence arguing for a role of affective touch as an interoceptive modality for the sense of body ownership, a potential relationship between the bodily pleasure raised by affective touch and the extent to which participants were aware of their body from within (i.e. interoceptive sensitivity) was hypothesised. However, as tested in the present study, this prediction could not be confirmed. Correlational analysis showed a non-significant relation between the performance on the heartbeat detection task and on the affective touch task. Therefore, these two interoceptive modalities might underlie different aspects of interoception. These results are discussed in more details below.

Chapter 4 presented an investigation of the neurobiology of affective touch. This double-blind, placebo-controlled, randomised, cross-over study aimed to explore the effect of intranasal oxytocin on the perception of affective touch and body awareness, as measured by means of the heartbeat detection task and the rubber hand illusion. The importance of tactile social interactions on physical and psychological wellbeing, and in particular slow touch (i.e. massage), is supported by clinical and experimental studies (e.g. Field, 2010 for a review). However, the neurobiological mechanisms of touch, and in particular affective touch, are still under investigation. Animal studies have associated the perception of affective touch with the release of oxytocin (Uvnäs-Moberg et al., 2015 for a review); more recently these findings have been partially extended to humans too (e.g. Morhenn et al, 2012). The study described in Chapter 4 attempted to further investigate the neurobiology of affective touch by exploring the effect of intranasal oxytocin and placebo on the perception of slow (CT optimal) vs. fast (non-CT optimal) strokes delivered on participants' forearms. The findings highlighted a trend for oxytocin compared to placebo to improve the discrimination between slow and fast touch; however the results were not statistically significant and future studies should investigate this further on a larger sample. Additionally, the performance on the heartbeat detection task following the self-

administration of oxytocin and placebo were compared in order to investigate any effect of the active compound on interoceptive awareness. No differences in performance on the heartbeat counting task were found following the self-administration of oxytocin or placebo. This finding supports the existing idea of interoceptive sensitivity as a rather fixed trait (Schandry, 1981; Tsakiris et al., 2011, but see Ring, Brener, Knapp & Mailloux, 2015). Finally, the sense of body ownership was manipulated and measured by means of the classical rubber hand illusion. No differences were found in the occurrence of the illusion following the self-administration of oxytocin vs. placebo, suggesting that this multisensory integration process is resistant to the effect of intranasal oxytocin. However, given the small sample size and limited statistical power observed in this study, the results and their interpretation should be taken with caution and further investigated in future research.

Chapter 5 applied some of the above methodologies to investigate affective touch in a clinical population characterised by body image distortions, lack of awareness and social difficulties, i.e. anorexia nervosa. Participants with anorexia nervosa and healthy controls were asked to rate the pleasantness of the touch that they perceived on their forearms, while simultaneously looking at faces displaying different facial expressions (accepting, neutral and rejecting faces), which are known to differently engage the attentional resources in anorexia nervosa compared to healthy controls. Results showed that participants with a diagnosis of anorexia nervosa perceived affective touch as less pleasant compared to healthy controls. No differences between the two groups were found in the perception of fast, emotionally neutral touch. Therefore, this finding seemed to suggest a specific impairment in the perception of touch mediated by the CT afferents system. Hence, these data might indicate a potential involvement of a distorted affective touch system in the disordered body image and social anhedonia which characterise this clinical population. Contrary to the prediction, no differences were found between anorexia nervosa participants and healthy controls in the social modulation of facial expressions, in the sense that both groups showed an increase in pleasantness ratings when touch was presented together with accepting faces compared to rejecting faces. These data might suggest an intact top-down modulation of

interpersonal touch in anorexia nervosa, and therefore open novel avenues to the development of different therapeutic approach to anorexia nervosa by means of this unimpaired channel.

The relationship between affective touch and body awareness in the context of social cognition was further investigated and discussed on **Chapter 6** and **Chapter 7**. In **Chapter 6**, the focus was on the *distinction* between self and other and the effect on bodily pleasure and cardiac awareness. Participants completed a heartbeat counting task and an affective touch task while they were looking at themselves or someone else in the mirror. The participants were split in two groups (high vs. low perceivers) based on whether their ability to count their own heartbeat while looking at a blank screen was above or below the median of the group (see Ainley et al., 2012). The findings showed a significant difference in interoceptive sensitivity between high and low interoceptive sensitivity groups also in the self- and other-mirror observation conditions, respectively. Previous studies showed that observing the self in a mirror can improve interoceptive sensitivity (measured using the heartbeat counting task) compared to a blank screen condition, but only in participants with low interoceptive sensitivity at baseline (Ainley et al., 2012). The study reported in Chapter 6 failed to replicate the findings of Ainley and colleagues, suggesting that visual feedback does not affect performance on the heartbeat counting task in either of the two groups. It should be noted that the sample of the study presented in Chapter 6 is much smaller than the sample tested in the study of Ainley and colleagues (64 vs. 129 participants); hence this could explain the discrepant findings, which are discussed in more depth below. Performance on the affective touch task indicated that perceiving touch whilst looking at someone else in a mirror (and being looked back at) reduced the perceived pleasantness, compared to looking at a blank screen or at one's own face in the mirror. To a certain extent, this finding was in line with recent evidence showing that exteroception, but not interoception, can be affected by the awareness of being watched (Durlik et al., 2014). In fact, the performance on the heartbeat detection task did not seem to be affected by a condition in which a recording camera was on ('being watched condition'); in contrast the tactile perception was enhanced when there was social self-focus. Similarly, the present study

showed that being observed by someone else reduced the perceived pleasantness of tactile stimulation, whereas it did not affect the performance on the heartbeat counting task. This could suggest that being observed by someone else (not the person performing the touch) does affect the perception of touch, since the nature of tactile stimulation itself is interpersonal, and therefore probably more sensitive to social manipulation.

In contrast, in **Chapter 7**, the effect of the *togetherness* of self and other on bodily pleasure was investigated. Namely, participants were asked to rate the pleasantness of touch while perceiving it together (synchronously or asynchronously) with someone else. The results showed that visual feedback of synchronous tactile stimulation on another person's arm increased the perceived pleasantness of the touch more than asynchronous touch. Moreover, this effect seemed to apply only when the touch was delivered at CT optimal velocities, with no effect of synchronicity found when touch was applied at fast, CT-non optimal velocities. Finally, no effect of visual feedback was found, in the sense that there were no differences in pleasantness ratings reported after looking at the participant's own arm or the confederate's arm being stroked in synchrony, for both CT- and CT-non-optimal velocities. This seemed to suggest that the mere knowledge of someone else being touched in a pleasant way in synchrony to the participant was enough to increase the pleasantness compared to the asynchronous condition.

8.3. Methodological discussion

8.3.1. Affective touch task

Only females have been tested in all the studies presented in this thesis; this choice was made because all the experimenters were females. Therefore, given the evidence showing the influence of the person delivering the touch on the perceived pleasantness (e.g. Scheele et al., 2014), only females were recruited. It would be of interest to replicate the same findings on a male sample only. There is evidence showing gender differences in the perception of touch; that is females tend to prefer same gender-matched touch, whereas males would rather receive touch by females (Stier & Hall,

1984). Additionally, women seem to respond generally more positively than men to touch. To the author's knowledge, no study to date has systematically investigated gender differences in the perception of affective touch. Exploring this outstanding question would enrich the current knowledge on affective touch, and on its anticipation and desirability. This exploration could be brought a step further by investigating the perception of affective touch among romantic partners. In fact, a recent study showed that the mere desire for touch among couples activated the posterior insular cortex, and therefore this anticipatory mechanism could mediate the sensory affective processing of the subsequent skin-to-skin contact (Ebisch, Ferri & Gallese, 2014).

Affective touch has been traditionally investigated by means of tactile strokes applied with a soft brush. Two main kinds of tactile modalities are usually used to deliver the touch; by human hand (e.g. Björnsdotter et al., 2009) and by machine (e.g. Löken et al., 2009). The latter one is preferred for experiments in which it is necessary to precisely control for the velocity and pressure of the tactile stimulation in order to detect very small differences. The advantage of manual touch is that it allows the experimenter to control for the velocity of touch and pressure with a good degree of precision (although not as precisely as the machine method), and in addition, it could be argued that manual touch has a higher ecological validity. In fact, affective touch is, by its very nature, an interpersonal modality and therefore it usually takes place in the context of human interactions. The affective touch procedure applied throughout all the studies presented in this thesis used the manual technique. The experimenters were all females and they all received an identical training; therefore the same technique to control for velocity and pressure was applied throughout all the studies. Although careful training procedures were followed during all experiments to ensure the consistency of touch in terms of experimental factors such as speed and pressure, further objective tests of reliability were not applied. For example, a random sample of testing session could have been video-recorded and second rated to verify that the velocities of touch were applied properly. However, there is a high internal consistency in the experimenters within an experiment, despite differences in experimenter between experiments. In fact, affective touch procedures completed by different experimenters lead to the same pattern of

results; this could provide additional confidence to the methodology used in this thesis. The total number of female experimenters involved in this thesis was seven, and the author provided consistency across all the experiments.

In all the studies of this thesis CT-optimal/slow touch was delivered at 3 cm/s, whereas non CT-optimal/fast touch was delivered at 18 cm/s. The dimension of the tactile area in terms of length and width and the duration of each trial were kept constant. As a consequence, the slow touch resulted in one single stroke, while fast touch resulted in six separate strokes. It could be argued that within the 3 seconds window of duration of the tactile stimulation the brush was in touch with the skin for a 'longer' total time in the slow touch condition compared to the fast touch. In fact, in the latter case, there was a small time window between the six strokes in which the brush was not in contact with the skin. Therefore, in the studies presented here the time and spatial information about the touch have been kept constant when both the velocities were applied. It could be argued that an alternative way to complete the affective touch task could have been by maintaining constant the number of strokes among the two velocities, manipulating the length of the area which was being stroked and the time length of the trial. To the author's knowledge, there are no studies showing which experimental choices are optimal in this context. The experimental choice made in this thesis was driven by practical motivation and it was kept constant in all the studies.

Finally, the rating scale used in the affective touch task presented two anchor words; 'not at all pleasant' and 'extremely pleasant'. Participants were asked to provide a number between 0 and 100 (0 and 10 in the case of the study of Chapter 7). The anchor words were chosen considering the fact that a soft brush stroke cannot really be rated as unpleasant, regardless of the velocity of touch. Therefore, the use of a word label related to 'unpleasantness' was avoided to maintain the ratings more balanced and not biased towards the 'pleasant' anchor word. Additionally, different aspects of the rewarding experience derived by affective touch could be considered in future studies, such as comfort, softness and 'wanting'.

8.3.2. Rubber hand illusion

The outcome measures of the rubber hand illusion considered in this thesis were: the embodiment questionnaire (subjective measure); the proprioceptive drift (objective measure) and the change in temperature (physiological measure – in Chapter 3 only). Interestingly, a dissociation between the subjective and objective measures of the rubber hand illusion has been proposed (Rohde et al., 2011; Abdulkarim & Ehrsson, 2016). Although classic rubber hand illusion studies have found that a reliable behavioural measure of the illusion is the degree to which one's arm is felt to be closer in space to the rubber hand (i.e. proprioceptive drift; Botvinick & Cohen, 1998; Tsakiris & Haggard, 2005), the findings presented in this thesis were consistent with recent studies showing a dissociation between subjective (embodiment questionnaire) and behavioural (proprioceptive drift) measures of body ownership (Rohde et al., 2011; Abdulkarim & Ehrsson, 2016). Specifically, a recent study explored the relationship between the sensed hand position and subjective feeling of ownership in the rubber hand illusion (Abdulkarim & Ehrsson, 2016), finding that the perceived position of the participant's hand (experimentally manipulated) does not play a fundamental causal role in producing the illusion of ownership. The results of Abdulkarim and Ehrsson's study demonstrated that it is possible to induce the rubber hand illusion without the proprioceptive drift component. However, it remains unclear whether the proprioceptive drift and the subjective feeling of ownership are two completely separated processes, and whether the proprioceptive drift is a potential consequence of the feeling of ownership itself. This thesis seems to suggest that the enhancement in embodiment due to interoceptive signals does not have as a consequence a spatial update of the felt location of the participant's hand. This could be due to the fact that interoceptive signals are poor in discriminative information and therefore they do not affect spatial information.

Another factor to take into account in the context of proprioceptive drift is the methodology by which it is measured. In all of the studies reported on this thesis participants were asked to point with their right index finger to the position where they felt that their left index finger was located inside the box; in Chapter 2 this was done with eyes open, and in Chapters 3 and 4 with eyes closed. This procedure requires the

participant to perform an active movement toward their own hand. Therefore, it is possible that this procedure could have cancelled or at least reduced the shift of the participant's own hand towards the rubber hand, and provides a possible explanation for why no proprioceptive drift was found in the studies reported in this thesis. Rubber hand illusion studies conducted by other research groups might use different methodologies, which do not involve a movement of the participant's upper limb after induction of the illusion, and which might therefore, explain findings of proprioceptive drift towards the rubber hand.

The change in temperature has been found to be related to the embodiment of the rubber hand; in fact, it has been proposed that participants lose ownership of their own hidden hand and hence the hand temperature drops. However, few existing studies, and the one described in Chapter 3, failed to replicate the original findings showing a physiological change (i.e. temperature change) in the hand as a consequence of the illusion induction (Moseley et al., 2008). One potential explanation of this inconsistency with the original study of Moseley and colleagues could be the implementation of a different methodology. In fact, in the present study it was observed whether there was a change in temperature before and after the induction of the illusion in the stimulated hand only (as in Tsakiris et al., 2011 and Rohde et al., 2013). In contrast, Moseley and colleagues (2008) observed the difference in temperature between the two hands (i.e. stimulated versus non-stimulated); therefore their results argue for a difference in temperature between the stimulated and the non-stimulated hand after the induction of the rubber hand illusion rather than focusing on the stimulated hand only. Taken together this evidence supports the idea proposed by Rohde and colleagues (2013) that the drop in temperature is observed only when following a specific experimental procedure (i.e. hand stroking and comparison between the two hands). Therefore, this phenomenon cannot be considered a reliable indicator of the subjective experience of owning the rubber hand/ disowning the real hand.

8.3.3. Heartbeat detection task

Despite the renewed interest in interoception, there is still inconsistency about the methods to be used to assess interoceptive ability. A recent theoretical account attempted to clarify the different word labels used to quantify interoception and their relationship (Garfinkel, Seth, Barrett, Suzuki & Critchley, 2015). Firstly, *interoceptive accuracy* refers to paradigms that objectively quantify individual differences in behavioural performance. Heartbeat detection tasks have been the preferred methods used to determine individual differences in interoceptive accuracy (Schandry, 1981), mainly because heartbeats are distinct and frequent internal events that can be easily measured. These procedures usually require the participants to count their own heartbeats without taking their pulse or feeling their chest during specific time (“Heartbeat Tracking Task”; Schandry, 1981). Another detection task is the one requiring participants to report the synchrony of heartbeats with externally originated stimuli (“Heartbeat Discrimination”; Brener & Kluitse, 1988). While some studies found these two heartbeat detection procedures to be correlated in individuals (e.g. Hart, McGowan, Minati & Critchley, 2013), these two methods often show different results and it has been proposed that they might involve different processes. While the counting task depends more on internal monitoring mechanisms, the discrimination task is based on integration between external and internal information (e.g. Schulz, Lass-Hennemann, Sütterlin, Schächinger & Vögele, 2013). Secondly, *interoception sensibility* represents the participants’ subjective rate of the extent to which they can feel their internal sensations. This sensibility can be measured by self-report questionnaires or by subjective scores of the participants’ performance on the interoceptive accuracy tasks described above. A third dimension adopted to quantify interoception is *interoceptive awareness*, which is a combination of interoceptive accuracy (e.g. heartbeat perception task performance), with a measure of interoceptive sensibility (e.g. subjective confidence in performing the task). This method provides a measure of metacognitive awareness of interoceptive ability (Garfinkel & Critchley, 2013). Garfinkel and colleagues recently attempted to empirically determine the relationships between interoceptive accuracy, sensibility and awareness (Garfinkel et al., 2015). The results

showed that these three dimensions are distinct and dissociable, and only partially correlate.

However this debate is beyond the scope of this thesis and it has been briefly reported only to contextualise the interoceptive task used in this thesis. The heartbeat counting task has been used throughout this thesis to measure interoceptive sensitivity (or awareness). The result at the heartbeat counting task has been named interoceptive sensitivity or awareness; these two terms have been consistently used as synonymous and interchangeable.

Additionally, recent evidence also challenges the validity of the heartbeat detection task as measuring a reliable trait, since performance on this task seems to be sensitive to changes such as beliefs (Ring & Brener, 1996), stress (Schulz et al., 2013), contingent feedback and physical exercise (Ring et al., 2015). However, the same identical task has been used throughout all the studies reported here and this provides reliable consistency within this thesis.

Furthermore, heartbeat baseline measurements have been collected for a time window of 3 minutes. The author came to knowledge that a 5 minutes baseline is more informative of the heart rate variability after data collection had been performed. Therefore, in future studies a baseline of 5 minutes should be recorded as it is more informative of the heart rate variability.

8.3.4. Social modulation: facial expressions, mirror observation and synchronous experiences

In this thesis the social modulation of affective touch has been explored through two different modalities; one *offline* and one *online*. *Offline* social modulation means that the social modulation is achieved without the presence of another person (i.e. photographs); whereas in order to produce an *online* social modulation, the presence of another person and social interaction is necessary. Specifically, Chapter 5 used an *offline* social modulation method to explore the effect of looking at faces showing different facial expression in the perception of tactile pleasantness. The strength of this method is its consistency; in fact, presenting facial expressions through photographs means that

these are always the same and therefore all the participants looked at exactly the same facial expressions presented under the same conditions. However it could be argued that the social modulation achieved by showing pictures is somehow “weaker” than an online social modulation, since participants are aware that there is no a real person behind that facial expression, and as a consequence the emotional experience is not felt as strongly as in a real social interaction situation.

Chapter 6 and 7 used *online* modalities of social manipulation. In particular, in the study presented in Chapter 6 participants were asked to look at another person’s face, whose reflection was presented in a mirror. The confederate was asked to keep a neutral facial expression; however, contrary to an offline social manipulation, some variations in these facial expressions between participants could occur and are beyond experimental controls. The strength of this manipulation is that the social scenario is real, in the sense that participants are asked to look at a real person present in the experimental room. The same advantage can be reported for the method used in Chapter 7, when participants were perceiving touch in synchrony or out of synchrony with a confederate who was present in the room.

8.4. The role of affective touch in the representation of the bodily self

As reviewed in section 1.2., the organisation of the tactile afferents systems reflects the duality of the human skin, subserving both discriminative and affective functions. On the one hand, we need to be able to rapidly identify a stimulus touching the body surface in order to react accordingly (i.e. discriminative touch mediated by A β afferents); on the other hand the ability to create social bonds and to perceive our body from within is equally fundamental to our survival (i.e. affective touch mediated by CTs afferents).

The findings of Chapter 2, replicated in Chapter 3, showed the key role played by pleasant, affective touch to the sense of body ownership. To the extent that the sense of body ownership is considered a constitutive aspect of self-consciousness (Gallagher, 2000; Blanke, 2012; Dijkerman, 2015), these findings highlight the importance of

affective touch to the embodied psychological “self” (Craig, 2009; Damasio, 1999). Specifically, Chapter 2 and 3 showed that dynamic, slow-velocity affective touch can have a fundamental role in the malleability of our sense of body ownership. Following the definition of affective touch as an interoceptive modality, this finding might suggest a centrality of interoception and embodied affectivity in self-consciousness. Furthermore, affective touch seemed to increase the subjective but not the objective measure of the illusion (see the methodological discussion above). One possibility is that an embodiment of an external body part mediated by interoceptive signals (i.e. affective touch) does not necessarily involve a spatial update of one’s own hand location. This conclusion may also relate to the more general observation that interoceptive pathways mainly convey homeostatic information that are relatively poor in spatial and discriminatory properties in relation to exteroceptive signals (Craig, 2002). A recent study replicated this finding, confirming an enhancement in the subjective embodiment of the rubber hand when touch was delivered at slow compared to fast velocities (Lloyd et al., 2013). However, subsequent findings by van Stralen and colleagues (2014) showed a different pattern of results, namely that affective touch enhanced the proprioceptive drift but not the subjective embodiment of the rubber hand. This disparity in findings should be acknowledged and taken into account in the wider discussion on the role of affective touch in body representation, in the sense that two independent processes may underlie these two measures of the illusion (van Stralen et al., 2014; see also the methodological discussion about the rubber hand illusion above).

The findings of Chapter 2 showed that participants generally embodied a confederate’s hand to a greater extent than a rubber hand, but this difference was unrelated to visuotactile congruency or stroking velocity. These findings suggest that the top-down knowledge and corresponding visual evidence that one is observing another person’s arm, are not sufficient to influence the effect of multisensory integration of congruent visual and tactile signals on body ownership (see also Longo et al., 2009), even if the tactile stimulation carries interoceptive information. Tsakiris and Haggard (2005) investigated the necessary condition for the rubber hand illusion to occur. As discussed in Chapter 7, it is necessary that the rubber hand and the participant’s own

hand are placed in a congruent condition (i.e. the illusion is abolished when the rubber hand is rotated of 90°). Furthermore, the embodiment process taking place during the illusion is influenced by the object that is placed in front of the participants; that is, the illusion is abolished when the rubber hand is substituted by a wooden stick for instance. This finding suggests that simple synchrony between tactile and visual stimulation between one's own hand and a neutral object is not sufficient for eliciting the rubber hand illusion (Tsakiris and Haggard, 2005); on the contrary, participants are able to embody only objects which are congruent with their existent knowledge of the body. In this context, the finding of Chapter 2 showed that top-down knowledge does not override the bottom-up multisensory integration involving interoceptive information provided the general visual representation is of an arm.

Existing research has also shown that slow, CT optimal touch can enhance embodiment of the rubber hand illusion only when tactile stimulation is delivered on the hairy skin, but not glabrous skin (van Stralen et al., 2014, but see Lloyd et al., 2013 for different results on glabrous skin). Therefore, the role of affective touch in the sense of body ownership seemed to specifically relate to the involvement of interoceptive information mediated by slow, caress-like touch. In this context, it has been hypothesised that the effect of affective touch on the rubber hand illusion could be mediated by the insula. In fact, CT optimal touch activated the insular cortex (Olausson, Wessberg, McGlone & Vallbo, 2010; see Chapter 1), which is a core area for the processing of interoceptive information and emotional salience experiences, and it contributes ultimately to the awareness of our body. The insular cortex has also been found to mediate the embodiment process taking place during the rubber hand illusion (Tsakiris et al., 2007). The authors used a positron emission tomography to investigate the neural correlates of the sense of body ownership during the illusion. Remarkably, body ownership was related to activity in the right posterior insula; in contrast, when the rubber hand was not successfully embodied this activation was not observed (Tsakiris et al., 2007; but see Ehrsson et al., 2004).

The data presented in Chapter 5 provided further support to the importance of affective touch in constructing body representation and a healthy sense of bodily self-

consciousness. The perception of affective touch was investigated in a clinical sample characterised by body image distortion, lack of awareness and difficulties in social processing, i.e. anorexia nervosa. The results showed that individuals with anorexia nervosa perceived affective touch as less pleasant compared to healthy controls. Furthermore, this difference between groups was specific to CT-optimal (i.e. slow) stroking velocities; although patients with anorexia nervosa rated CT-optimal touch as more pleasant than non-CT optimal touch, there was no significant difference between groups when touch was delivered at a non-CT optimal speed (i.e. a fast velocity). Therefore, the reduced pleasantness of interpersonal touch may at least in part relate to a dysfunctional CT afferent system. Given the unique contribution of affective touch to the multisensory integration processes that underlie the subjective sense of body ownership, this finding may have implications for the distorted body representation observed in anorexia nervosa. One other study also attempted to investigate the sense of body ownership in people with anorexia nervosa by investigating the extent to which they are susceptible to the rubber hand illusion (Eshkevari et al., 2012). The results showed that anorexia nervosa participants experienced the rubber hand illusion to a stronger level compared to healthy controls, both from the objective (i.e. proprioceptive drift) and subjective (i.e. embodiment questionnaire) points of view. Most importantly, people with anorexia nervosa showed a higher visual capture (i.e. a component of body perception which is purely visual, independent of any tactile input) compared to healthy controls. This finding might support the idea that in anorexia nervosa the embodiment of the rubber hand seems to be more strongly driven by a visual component compared to healthy control.

Taken together, the results from Eshkevari and colleagues' study and the one from Chapter 5 raise the possibility that an enhanced susceptibility to visual signals about the body, and related body distortions in anorexia nervosa, may in part be linked to their weakened interoceptive perception. A reduced body awareness might lead to a body representation which relies less on interoceptive signals from within the body and is more strongly influenced by externally driven information.

8.5. Integration of interoceptive and exteroceptive signals in bodily self-consciousness

We usually take the ability to identify our body as our own for granted, but in order to identify our limbs as our own and as part of our body, information coming from outside our body (exteroceptive stimuli) needs to be integrated with information from inside our body (interoceptive stimuli). Recent research has shown how important it is to successfully integrate these two aspects in order to develop a coherent sense of self (Aspell et al., 2013). More generally, the integration of different sensory modalities (multisensory integration, see Maravita et al., 2003 for a review) is a key component of the sense of body ownership (Tsakiris & Haggard, 2005). In this context, an important outstanding question is how do we integrate interoceptive information from within the body with exteroceptive channels providing information about our body from the outside? This outstanding issue has been investigated in Chapters 3 and 6.

Specifically, Chapter 3 investigated the relationship between interoception and exteroception in the context of the rubber hand illusion. Two interoceptive modalities, and their reciprocal relationship, were considered, namely affective touch and cardiac awareness. The study aimed to explore whether the perception of interoceptive signals such as affective touch during the rubber hand illusion, and their integration with exteroceptive signals, would influence the sense of body ownership differently depending on individual differences in interoceptive sensitivity, as measured by a heartbeat counting task.

Recent studies have investigated multisensory integration across interoceptive (i.e. cardiac awareness) and exteroceptive modalities in the rubber hand illusion. Specifically, Tsakiris and colleagues (2011) showed that interoception sensitivity, in the sense of how good or bad participants perform in a heartbeat counting task (Schandry, 1981), can predict the malleability of the sense of body ownership. In particular, participants with low interoceptive sensitivity seem to acquire ownership of the rubber hand to a greater extent compared to people with high interoceptive sensitivity. This effect seems to be due to a much more malleable sense of bodily self in the low

compared to high interoceptive sensitivity participants (Tsakiris et al., 2011). This finding has been partially replicated and extended also in the context of the virtual body illusion (Aspell et al., 2013) and virtual rubber hand illusion (Suzuki et al., 2013). In both studies, cardio-visual feedback was provided in synchrony or out-of-synchrony with the participants' own heartbeats, with only the synchronous condition increasing self-identification with the virtual body (Aspell et al., 2013) and embodiment of the rubber hand (Suzuki et al., 2013). Furthermore, although Suzuki and colleagues (2013) found that this effect was modulated by the participants own interoceptive sensitivity, the direction of this finding seems to partially contradict the previous ones (Tsakiris et al., 2011). That is, Suzuki and colleagues observed a positive correlation between interoceptive sensitivity and proprioceptive drift in their virtual rubber hand study, indicating that better interoceptive awareness produced greater embodiment of the rubber hand; however this discrepancy in findings could be potentially due to the involvement of different methodologies, such as the implementation of different tasks to assess interoceptive sensitivity, the difference in sample size (21 vs. 46 participants) and the use of a virtual rubber hand paradigm rather than the classic one in Suzuki and colleagues' study (2013).

The findings of the experiment reported in Chapter 3 failed to support the ones from these previous studies; that is, no difference was found between the low and high interoceptive sensitivity group in either the subjective/explicit or objective/implicit outcome measures of the rubber hand illusion. Hence, it could be hypothesised a potential dissociation between off-line interoception (i.e. cardiac awareness as a trait), and exteroceptive multisensory integration interplay taking place between vision and touch during the rubber hand illusion. On the contrary, the relationship between on-line interoception (i.e. affective touch as part of a multisensory integration paradigm) and exteroception (vision in the same multisensory integration paradigm) is supported by the data, confirming previous findings in this direction (see Chapter 2; Lloyd et al., 2013; van Stralen et al., 2014).

Chapter 6 investigated the interplay between the aforementioned interoceptive modalities and exteroception in the context of social modulation. Participants were

asked to complete the heartbeat detection task and a pleasant touch task under three different visual feedback conditions: blank screen, observation of the self (i.e. face) in a mirror (self-mirror condition), and observation of another face in a mirror (other-mirror condition) to investigate the effect of exteroceptive/visual feedback on interoception. Based on the previous findings of Ainley and colleagues (2012), participants with high interoceptive awareness were expected to be less susceptible to exteroceptive manipulation, given the fact that they rely to a greater extent on their own internal signals. That is, it was anticipated to observe an improvement in the performance on the heartbeat detection task and pleasant touch task following mirror-observation only in people with low interoceptive sensitivity at baseline. However, the results of Chapter 6 failed to replicate these findings. Additionally, given the varied and inconsistent range of evidence in the context of exteroceptive modulation of interoceptive perception (see above), it remains unclear whether the improvement in interoceptive sensitivity is more guided by eye contact or by self-related information. Therefore, this study investigated whether the same increase in interoceptive sensitivity expected in the self-mirror condition would also occur when making eye contact with someone else in a mirror. The results were in line with recent evidence indicating that exteroception, but not interoception, can be affected by looking at someone else and being looked back at (Durlík et al., 2014).

The secondary aim of the study presented in Chapter 6 was to further investigate the use of pleasant touch as a measure of interoception, by comparing the effect of the above mentioned manipulations on the perception of pleasant touch, as well as the more widely used measure of interoception (i.e. the heartbeat detection task). As in Chapter 3, the relationship between these two measures could not be confirmed, since correlational analyses did not show any systematic relationship between these two interoceptive modalities, as assessed by means of the heartbeat detection task and pleasant touch task

To summarise, there was a lack of systematic relation between the performance on the affective touch task and heartbeat detection task in all of the experiments presented in Chapters 3 and 6. This might suggest that these two modalities reflect

different facets of interoception. In fact, the heartbeat detection task generates a sensitivity score, which provides us with a measure of how well or poorly participants are able to feel their body from within. In contrast, pleasant touch is measured by subjective ratings of pleasantness expressed by means of a rating scale and hence it is a different kind of measure. Cardiac awareness originates within the body, whereas the bodily pleasure derived from affective touch is triggered by tactile, and therefore, external stimulation; therefore these modalities might refer to different aspects of interoception. This fundamental difference implies the interpersonal and social nature of affective touch, which does not belong to the heartbeat counting task. Consequently, also the neurobiological mechanisms which underlie these interoceptive modalities might be different and further support the results of this study. One of the implications of the findings presented here is that interoceptive sensitivity measured by means of the heartbeat detection task seems to not be affected by visual manipulations, providing further support to the idea that it represents a rather fixed trait and it can be considered a reliable measure of one aspect of interoception.

8.6. A neurobiological basis for interoceptive bodily signals

As introduced in Chapter 1, touch is one of the first senses to develop and we are constantly under tactile stimulation from an early stage of our existence. Human tactile contact, just like grooming and tickling behaviors in other mammals, is increasingly understood to be central to a healthy emotional, cognitive and physical development (see Chapter 1). Studies in humans show that the reported frequency of physical contact with partners is correlated with elevated oxytocin level and lowered blood pressure in women (Light et al., 2005), and supportive physical contact from a partner has been shown to reduce the response to an acute stress (Ditzen et al., 2007). Therefore, there is some evidence supporting the role of tactile stimulation, probably paired with oxytocin release, in reducing stress and promoting a healthy development in humans (for a review, Walker & McGlone, 2013). Also, a recent study showed that self-reported frequency of maternal stroking over the first weeks of life reduced the association

between prenatal depression and adverse mental health outcomes in infancy (Sharp et al, 2012). Accumulating clinical evidence supports the beneficial role of affective touch delivered through massage in healthy individuals as well as clinical populations, in promoting psychological and physical well-being (see Field, 2010, for a review).

Accordingly, the study of Chapter 4 was designed to investigate the neurobiology of affective touch by exploring the effect of intranasal oxytocin and placebo on the perception of slow (CT optimal) vs. fast (non-CT optimal) strokes delivered on participants' forearms. The findings highlighted a trend for oxytocin compared to placebo to improve the discrimination between slow and fast touch; however the results are not significant and future studies should investigate this further on a bigger sample. This pattern of results could be considered in line with a recent account of the effect of oxytocin on human behaviour, according to which oxytocin might increase the precision (i.e. the difference between top-down expectations and bottom-up experiences) of interoceptive signals (Quattrocki & Friston, 2014). This account, developed in a predictive coding framework, argues that oxytocin might sharpen the salience of signals conveying homeostasis and socially relevant information, facilitating the development of the emotional and social self (Quattrocki & Friston, 2014). However, it must be noted that the study described in Chapter 4 failed to detect any difference in interoceptive sensitivity, as measured by means of the heartbeat counting task, following self-administration of oxytocin compared to placebo. As mentioned above, this finding is in line with the hypothesised lack of systematic relation between interoceptive sensitivity in the sense of cardiac awareness and affective touch perception. Hence this could further support the idea that different neurobiological mechanisms might underlie these modalities.

The results of this study contribute to the ongoing debate about the effect of intranasal oxytocin on the perception of touch, and affective touch in particular. To the author's knowledge, to date only a handful of studies have attempted to specifically investigate the effect of oxytocin on the perception of social, affective touch. Although the results are not consistent (see Chapter 4), these studies offered novel avenues to further explore the effect of oxytocin on the perception of affective touch, also in

relation to other interoceptive modalities and bodily self-consciousness. For instance, a recent behavioral study did not find any effect of intranasal oxytocin on the hedonic experience of affective touch; in contrast this study found an effect of facial expression on the hedonic experience of touch (Ellingsen et al, 2014; see also below). However, it should be pointed out that the study did not control for contextual effects that could have played a role in the experimental setting, such as the gender of the person delivering the touch (see also Chapter 4 for an extensive discussion on this point). Another study (Ellingsen et al., 2013) investigated the effect of positive expectations on an inactive nasal spray (i.e. placebo). The results showed that the placebo enhanced the perceived pleasantness of touch, and reduced the unpleasantness of painful touch, confirming previous data on the so-called placebo analgesia effect. This evidence supports the strengths of top-down modulation in the context of oxytocin research and provides important suggestions for the optimal methodology to be used. On the basis of this evidence, the study described in Chapter 4 followed a double-blind procedure, so that both the experimenter and the participant were blind to the nature of the nasal spray to avoid any potential top-down influence on the active compound.

Scheele and colleagues (2014) investigated whether the effect of intranasal oxytocin on the perception of interpersonal touch was dependent on the person delivering the touch, and the extent to which this effect was correlated with autistic traits. The results showed that oxytocin increased the perceived pleasantness of female but not male touch and this effect was negatively correlated with autistic-like traits. This study provides evidence for the importance of the context in which touch is delivered, particularly in terms of the gender of the person delivering the touch. Following this evidence, the study described in Chapter 4 tested only heterosexual females and all the experimenters involved were gender matched to control for any unwanted dynamic which could have influenced the pleasantness of the touch.

In summary, further studies should explore the neurobiological basis of affective touch taking into account the factors that might play a role and have an influence on the effect of intranasal oxytocin and in the perception of affective touch per se, such as individual differences, expectations and contextual aspects. Additionally, other

neurobiological circuits such as the dopaminergic system which might mediate the hedonic experience of touch and interact with the oxytocinergic system, should be taken into account.

8.7. The social modulation of bodily pleasure

As human beings, we are constantly exposed to social interaction with others. Chapter 1 described animal studies supporting the importance of others in the way we become aware of ourselves; for instance we might need others to be able to recognise ourselves in the mirror. Chapter 2 showed that affective touch might play a pivotal role in the way we acquire ownership of our own body. However, affective touch has also been found to contribute to social affiliation, facilitating bonding and emotional communication among individuals (see Chapter 1). The influence that social factors can have on the subjective experience of bodily pleasure was specifically investigated in Chapters 5, 6 and 7.

Chapter 5 investigated the perception of affective touch while simultaneously displaying different facial expressions, namely accepting, rejecting and neutral faces. The simultaneous display of accepting faces enhanced the perceived pleasantness of touch, while there were no statistically significant differences between rejecting and neutral faces. That is, a positive social modulation (i.e. accepting faces) is more likely to affect the perception of tactile pleasantness. Additionally, contrary to the prediction, the perception of affective touch was not differently affected by social stimuli in healthy controls and people with anorexia nervosa. This could suggest that, even when there is a distorted perception of affective touch and body representation, a positive top-down modulation is still possible. However, the study presented in Chapter 5 showed that the effect was not specific for the CT-optimal/slow touch. In line with this finding, a recent study showed an increase in pleasantness ratings only when affective touch was presented simultaneously with smiling faces compared to neutral faces (Ellingsen et al., 2014; see also above). However, Ellingsen and colleagues (2014) also found a negative social modulation in the sense that displaying angry faces reduced the pleasantness of

concomitant touch. Interestingly, the experience of the touch itself modulated the perception of the faces, in the sense that perceiving affective touch increased the attractiveness and friendliness of the neutral and happy faces. The social nature of affective touch was strengthened by additional findings showing that the social modulation of touch was stronger when touch was applied by an experimenter compared to a tactile machine (Ellingsen et al., 2014). These results are in line with studies showing that the believed identity of the toucher can affect the perceived pleasantness of the touch (Gazzola et al. 2012; Scheele et al., 2014). Taken together this evidence supports the influence of top-down social factors in the perception of interpersonal affective touch.

However, the studies discussed so far investigated the social modulation using only *offline* paradigms (i.e. pictures of other people), which do not involve the actual presence of another person in the experimental setting (in addition to the experimenter). In contrast, *online* paradigms must involve the actual presence of another person (i.e. mirrors or social interactions) in order to investigate the social modulation of pleasant touch. In Chapter 6, the effect of looking at *someone else* in the mirror on the perceived pleasantness of touch was investigated in comparison to a *self-reflection* condition. The results showed that perceiving touch whilst looking at someone else (and being looked back at) reduced the perceived pleasantness compared to looking at a blank screen or at one's own face at the mirror. This could suggest that being observed by someone else (not the person performing the touch) does affect the perception of touch generally, since the nature of tactile stimulation itself is interpersonal, and therefore probably more sensitive to social manipulation. However, this social modulation did not specifically influence affective touch, since neutral touch was modulated by the visual feedback in a comparable manner. This could suggest that top-down social modulation affect both affective and emotional neutral touch in a similar fashion.

Chapter 6 investigated affective touch in a self *versus* other context, while Chapter 7 sought to explore the perception of tactile pleasantness in a self *and* other context (see Schilbach, Timmermans, Reddy, Costall, Bente et al., 2013 for similar considerations under the remit of 'Second-person Neuroscience'). Participants were

asked to rate the pleasantness of tactile stimuli perceived either in synchrony or out of synchrony with another person. Synchronous touch was perceived as more pleasant compared to asynchronous touch, but only when it was delivered at CT optimal/slow velocity. That is, the involvement of interoceptive information is fundamental in order to perceive the synchronous touch experience as more pleasant. This study controlled for any potential embodiment process taking place as a consequence of the synchronous touch between the two hands by placing the other hand in an incongruent position (i.e. 90 degrees) with respect to the participant's hand. Furthermore, the visual focus did not play a role on this effect in the sense that the mere knowledge rather than direct vision of the other person being synchronously touched seems to be sufficient to enhance the perceived pleasantness. Existing research in anthropology and social psychology suggest that synchronous activity could be involved in the development of positive emotions in social relations (see below). In line with this evidence, the findings of Chapter 7 showed that synchronicity could have a specific importance in modulating pleasantness perception of interpersonal affective touch. Specifically, synchronous activities have been found to diminish the boundaries between the self and other group's members (Wiltermuth & Heath, 2009), promote social understanding (Wheatley et al., 2012) and increase affiliation (Hove & Risen, 2009). In addition, 'synchronicity' has an important role in development. In this context, synchronicity has been considered as 'affect synchrony', or congruency (e.g. coordination of affective expressions during face-to-face interactions) between mother and infant can promote the emergence of self-control and self-regulation which represent key aspects for later socialisation (Feldman et al., 1999; Fonagy, Gergely & Target, 2007; Beebe, Lachmann, Markese, Buck, Bahrnick et al., 2012). The notion of synchronicity used in these studies is not the same as in psychophysical studies, since they mainly referred to psychoanalytically inspired approaches which provided support to the role of 'congruent' interactions between infants and caregivers (Fonagy et al., 2007) with some emphasis to the role of maternal touch for future pattern of relating (Beebe et al., 2012). However, although different, these definitions of synchronicity can be found to be related in future studies. For instance, developmental studies suggested that infants as young as 3–5 months show

sensitivity to body-related and proprioceptive-visual synchrony (Rochat & Morgan, 1995). In such paradigms, infants tend to respond differentially to experimentally controlled and visually presented feedback of their body parts moving synchronously and in spatial congruency to their own movements compared to asynchronous or incongruent movements. A recent study found that newborns are able to detect visual-tactile synchrony in stimuli directed to their own faces and are able to discriminate synchrony from visual-tactile asynchrony (Filippetti, Johnson, Lloyd-Fox, Dragovic & Farroni, 2013). Therefore, the relation between affective synchronicity and multisensory integration might offer an interesting avenue for future studies.

The finding of the study presented in Chapter 7 suggested that perceiving pleasant touch in synchrony with someone else increased the hedonic tactile experience. Future studies should investigate this further in order to explore the implications of these 'shared touch experience'. For instance, it could be of great interest to manipulate the gender of the other person or to explore whether the shared touch experience would be stronger if the other person is a significant one compared to a stranger.

8.8. Conclusion

The main aim of the present thesis was to explore the role of affective touch to the representation of the body, as a fundamental aspect of bodily self-consciousness. It has been shown that affective touch provides an important contribution to body representation. In addition to the widely-accepted role of affective touch in social affiliation, this finding further strengthens the importance of this interoceptive modality in bodily self-consciousness, and by implication in self-other distinction. To the extent that interoceptive and exteroceptive information contribute to the way we become aware of our body, here their relationship has been investigated in the context of the sense of body ownership. This finding can have important implication in the context of disorders of body representation and awareness (e.g. anosognosia for hemiplegia and somatoparaphrenia). The case of a stroke patient has been reported who reported increased sense of arm ownership after slowly stroking her arm (van Stralen, van

Zandvoort & Dijkerman, 2011). This finding could also have important implication in the case of phantom limb syndrome.

Clinical evidence showed that people with anorexia nervosa perceived affective touch only as less pleasant compared to healthy controls; this has been linked to their distorted body image and social anhedonia. The finding of this thesis might have some clinical implications for therapeutic approach to anorexia nervosa. In particular, the fact that participants with anorexia nervosa can be positively influenced by top-down information in a similar fashion as healthy controls, might suggest the importance of social context. Importantly, top-down modulation in the sense of facial expression seems to affect tactile interaction and this could suggest the importance of social environment also in the context of therapeutic setting.

Additionally, this thesis contributed to the debate on the neurobiological basis of affective touch by showing that intranasal oxytocin does not influence the perceived pleasantness of slow (CT-optimal) touch. Moreover, oxytocin did not influence body representation or cardiac awareness measures. However, it would be of interest to follow up this finding in disorders characterised by reduced oxytocin release such as anorexia nervosa and autism spectrum disorders. Finally, this thesis provided evidence of top-down social modulation of affective touch. Both online and offline paradigm have shown that social information can influence the way bodily pleasure is perceived. It would be of interest to follow up these results by investigating the top-down social modulation of affective touch in disorders characterised by social processing impairment such as autism spectrum disorders.

The findings presented in this thesis contributed to current knowledge about the role and perception of affective touch, particularly in relation to self-consciousness and social cognition, paving the way for future experimental, pharmacological and clinical research.

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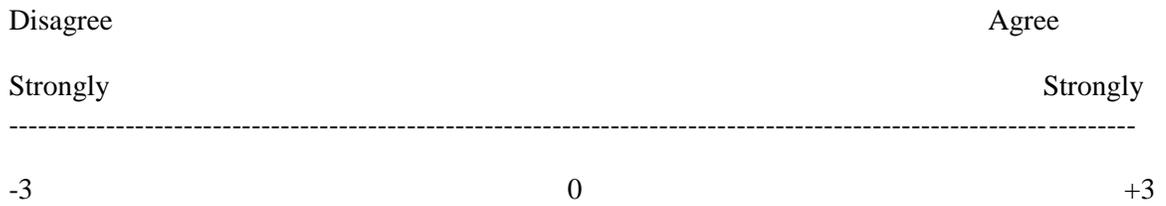
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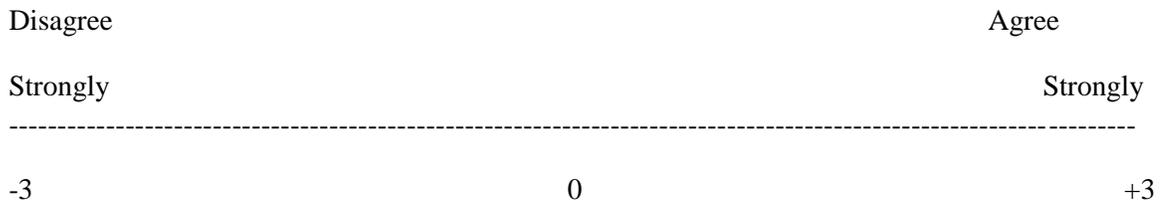
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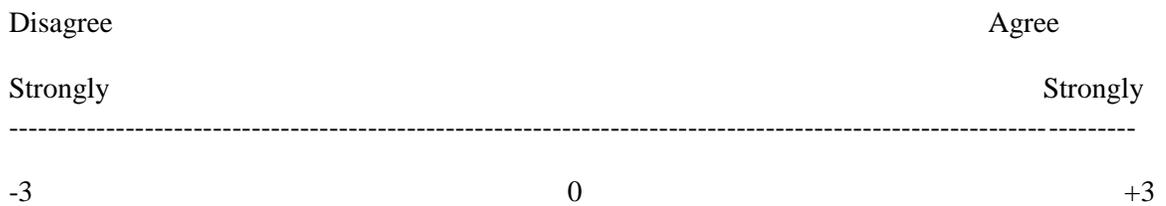
5. It seemed like the rubber hand was part of my body



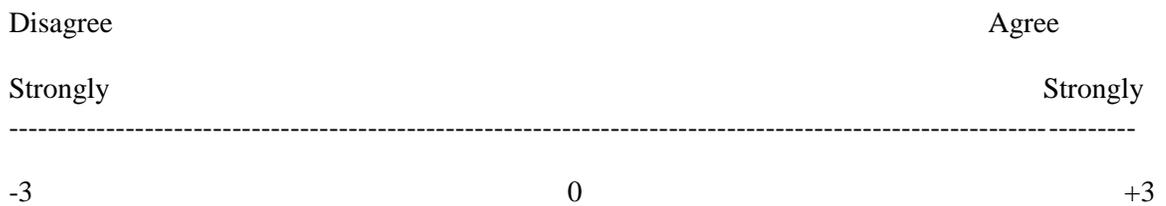
6. It seemed like my hand was in the location where the rubber hand was



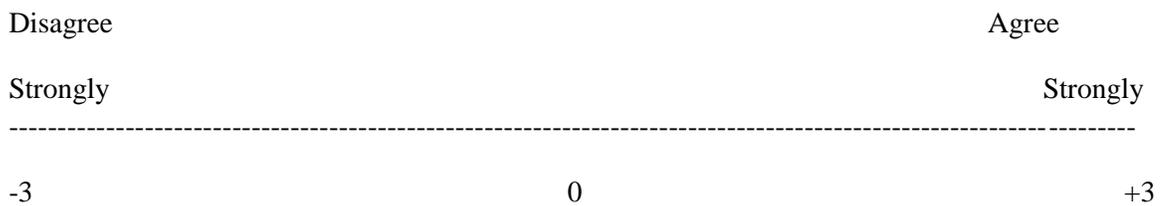
7. It seemed like the rubber hand was in the location where my hand was



8. It seemed like I could have moved the rubber hand if I had wanted



9. It seemed like I was in control of the rubber hand



10. I found that experience enjoyable

Disagree

Agree

Strongly

Strongly

-3

0

+3

11. I found that experience interesting

Disagree

Agree

Strongly

Strongly

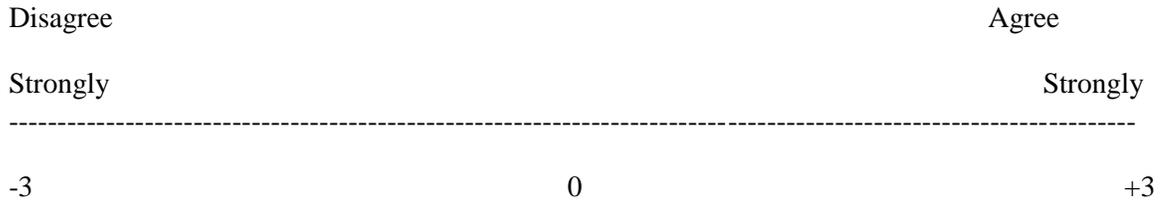
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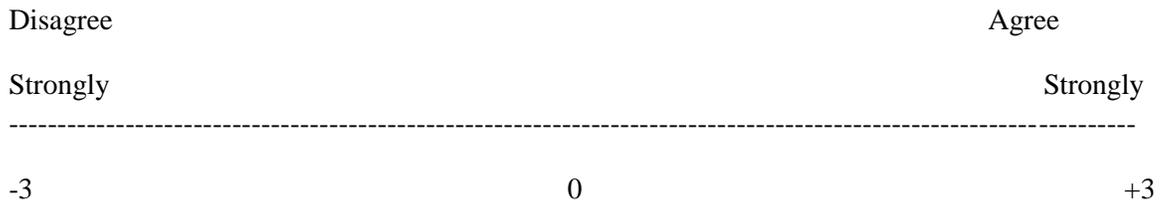
+3

Appendix 2. *Post embodiment questionnaire for studies in Chapters 2, 3 and 4*

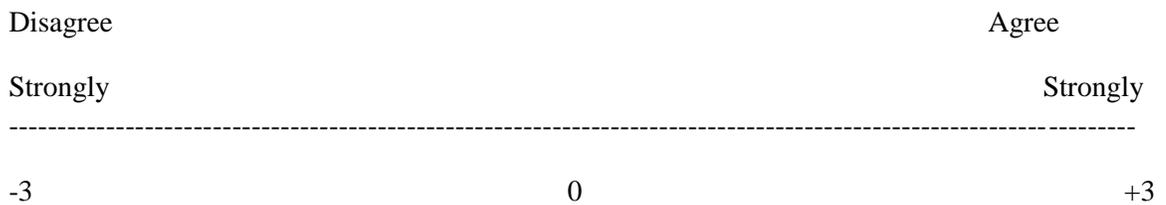
1. It seemed like I was looking directly at my own hand, rather than at a rubber hand.



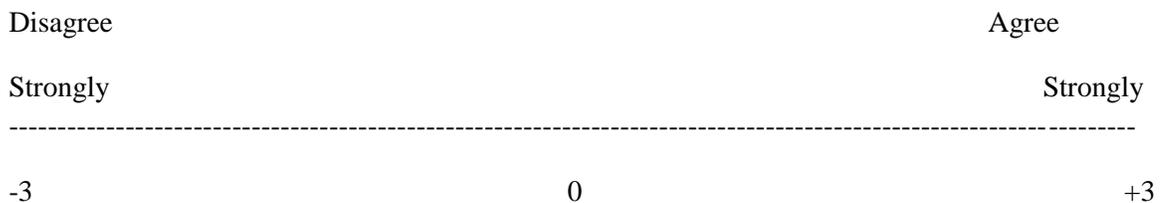
2. It seemed like the rubber hand began to resemble my own hand



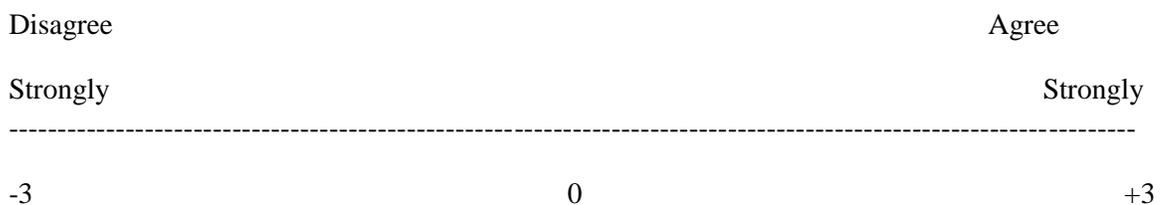
3. It seemed like the rubber hand belonged to me



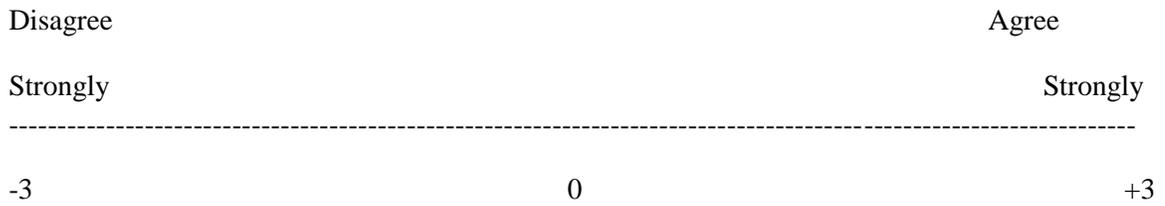
4. It seemed like the rubber hand was my hand



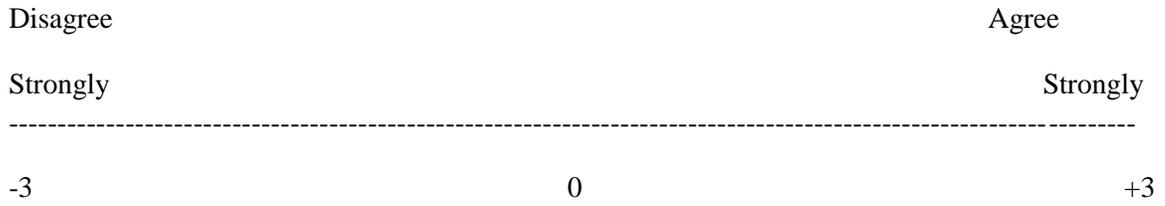
5. It seemed like the rubber hand was part of my body



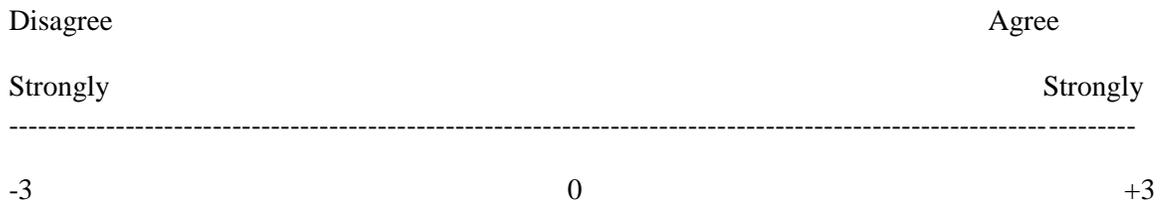
6. It seemed like my hand was in the location where the rubber hand was



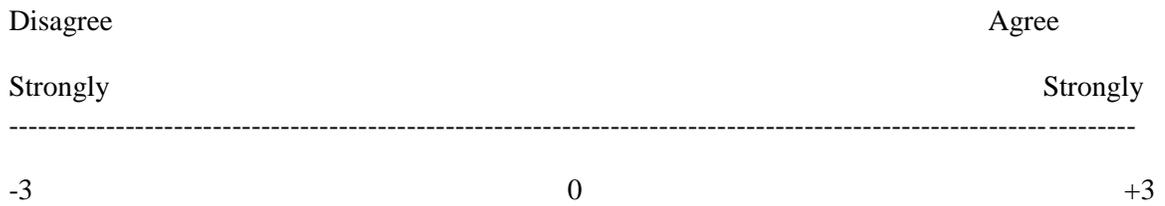
7. It seemed like the rubber hand was in the location where my hand was



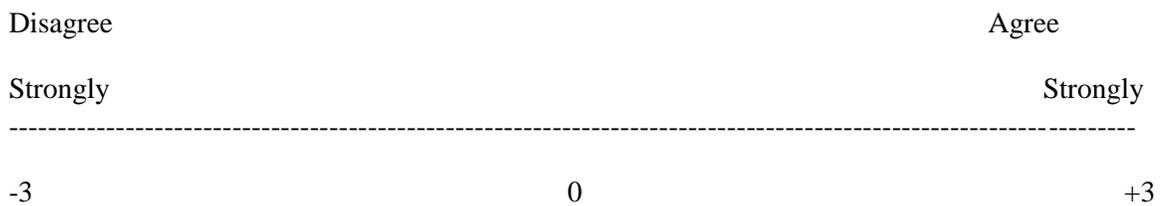
8. It seemed like the touch I felt was caused by the brush touching the rubber hand



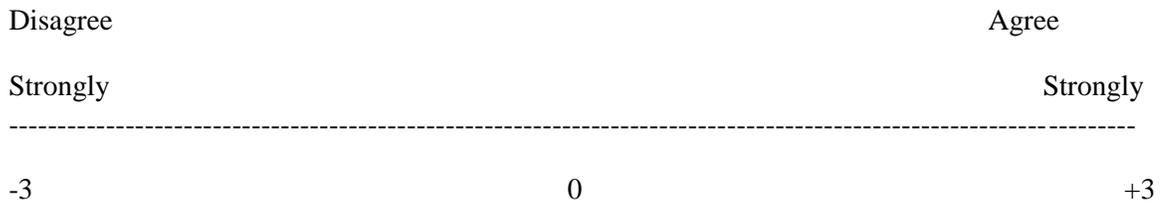
9. It seemed like I could have moved the rubber hand if I had wanted



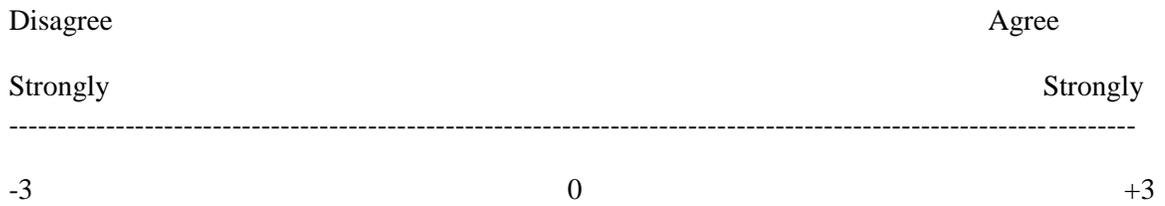
10. It seemed like I was in control of the rubber hand



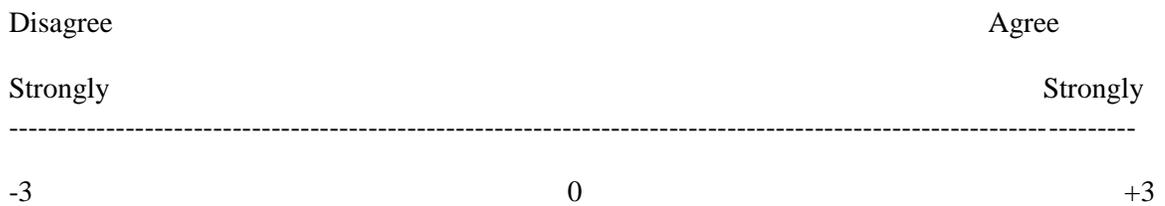
11. I found that experience enjoyable



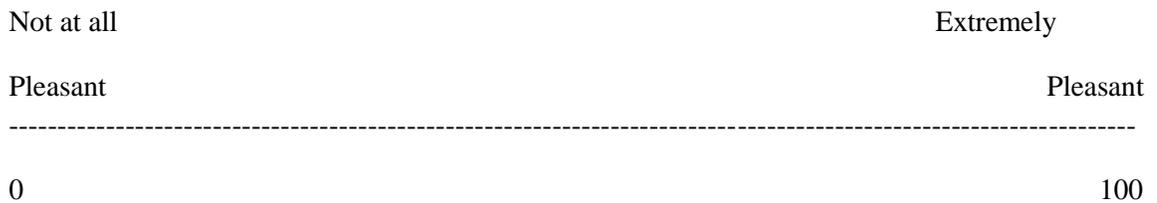
12. I found that experience interesting



13. The touch of the brush on my arm was pleasant



14. How pleasant the touch of the brush was on my arm?



Appendix 3. *Depression Anxiety Stress Scale (DASS 21) for study in Chapter 5*

DASS21				
Please read each statement and circle a number 0, 1, 2 or 3 which indicates how much the statement applied to you <i>over the past week</i> . There are no right or wrong answers. Do not spend too much time on any statement.				
<i>The rating scale is as follows:</i>				
0 Did not apply to me at all				
1 Applied to me to some degree, or some of the time				
2 Applied to me to a considerable degree, or a good part of time				
3 Applied to me very much, or most of the time				
1	I found it hard to wind down	0	1	2 3
2	I was aware of dryness of my mouth	0	1	2 3
3	I couldn't seem to experience any positive feeling at all	0	1	2 3
4	I experienced breathing difficulty (eg, excessively rapid breathing, breathlessness in the absence of physical exertion)	0	1	2 3
5	I found it difficult to work up the initiative to do things	0	1	2 3
6	I tended to over-react to situations	0	1	2 3
7	I experienced trembling (eg, in the hands)	0	1	2 3
8	I felt that I was using a lot of nervous energy	0	1	2 3
9	I was worried about situations in which I might panic and make a fool of myself	0	1	2 3
10	I felt that I had nothing to look forward to	0	1	2 3
11	I found myself getting agitated	0	1	2 3
12	I found it difficult to relax	0	1	2 3
13	I felt down-hearted and blue	0	1	2 3
14	I was intolerant of anything that kept me from getting on with what I was doing	0	1	2 3
15	I felt I was close to panic	0	1	2 3
16	I was unable to become enthusiastic about anything	0	1	2 3
17	I felt I wasn't worth much as a person	0	1	2 3
18	I felt that I was rather touchy	0	1	2 3
19	I was aware of the action of my heart in the absence of physical exertion (eg, sense of heart rate increase, heart missing a beat)	0	1	2 3
20	I felt scared without any good reason	0	1	2 3
21	I felt that life was meaningless	0	1	2 3

