Changes in Interoceptive Accuracy in Response to Social and Physical Threat

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University of London.

Declaration of Authorship

I, Caroline Annette Durlik, hereby declare that this thesis and the work
presented in it is entirely my own. Where I have consulted the work of others, this
is always clearly stated.
Signed:
Date:

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Abstract

This thesis examines state changes in interoceptive accuracy in situations characterised by negative affect and heightened self-focus. The experiments manipulate negative affect in social and non-social contexts, by evoking social and physical threat, respectively. State changes in interoceptive and exteroceptive somatosensory perception are simultaneously examined in several experiments comprising the present thesis, in order to establish whether potential changes in the interoceptive modality generalise to the exteroceptive somatosensory modality. The experiments in the current thesis measure interoceptive accuracy using a heartbeat tracking task and assess the perception of exteroceptive bodily signals using cutaneous electrical stimulation. Socially threatening contexts manipulated in the present thesis include ones which: evoke social anxiety (Experiment 1), heighten social awareness of the self (Experiment 2) and result in social rejection (Experiments 3 and 4). Experiment 5 additionally examines the effect of physical threat on interoception by employing a pain anticipation paradigm. The main findings of these experiments indicate that heartbeat tracking accuracy (HTA) increases in response to public speaking anticipation as well as in response to pain anticipation, while it decreases as a result of social exclusion. Social self-focus, manipulated using a video camera being turned on and off, does not affect HTA, nevertheless, increasing the sensitivity in detecting electrotactile stimuli. Overall, the results of the present thesis indicate that interoceptive accuracy functions as a state variable, which changes in response to negative affective contexts that manipulate social and physical threat. It is proposed that interoceptive accuracy changes as a function of affective and social self-focus in these contexts. The findings of the current thesis are important considering the role of interoception in cognitive-affective processing. Future research investigations should explore whether state changes in interoceptive accuracy are accompanied by simultaneous changes in neural activity in the interoceptive regions of the brain, such as the anterior insula.

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Chapter 1: Introduction

1.1 What is Interoception?

"The term interoception was coined by Sherrington in 1906, who defined it as the perception of signals from the inner organs of the body (i.e., visceroception) that is distinct from exteroception—the perception of signals originating outside of the body—as well as from *proprioception*—the perception of joint angles and muscle tensions relating to movement, posture and balance (Cameron, 2001; Vaitl, 1996). Interoception has been recently redefined as the "sense of the physiological condition of the entire body" (Craig, 2002, p.655), which in addition to visceroception (e.g., perception of cardiovascular, respiratory, gastrointestinal and genitourinary signals), also includes the perception of signals from the skin (e.g., affective touch, pain) and from the chemoreceptors of the body (e.g., taste, smell) (Criag, 2002, 2009). There are multiple pathways of interoception. The body's visceral afferents are conveyed through the lamina-I spinal-thalamo-cortical pathway, converging in the insular cortex. Light and slow stroking touch (i.e., pleasant touch) is interoceptively processed via C-Tactile afferents—slow-conducting unmyelinated afferent fibres, which also project to the insular cortex (Olausson, Wessberg, Morrison, McGlone, & Vallbo, 2010). The other interoceptive pathway involves skin afferents projecting to the somatosensory cortices (Couto et al., 2014; Khalsa, Rudrauf, Feinstein, & Tranel, 2009). In the insular and somatosensory cortices, interoceptive signals are integrated into a cortical representation of the homeostatic state of the body, giving rise to bodily sensations (Craig, 2002, 2009). The cortical representation of the interoceptive state of the body has been proposed to be the basis of consciousness, the sense of self and subjective feeling states (Craig, 2002, 2010; Damasio, 2010; Seth, 2013). Converging evidence from imaging and behavioural studies emphasises the importance of interoceptive processes in cognitive (e.g., Dunn et al., 2010; Garfinkel, Barrett et al., 2013; Garfinkel, Tiley, O'Keeffe, & Critchley, 2013; Werner, Schweitzer et al., 2013; Werner, Peres, Duschek, & Schandry, 2010) and emotional experience (e.g., Wiens, 2005; Wiens, Mezzacappa, & Katkin, 2000).

1.2 How is Interoception Measured?

Interoceptive accuracy, the accuracy in perceiving inner bodily signals, has been most frequently quantified by means of heartbeat perception tasks, including heartbeat tracking—where participants are asked to silently count, and later report, the number of heartbeats they feel within a given time interval (e.g., Schandry, 1981)—and heartbeat discrimination—where participants are asked to judge whether a string of auditory tones matches their own heart rhythm (e.g., Brener & Kluvitse, 1988; Katkin, Reed, & Deroo, 1983; Whitehead, Drescher, Heiman, & Blackwell, 1977). In both of the above heartbeat perception tasks, participants are connected to equipment monitoring their true heart rate; participants' subjective reports are then are compared to their actual cardiac measurements to determine perception accuracy. Performance on heartbeat tracking and heartbeat discrimination tasks has been found to be correlated (e.g., Garfinkel, Seth, Barrett, Suzuki, & Critchley, 2015; Hart, McGowan, Minati, & Critchley, 2013; Knoll & Hodapp, 1992), however, a significant relationship is not always found (e.g., Phillips, Jones, Rieger, & Snell, 1999; Schulz, Lass-Hennenmann, Sutterlin, Schachinger, & Vogele, 2013). Garfinkel et al. (2015) note the fact that the studies in which the two measurements are not significantly correlated often have small sample sizes (Garfinkel et al., 2015). Additionally, Garfinkel et al. highlight that heartbeat tracking and heartbeat discrimination may be reliant on shared, but also on distinct underlying mechanisms, with heartbeat tracking relying primarily on internal monitoring of heartbeat sensations, and heartbeat discrimination additionally requiring a comparison of internal (heartbeat) and external (auditory tones) information to be made. Even though individuals tend to underreport the number of heartbeats on the heartbeat tracking task (e.g., Ehlers, Breuer, Dohn, & Fiegenbaum, 1995), measured accuracy tends to be higher on the heartbeat tracking task than on the heartbeat discrimination task (Schulz, Lass-Hennenmann et al., 2013). Also, factors such as stress might differentially affect the two measures (e.g., Schulz, Lass-Hennenmann et al., 2013), further highlighting that the two tasks might be reliant on related, yet somewhat distinct processes.

1.3 Inter-Individual Differences in Interoception

The ability to accurately perceive interoceptive signals (i.e., heartbeats) has been found to vary significantly across individuals (e.g., Blascovich et al., 1992; Cameron, 2001; Schandry & Bestler, 1995) and shows high test-retest reliability (Mussgay, Klinkenberg & Ruddel, 1999), thus is considered to be stable trait variable (Cameron, 2001). The basis of inter-individual differences in the ability to accurately perceive interoceptive signals is not yet fully understood (Verdejo-Garcia, Clark, & Dunn, 2012), however, it is likely that the relative strength of interoceptive signals arising in the body (determined by physiological parameters such stroke volume and cardiac output) plays a significant role in determining interoceptive accuracy (Craig, 2003; Cameron, 2002). Accuracy on the heartbeat discrimination task and on the heartbeat tracking task has been found to be inversely related to heart rate (e.g., Ainley, Tajadura-Jimenez, Fotopoulou, & Tsakiris, 2012; Fairclough & Goodwin, 2007; Knapp-Kline & Kline, 2005; Stevens et al., 2011), likely due to decreasing stroke volume of individual heartbeats with increasing heart rate (Schandry, Bestler, & Montoya, 1993). Factors that have been suggested to affect accuracy in perceiving interoceptive signals include sex, fitness, body composition and age (Cameron, 2001; Vaitl, 1996). However, the exact nature of these effects is not entirely understood, with studies providing disparate results. Khalsa, Rudrauf and Tranel (2009) observed an inverse relationship between age and heartbeat discrimination accuracy. On the contrary, Eley, Stirling, Ehlers, Gregory and Clark (2004) found a lack of a significant relationship between age and heartbeat tracking accuracy, although, in a sample of children. Males have been found to be more accurate in heartbeat discrimination than females in some (Jones & Hollandsworth, 1981; Katkin, Blascovich, & Goldband, 1981; Whitehead et al., 1977), but not all studies (e.g., Eley et al., 2004; Herbert & Pollatos, 2014; Khalsa, Rudrauf, & Tranel, 2009; Rouse, Jones, & Jones, 1988). While some studies have found individuals with a high body mass index to be significantly lower in heartbeat discrimination accuracy (e.g., Montgomery & Jones, 1984; Rouse et al., 1988) as well as in heartbeat tracking accuracy (e.g., Herbert & Pollatos, 2014), other studies failed to observe this relationship (e.g., Eley et al., 2004; Khalsa, Rudrauf, & Tranel, 2009;

Koch & Pollatos, 2014; Tsakiris, Tajadura-Jimenez, & Costantini, 2011). Given the largely contradictory results, more research is necessary to understand the determinants of individuals' ability to accurately perceive interoceptive signals.

Researchers have categorized individuals into good and poor interoceptors by using cut-off points (e.g., Herbert, Muth, Pollatos, & Herbert, 2012; Herbert, Pollatos, & Schandry, 2007; Herbert, Ulbrich, & Schandry, 2007; Matthias, Schandry, Duschek, & Pollatos, 2009; Montoya, Schandry, & Mueller, 1993; Pollatos, Kirsch, & Schandry, 2005; Pollatos, Schandry, Auer, & Kaufmann, 2007) and median splits on interoceptive accuracy scores (Ainley, Maister, Brokfeld, Farmer, & Tsakiris, 2013; Ainley et al., 2012; Garfinkel et al., 2015; Ferri, Ardizzi, Ambrosecchia, & Gallese, 2013; Suzuki, Garfinkel, Critchley, & Seth, 2013; Tajadura-Jimenez & Tsakiris, 2014; Tsakiris et al., 2011). As randomly selected samples tend to be characterised by a small proportion of individuals with high interoceptive accuracy scores, median splits have been used as an alternative to cut-off points, consequently allowing for comparisons of individuals with lower and higher interoceptive accuracy. Even though there are disadvantages to dichotomising continuous variables and creating a situation where similar cases that are on opposite sides of the cut-point are considered to be different from one another, including potential loss of power to detect a difference and increased risk of identifying spurious effects (Altman & Royston, 2006), median splits can be useful in characterising data with an underlying dichotomy, as in the case of interoceptive accuracy. Good and poor interoceptors have been found to differ significantly on a number of variables pertaining to emotion processing (e.g., Pollatos, Herbert et al., 2007), decision-making (e.g., Werner, Jung et al., 2009) and attention (Matthias et al., 2009), to name a few. Moreover, baseline level of interoceptive accuracy has been found to moderate the effect of self-focus on state interoceptive accuracy, the effect of interpersonal multisensory stimulation on self-recognition (Tajadura-Jimenez & Tsakiris, 2014) and the adaptive modulation of autonomic response in social setting (Ferri et al., 2013), to name a few. Taken together, these results highlight the importance of taking into account individuals' baseline interoceptive accuracy when investigating the relationship between interoception and social, affective and cognitive processes.

1.4 Neural Correlates of Interoceptive Accuracy

The anterior insula is the key brain region associated with interoception, and with individual accuracy in detecting interoceptive signals (e.g., Critchley, Wiens, Rotshtein, Ohman, & Dolan, 2004; Pollatos, Schandry et al., 2007), although other areas, such as the anterior cingulate and somatosensory cortices, have also been implicated in interoceptive processing (Khalsa, Rudrauf et al., 2009). Critchley and colleagues (2004) measured brain activity of individuals performing a heartbeat discrimination task and an auditory note discrimination task, observing that when individuals were performing the heartbeat discrimination task, relative to the auditory note discrimination task, there was increased activity in the anterior insula, and in the anterior cingulate and somatosensory cortices. Notably, individual heartbeat discrimination accuracy was predicted by the level of activity in the right anterior insula/opercular cortex, and was also correlated with the volume of gray matter in this region. Similar results were obtained by Pollatos, Schandry et al., (2007) using the heartbeat tracking task and an auditory tone tracking task; Pollatos, Schandry and colleagues found that heartbeat tracking accuracy scores predicted the level of activity in the anterior insula and medial frontal/dorsal cingulate gyrus, while also engaging the thalamus, inferior gyrus, and somatomotor cortex.

Complimentary evidence implicating the insula in cardiac interoceptive accuracy comes from Ronchi et al. (2015), who observed that right insular resection decreased heartbeat tracking accuracy. Taken together, the results of empirical investigations of the neural correlates of interoceptive accuracy most consistently point to the anterior insula, and the co-activated anterior cingulate and somatosensory cortices. Critchley (2005) states that the anterior cingulate cortex likely integrates autonomic and visceral changes, which are then mapped and represented in the insula and the orbitofrontal cortices; the cortical representation of the interoceptive state of the body can be then accessed by conscious awareness and subsequently influence cognitive-affective processing.

1.5 Interoceptive Accuracy, Awareness and Sensibility

The link between interoception, emotion and cognition has been studied

by investigating the relationship between various aspects of cognitive and affective processing and objective, subjective and metacognitive dimensions of interoception: interoceptive accuracy, interoceptive sensibility and interoceptive awareness, respectively (see Garfinkel et al., 2015). It should be noted that in the interoceptive awareness and interoceptive sensitivity were used interchangeably to refer to interoceptive accuracy; however, recently, the theoretical issues implicated in conflating interoceptive accuracy and awareness, have been highlighted (see Ceunen, Van Diest, & Vlaeyen, 2013), which has resulted in a clarification and redefining of these constructs (Garfinkel & Critchely, 2013; then further redefined in Garfinkel et al., 2015). Garfinkel and colleagues (2015) define interoceptive accuracy as the "objective accuracy in detecting internal bodily sensations" (p. 67), which can be measured with objective body signal perception accuracy tasks, such as heartbeat perception tasks (e.g., Schandry, 1981; Brener & Kluvitse, 1988; Katkin et al., 1983; Whitehead et al., 1977). Interoceptive accuracy is distinct from interoceptive sensibility—the subjective, "self-perceived dispositional tendency to be internally self-focused and interoceptively cognisant"—and from interoceptive awareness the "metacognitive awareness of interoceptive accuracy" (Garfinkel et al., 2015, p. 67).

1.6 Interoception across Modalities

Interoceptive modalities include all categories of sensations that originate within the body, such as cardiac, respiratory, genital, urinary, gastric, intestinal sensations. A class of afferent fibres has been identified as monitoring the physiological state of all internal organs of the body (Craig, 2002, 2009). These fibres converge in the insular cortex, giving rise to the conscious and unconscious perception of interoceptive signals. Consequently, experiencing an array of visceral (e.g., cardiac, gastrointestinal) sensations has been found to activate the anterior insula (see Craig, 2009 for a review).

Few experimental studies have investigated interoceptive perception across modalities. Herbert, Muth et al. (2012) point out that there is a lack of research on the topic because interoceptive perception accuracy measurement is

limited by existing methodological possibilities. Further, empirical assessment of interoceptive accuracy across modalities has been complicated by the fact that not all visceral signals are easily perceived—for example, heartbeats tend to be perceived more easily than other visceral sensations (Kollenbaum, Dame, & Kirchner, 1996)—as well as by the fact that physiological responses of different visceral systems (during emotional experience, for example) have been observed to be only modestly associated with one another (Mauss, Levenson, McCarter, Wilhelm, & Gross, 2005).

Two studies to date (Herbert, Muth et al., 2012; Whitehead, & Drescher, 1980) have examined the association between visceral perception accuracy across modalities—focusing on the cardiac and gastrointestinal systems. Whitehead and Drescher (1980) found that heartbeat discrimination accuracy was significantly correlated with the ability to accurately detect stomach contractions. The results of Herbert, Muth et al. (2012) compliment the findings of Whitehead and Drescher, showing that heartbeat tracking accuracy is inversely related to the volume of ingested water during the Water Load Test—a widely used non-invasive method of assessing gastric sensation (Chen, Lin, Chen, & Huang, 2005; Jones, Hoffman, Sha, Patel, & Ebert, 2003; Koch, Hong, & Xu, 2000)—despite good and poor interoceptors not differing with respect to subjective reports of fullness or nausea after drinking. Herbert, Muth and colleagues (2012) concluded that these results are suggestive of individuals with higher cardiac perception accuracy requiring a lesser volume of ingested water, than individuals with lower cardiac perception accuracy, to experience the same level of fullness—likely due to stronger perception of the interoceptive cues signalling fullness. These results are supported by the findings of Herbert, Blechert, Hautzinger, Matthias and Herbert (2013), which show that, in comparison to individuals with lower heartbeat tracking accuracy, individuals highly accurate at tracking their heartbeats score higher on the intuitive eating scale (IES; Tylka, 2006), which assesses adaptive eating behaviour—eating behaviour that is guided by physiological signals of hunger and fullness, and one's ability to recognize them, rather than by external and emotional cues. As decreased ability to perceive internal signals of hunger and fullness might contribute to unhealthy body mass index, it follows that

individuals suffering from disordered eating (specifically, anorexic, overweight, and obese individuals) have been observed to have lower interoceptive accuracy scores than individuals with a healthy body mass index (Herbert & Pollatos, 2014; Pollatos et al., 2008). Overall, it can be concluded that cardiac and gastrointestinal perception accuracy correspond to one another within individuals, which is in line with the evidence indicating that the anterior insula supports the perception of cardiac signals (Critchley et al., 2004; Pollatos, Schandry et al., 2007), as well as the perception of gastrointestinal signals arising in the rectum, stomach, and oesophagus (Aziz, Schnitzler, & Enck, 2000; Moisset et al., 2010; Craig, 2009). Overall, while it has been assumed that cardiac interoceptive accuracy is a valid measure of general interoceptive perception accuracy, there definitely is a need for a larger number of empirical studies that investigate perception accuracy of interoceptive signals across various modalities.

1.7 Interoceptive and Exteroceptive Somatosensory Perception

A distinction can be made between bodily signals that are interoceptive and arise within the body (e.g., cardiac, respiratory, gastrointestinal signals) and bodily signals that are exteroceptive and arise on or outside of the body (e.g., external tactile signals) (Cameron, 2002; Craig, 2003; Leder, 1990). Interoceptive and exteroceptive signals are processed separately in the brain (e.g., Farb, Segal, & Anderson, 2013; Hurliman, Nagode, & Padro, 2005); however, interoceptive and exteroceptive somatosensory systems are highly interconnected (Simmons et al., 2013), jointly bringing about body awareness (Craig, 2009).

Tactile signals are generally perceived using the exteroceptive somatosensory system; however, affective touch has been identified as relying on the interoceptive system. Whereas sensory/discriminatory touch is processed exteroceptively via fast-conducting myelinated afferent fibres projecting to the somatosensory cortices, affective touch (slow and light stroking of the skin, which produces a pleasant subjective sensation) is processed interoceptively via slow-conducting unmyelinated afferent fibres, which project to the insular cortex (see Olausson et al., 2010 for a review). Similarly, while visceral pain is an interoceptive sensation originating within the body, cutaneous pain, resulting from

painful tactile stimulation, is at least partially exteroceptively processed (e.g., Lenz, Ohara, Gracely, Dougherty, & Patel, 2004; Strigo, Duncan, Boivin, & Bushnell, 2003). The interoceptive affective-motivational component of painful tactile stimulation—measured with pain unpleasantness ratings—is processed in the insular and anterior cingulate cortices; the exteroceptive sensory-discriminative aspect of painful tactile stimulation—measured with pain intensity ratings—is processed in the somatosensory cortices, which encode spatial, temporal, and intensive properties of noxious stimuli (see Rainville, 2002 for a review). The affective-motivational and sensory-discriminative dimensions of painful somatosensory experience (i.e., pain unpleasantness and pain intensity ratings) are usually correlated, but in some clinical contexts, such as myocardial infarction, they can be dissociated (Gaston-Johansson, Hofgren, Watson, & Herlitz, 1991).

It is not currently entirely clear how interoceptive accuracy is related to exteroceptive somatosensory perception. Pennebaker and Lightner (1980) propose that there is a competition of internal and external cues, resulting in shifts of attention from one source of information to the other (internal-to-external and external-to-internal), depending on environmental demands. This model implies that attention to internal sources of information increases perception of internallyoriginating signals, at the same time diminishing attention to external sources of information, consequently decreasing perception of externally-originating signals, and vice versa. However, Knapp, Ring, and Brener (1997) found that accuracy in detecting exteroceptive vibrotactile signals was correlated with heartbeat discrimination accuracy, suggesting that there might be a general sensitivity or sensory acuity to somatosensory stimuli that is not modality specific, and spans across the interoceptive and exteroceptive somatosensory modalities. Consequently, two opposite patterns of predictions can be made with regards to the potential relationship between interoceptive and exteroceptive somatosensory perception accuracy: accuracy in perceiving these two modes of somatosensory signals might be inversely related, which would be in line with the competition of cues model (Pennebaker & Lightner, 1980), or it might be positively correlated, reflecting general modality-nonspecific sensory acuity, in line with the results of

Knapp et al. (1997). As very few studies have examined the relationship between interoceptive accuracy and sensitivity to exteroceptive tactile stimuli (both, noxious and not), neither of the above hypotheses can be ascertained. Moreover, while research on multisensory integration has examined the way in which exteroceptive signals are integrated to shape body-awareness (e.g., vision and touch, or vision and audition; see Tsakiris, 2010 for a review), little is known about the way in which somatosensory signals are integrated across interoceptive and exteroceptive modalities. Recent empirical investigations demonstrate that combined interoceptive-exteroceptive signals can significantly alter ownership of a virtual hand (Suzuki et al., 2013), as well as the awareness of one's body in space (Adler, Herbelin, Similowski, & Blanke, 2014; Aspell et al., 2013), highlighting the importance of investigating the mechanisms through which somatosensory signals are integrated across interoceptive and exteroceptive modalities.

1.7.1 Interoception and Tactile Perception

Little is known about the way in which interoceptive accuracy is related to the accuracy in perceiving exteroceptive somatosensory stimuli; however, it has been shown that directing individuals' attention to interoceptive signals can significantly affect somatosensory decision-making. For example, Mirams, Poliakoff, Brown, and Lloyd (2012) investigated the effects of interoceptive versus exteroceptive attention on individuals' performance on the Somatic Signal Detection Task (SSDT; Lloyd, Mason, Brown, & Poliakoff, 2008). Mirams and colleagues observed that engaging in an interoceptive attention task, during which participants focused their attention on pulse sensations in their fingertips, resulted in a more liberal response criterion on the task—individuals were more likely to report a tactile stimulus, regardless of whether it occurred or not. On the contrary, engaging in an exteroceptive attention task, during which participants focused their attention on the grating orientation of tactile stimuli, resulted in a more conservative response criterion—individuals were less likely to report feeling a tactile stimulus, regardless of its occurrence. Mirams et al. concluded that the observed increase in the propensity to report a tactile stimulus following the interoceptive attention task could be potentially explained by interoceptive attention increasing the level of sensory noise and making it more difficult for an individual to distinguish between signal and noise (sensations originating outside and inside the body, respectively) when detecting a tactile stimulus. However, it should be noted that Mirams et al. utilised an atypical interoceptive attention task, in which participants were asked to focus their attention on pulse sensations in their fingertip. This methodology might account for an increased propensity to report a tactile stimulus on the fingertip, when completing the tactile perception afterwards. Additionally, Mirams et al. did not examine whether inter-individual variability in interoceptive accuracy was related to individuals' sensitivity in detecting the tactile stimuli, or to individuals' susceptibility to experience somatosensory distortion, as reflected by the number of false alarms made during the task. While the results of the study by Mirams et al. suggest that interoceptive attention might bias individuals toward reporting tactile sensations in their absence, these results do not provide direct support for the hypothesis that interoceptive attention contributes to individuals being less able to distinguish sensory noise from signal. Consequently, further research is necessary to establish the nature of the relationship between interoceptive and exteroceptive somatosensory perception.

1.7.2 Interoception and Pain Perception

Neuroimaging evidence suggests that painful somatosensory sensations are, at least partially, separately processed from interoceptive sensations (e.g., Lenz et al., 2004; Strigo et al., 2003). Only two studies to date have examined the relationship between interoceptive accuracy and sensitivity to pain. Werner, Duschek, Mattern and Schandry (2009b) investigated the relationship between heartbeat tracking accuracy and sensitivity to heat pain, failing to find an association. On the contrary, Pollatos, Füstös and Critchley (2012) observed that individuals with higher heartbeat tracking accuracy displayed higher sensitivity and lower tolerance to cutaneous pressure pain than individuals with lower heartbeat tracking accuracy. Moreover, Pollatos and colleagues found that individuals with higher heartbeat tracking accuracy exhibited more autonomic reactivity in response to pain, and rated the painful sensations as significantly more unpleasant than individuals with lower heartbeat tracking accuracy. The

results of Pollatos et al. suggest that high interoceptive accuracy is associated with higher sensitivity to pain and an increased affective (as opposed to sensory) response to pain, which is in line with neuroimaging evidence linking the insular and anterior cingulate cortices to the affective-motivational dimension of pain (Rainville, 2002). Interoceptive processes might also be involved in pain anticipation, as suggested by activation of brain regions associated with interoception (i.e., insula, anterior cingulate) during the anticipation of pain (Chua, Krams, Toni, Passingham, & Dolan, 1999; Ploghaus et al., 1999). Because only two studies to date (Pollatos et al., 2012; Werner et al., 2009b) examined the relationship between interoceptive accuracy and pain perception, producing contradictory results, the relationship between these two types of somatosensory processing remains unclear.

1.8 Interoception and Emotion

Interoception is central to the experience of emotion (Damasio, 1999). The view that visceral activity and emotional experience are inherently linked is referred to as *peripheralism* and was first proposed by William James (1884) who defined emotion as the perception of bodily signals in response to emotioneliciting stimuli. This controversial peripheralist view that "our feeling of . . . (autonomic) changes as they occur IS the emotion" (p.189-190) and that distinct patterns of bodily signals code for different emotions was also held by Carl Lange (1885)—a Dane who, independently of James, came up with similar ideas around the same time—and became known as the James-Lange theory of emotion. The James-Lange theory was challenged by Cannon (1927, 1931) who proposed an opposing account, claiming that physiological activity is largely too undifferentiated to constitute an emotion in itself and that the human body does not have a sufficient number of distinct afferents to generate distinct emotions solely on the basis of autonomic signals. Cannon presented supporting evidence for his theory showing that emotion-based behaviour in animals was not affected by complete separation of the viscera from the brain as well as that emotions could not be generated solely by artificial hormonal induction of physiological activity. Whereas, these claims have been undermined by future research (e.g.,

Ekman, Levenson, & Friesen, 1983), at the time, Cannon's claims could not be disputed and the role of bodily perception in emotional experience was not considered as essential to emotional experience. It was not until the work of Schachter and Singer (1962) that the role of physiological signals was reconsidered in the research literature on emotion. Schachter and Singer (1962) investigated cognitive evaluations of physiological feedback, finding that similar patterns of physiological activity could be experienced either as happiness or as anger, depending on the social and/or cognitive context. This result led them to redefine emotional experience as being situation-dependent and resultant from the interaction of autonomic arousal and environmental cues perceived as relevant at the time by the individual. The appraisal theory of Schachter and Singer, therefore, posits the perception of bodily changes as prerequisite, but not sufficient, for the experience of emotions.

The peripheralist tradition of James and Lange has been continued by Damasio (1996) and the Somatic Marker Hypothesis, in which Damasio proposes that various somatic markers from the body influence emotions and, consequently, cognitive processes such as decision-making, or working memory formation and retrieval. Damasio hypothesises that a specific visceral event (e.g. rapid heart rate) gets represented with a particular 'somatic marker' within the emotional neurocircuitry of the brain (involving mainly the ventromedial prefrontal cortex); then, in situations of uncertainty, somatic markers associated with previously encountered events that are similar to the presently faced uncertain event get reactivated to allow for quicker information processing, decision making and consequent execution of adequate behaviour. It has to be noted that the existence of specific somatic markers associated with particular emotions has not been empirically supported (see Cacioppo, Berntson, Larsen, Poehlmann & Ito, 2000 for a meta-analytic review), however, somatosensory information is of crucial importance as it constitutes a basic building block of emotion in that the somatovisceral of the signals state body core affect—feelings pleasure/displeasure (i.e., valence) and activation/deactivation (i.e., arousal) (e.g., Barrett & Lindquist, 2008; Barrett & Bliss-Moreau, 2009).

In the last years, there has been growing support for the constructionist

model of emotion, which holds that emotions are situated conceptualisations of bodily changes (Barrett 2011, 2013; Lindquist, 2013). Barrett (2015) explains that while appraisal theories assume that ambiguous physiological arousal in a specific situation gets interpreted by the perceiver, which then results in an emotional response in a linear and recursive manner, in the psychological construction model, emotions emerge in a non-linear manner, when the whole array of bodily sensations is interpreted in light of the current context, using conceptual knowledge about specific emotions. Taken together, even though there is no oneto-one correspondence between physiological activity and subjective emotional experience (as suggested by James and Lange), it is likely the interaction between the perception of bodily signals—interoception—and cognitive, social, and other contextual variables, that gives rise to subjective feeling states. Nevertheless, if the peripheralist account of emotion is considered, it follows that individuals who are more aware of, and better able to detect, physiological changes taking place in their bodies, would be more influenced by these in their emotional experience than those individuals who are less aware of, and less able to detect bodily signals. Indeed, several lines of investigation suggest that the experience of emotion is shaped by an individuals' ability to accurately perceive internal body signals their interoceptive accuracy—including self-reported, physiological, neuroimaging, behavioural and clinical evidence. There is no one-to-one correspondence between physiological activity and subjective emotional experience (Mauss et al., 2005; Steptoe & Noll, 1997).

1.8.1 Interoception and Subjective Reports of Emotion

High interoceptive accuracy has been associated with an amplified subjective experience of emotions. Herbert, Pollatos and Schandry (2007) observed that individuals with higher heartbeat tracking accuracy rated affective (both pleasant and unpleasant), but not neutral, visual stimuli as significantly more arousing than individuals with lower heartbeat tracking accuracy. The positive correlation between heartbeat tracking accuracy and arousal ratings associated with affective images remained significant after controlling for valence ratings of the images. Additionally, no differences in valence ratings of the images were found between individuals with higher and lower heartbeat tracking

accuracy. Consequently, Herbert and colleagues concluded that cardiac interoceptive accuracy is likely related only to the intensity, and not valence of emotional experience.

The association between cardiac interoceptive accuracy and increased intensity of subjective emotional experience has been ascertained by an array of studies using affective images (Dunn et al., 2010; Hantas, Katkin, & Blascovich, 1982; Pollatos et al., 2005; Pollatos, Gramann, & Schandry, 2007; Pollatos, Herbert et al., 2007; cf. Eichler, Katkin, Blascovich, & Kelsey, 1987), and ones using emotion eliciting videos (Wiens et al., 2000), while assessing cardiac interoceptive accuracy with various measures. Barrett, Quigley, Bliss-Moreau, and Aronson (2004) examined inter-individual variability in cardiac interoceptive accuracy as it relates to two aspects of expressing individual emotional experience: arousal and valence. They found that cardiac interoceptive accuracy, as assessed with a heartbeat discrimination task, is positively associated with an arousal focus—or the extent to which individuals emphasize activation and deactivation when describing their emotional states over time, but is unrelated to valence focus—the extent to which individuals use emotion adjectives to convey feelings of pleasure and displeasure when describing their emotional experiences over time (Feldman, 1995; Barrett, 1998). Pollatos, Traut-Mattausch, Schroeder and Schandry (2007) observed that cardiac interoceptive accuracy, as measured with heartbeat tracking, mediates the relationship between trait anxiety and arousal ratings of unpleasant affective pictures. Further, Dunn et al. (2010) found that cardiac interoceptive accuracy, also measured with heartbeat tracking, moderates the relationship between changes in heart rate and self-reports of arousal in response to affective stimuli. Taken together, these results suggest that accuracy in perceiving cardiac interoceptive signals is closely linked to subjective emotional experience, and particularly to the perceived intensity of emotional experience. Additionally, it seems that the stronger an individual's perception of physiological changes taking place in his or her body, the more these changes influence how the individual feels.

1.8.2 Interoception and Physiological Reactivity to Emotion

The relationship between interoceptive accuracy and emotion-evoked physiological reactivity is complex and not yet fully understood. One line of research suggests that high interoceptive accuracy might be associated with increased physiological reactivity in emotional situations. For example, Eichler and Katkin (1994) found that individuals who were higher in cardiovascular reactivity to mental arithmetic stress were more interoceptively accurate, as measured with a heartbeat discrimination task; Herbert, Pollatos, Flor, Enck and Schandry (2010) found that individuals with higher heartbeat tracking accuracy displayed higher sympathetic reactivity to mental stress and more vagal reactivity during emotional picture presentation than individuals with lower heartbeat tracking accuracy have been observed to exhibit amplified heart rate deceleration in response to affective images, which is suggestive of increased autonomic reactivity to emotive stimuli (Pollatos, Herbert et al., 2007; Pollatos & Schandry, 2008).

Whereas the above results suggest that interoceptive accuracy is associated with greater emotion-related autonomic reactivity, multiple other studies failed to observe significant differences in emotion-related physiological reactivity measures between individuals higher and lower in cardiac interoceptive accuracy (Schandry, 1981; Ferguson & Katkin, 1996; Wiens et al., 2000; Werner, Duschek, Mattern, & Schandry, 2009a; Werner, Kerschreiter, Kindermann, & Duschek, 2013). Studies indicating a lack of differences in emotion-related autonomic reactivity in individuals with high and low interoceptive accuracy suggest that individuals who are more interoceptively accurate subjectively experience emotions as more intense not necessarily because of increased physiological arousal, but perhaps because of a more accurate perception of physiological changes associated with emotional reactions. Nevertheless, more research is necessary to determine the nature of the relationship between interoceptive accuracy and emotion-related physiological reactivity.

1.8.3 Interoception and Emotion: Neuroimaging Evidence

The same brain regions that have been linked to interoception—the insula,

the anterior cingulate and somatosensory cortices (e.g., Critchley et al., 2004)—have also been associated with the subjective experience of emotion (e.g., Damasio et al., 2000). Zaki, Davis and Ochsner (2012) found overlapping activity in these interoception-related brain areas within individuals when they performed a heartbeat perception task and when they watched emotion eliciting videos, and rated their emotional responses to those videos. Zaki et al. further observed a strong positive correlation between brain activity and intensity of emotional experience—both at group-level and individual participant-level. The finding that interoceptive and emotion processing recruit a shared neural network is not surprising considering that somatosensory information is one of the basic components of emotion (e.g., Barrett & Lindquist, 2008; Barrett & Bliss-Moreau, 2009).

Studies measuring the brain's event-related potentials (ERPs) in response to affective visual stimuli have found that cardiac interoceptive accuracy, measured via heartbeat tracking accuracy, was directly associated with the magnitude of the P300 and slow wave latency ERP components (Herbert, Pollatos, & Schandry, 2007; Pollatos et al., 2005). The P300 and slow wave ERP components index heightened and sustained attentional processing of salient stimuli (Keil et al., 2002); greater positivity in the P300 and late positive slow wave latencies are characteristic of arousal-related responses to emotionally salient stimuli (e.g., Cuthbert, Schupp, Bradley, Birbaumer, & Lang, 2000). Herbert, Pollatos and Schandry (2007) observed that individuals with higher heartbeat tracking accuracy show greater amplitude of the P300, and greater slow wave positivity in response to emotional (both pleasant and unpleasant), but not neutral, visual stimuli than individuals with lower heartbeat tracking accuracy. Consequently, the pattern of results obtained by Herbert and colleagues suggests that individuals with higher cardiac interoceptive accuracy show enhanced neural processing of emotional stimuli.

1.8.4 Interoception and Affective Psychopathology

Altered interoceptive processing has been implicated in affective psychopathology. Depression has been linked to low interoceptive accuracy

(Dunn, Dalgleish, Ogilvie, & Lawrence, 2007; Furman, Waugh, Bhattacharjee, Thompson, & Gotlib, 2013; Pollatos, Traut-Mattausch, & Schandry, 2009). Depressed individuals have been found to exhibit reductions in the amplitude of the heartbeat evoked potential (Terhaar, Viola, Bar, & Debener, 2012, reflective of cortical processing of cardiovasuclar signals (Pollatos & Schandry, 2004) as well as dampened insula activity when directing attention to interoceptive (i.e., cardiac, respiratory and gastrointestinal) signals (Avery et al., 2014). Harshaw (2015) proposes that altered integration of interoceptive and exteroceptive signals might be at the core of various depressive symptoms such as anhedonia and social deficits; although empirical evidence is required to directly test this theory. Taken together, studies investigating interoceptive accuracy in depression suggest that depression is associated with reduced accuracy at perceiving interoceptive signals.

Anxiety psychopathology, on the contrary, has been linked to heightened interoceptive accuracy (see Domschke, Stevens, Pfleiderer, & Gerlach, 2010 for a comprehensive review). Cognitive theories of anxiety suggest that increased interoceptive accuracy might increase the likelihood of somatic sensations being misinterpreted as threatening and dangerous (Clark, 1986)—via somatosensory amplification (the experience of common bodily sensations as noxious and unpleasant (e.g., Bischoff, 1989; Brown, 2004)—contributing in that way to panic and health anxiety, for example. However, Mailloux and Brener (2002) failed to find a positive association between heartbeat discrimination accuracy and scores on the Somatosensory Amplification Scale (SSAS; Barsky, Wyshak, & Klerman, 1990), instead observing that individuals with higher heartbeat discrimination accuracy tend to be low in somatosensory amplification. Moreover, low interoceptive accuracy has been observed in individuals affected by various anxiety conditions, such as obsessive-compulsive disorder (Weiss & Pollatos, 2014), health anxiety (Krautwurst, Gerlach, Gomille, Hiller, & Witthöft, 2014), and closely related to health anxiety—somatoform disorders (Schaefer, Egloff, & Witthoeft, 2012). Additionally, even though several studies found increased interoceptive accuracy in individuals with panic symptoms (Ehlers & Breuer, 1992; Ehlers et al., 1995), not all studies found an association, with several studies

indicating an inverse relationship between the two (e.g., Asmundson, Sandler, Wilson, & Norton, 1993; Ehlers, Margaf, Roth, Taylor, & Birbaumer, 1988; Kroeze & van den Hout, 1998). Mailloux and Brener (2002) propose that individuals with low interoceptive accuracy might experience difficulty in perceiving a range of somatic sensations that result from normal physiological functioning, as a result misidentifying these sensations as being threatening or dangerous, which then could lead to anxiety. Overall, more research is necessary to establish whether anxiety conditions are associated with heightened or lowered interoceptive accuracy.

The relationship between anxiety and interoceptive accuracy might be unclear due to several confounding factors such as use of medication, and comorbid conditions, which could be differentially associated with interoceptive accuracy—for example, depression (Dunn et al., 2007). Additionally, interoceptive accuracy has been found to be directly associated with traits such as anxiety sensitivity (Stewart, Buffett-Jerrott, & Kokaram, 2001), emotional lability (Schandry, 1981)—but also emotional intelligence (Schneider, Lyons, & Williams, 2005)—while being inversely related to variables such as alexithymia (Herbert, Herbert, & Pollatos, 2011), and antisocial behaviour (Nentjes, Meijer, Bernstein, Arntz, & Medendorp, 2013). The simultaneous opposing associations between variables implicated in affective psychopathology and interoceptive accuracy undoubtedly contribute to contrasting results of studies investigating interoceptive accuracy in individuals affected by various anxiety conditions. Further research is necessary to delineate the mechanisms governing the complex interplay between interoceptive accuracy and affective psychopathology by taking into account moderating factors such medication use, presence of comorbid conditions, and interactions with various other inter-individual difference variables.

1.9 Interoception and Cognitive-Affective Processing

Interoceptive accuracy has been associated with aspects of cognitive processing. Enhanced interoceptive accuracy has been related to improved memory (Garfinkel, Barrett, et al., 2013; Garfinkel, Tiley et al., 2013; Werner et

al., 2010) as well as improved decision-making (Dunn et al., 2010; Werner, Schweitzer et al., 2013). It has been suggested that high interoceptive accuracy might be associated with by general enhancement in attentive ability. Pollatos, Matthias and Schandry (2007) observed that individuals with higher heartbeat tracking accuracy show increased attentional processing of visual stimuli, as reflected by higher P300 amplitudes in response to target stimuli in a visual oddball paradigm in comparison to individuals with lower heartbeat tracking accuracy. Further, Matthias et al. (2009) observed that individuals with higher heartbeat tracking accuracy performed significantly better on tasks assessing selective and divided attention than individuals with lower interoceptive accuracy (although, Ainley, Brass and Tsakiris, 2014 failed to replicate this relationship). It might be the case that interoceptive accuracy is reflective of a general ability to orient and direct their attention to various stimuli—both interoceptive and exteroceptive—although further research is necessary to ascertain this hypothesis.

Because individuals with higher interoceptive accuracy have been found to subjectively experience emotions as more intense, it is not surprising that high interoceptive accuracy affects performance on a range of cognitive tasks, which involve emotion processing. Werner, Mannhart, Reyes Del Paso and Duschek (2014) found that individuals with higher heartbeat tracking accuracy show increased interference of negative affective words on the Emotional Stroop Task than individuals with lower heartbeat tracking accuracy. Individuals with higher heartbeat tracking accuracy have been shown to have better implicit memory for affective words, as assessed by means of primed and unprimed word stem completion (Werner et al., 2010), as well as better explicit memory of affective images (Pollatos & Schandry, 2008) than individuals with lower heartbeat tracking accuracy. Lastly, individuals with higher heartbeat discrimination accuracy have been found to show more pronounced facial expressiveness in response to affective images than individuals with lower heartbeat discrimination accuracy (Ferguson & Katkin, 1996). Taken together, these results show that individuals with higher cardiac interoceptive accuracy are more affected by emotion-related information during cognitive tasks than individuals with lower cardiac interoceptive accuracy. Unsurprisingly, interoception has also been implicated in intuitive decision making, affective learning, and emotion regulation.

1.9.1 Intuitive Decision-Making

Interoceptive signal perception has been implicated in intuitive decisionmaking. The Somatic Marker Hypothesis (Damasio, 1996) suggests that intuition is, at least in part, influenced by emotion-related physiological signals. Indeed, Werner, Jung et al. (2009) found that individuals with higher heartbeat tracking accuracy showed superior intuitive decision making performance on an Iowa Gambling Task (Bechara, Damasio, Tranel, & Damasio, 1997). Specifically, Werner et al. observed that individuals with higher heartbeat tracking accuracy made a significantly more choices resulting in net gains (as opposed to losses) than individuals with lower heartbeat tracking accuracy. Wölk, Sutterlin, Koch, Vogele and Schulz (2014) found that heartbeat tracking accuracy was positively related to performance on the Iowa Gambling Task in individuals without psychiatric conditions, but was inversely related to performance on the task in individuals with panic disorder. The results of the study by Wölk and colleagues suggest that higher interoceptive accuracy might not necessarily lead to improved intuitive decision-making. Dunn and colleagues (2010) found that individuals with higher heartbeat tracking accuracy are more reliant on anticipatory bodily signals, such as electrodermal activity and heart rate, when making decisions under uncertainty. As anticipatory bodily signals can favour choices that may or may not be advantageous, reliance on these signals during the task can result in either superior or poorer performance.

1.9.2 Affective Learning

The involvement of interoceptive processes in affective learning is evidenced by masked fear conditioning paradigms. During masked fear conditioning, individuals are classically conditioned to fear stimuli that they are not consciously aware of; once conditioned, individuals report significantly higher shock-expectancy ratings, and display significantly higher skin conductance responses when presented with the visual stimuli that were previously paired with electric shocks than when presented with visual stimuli which were not previously

paired with shocks (Parra, Esteves, Flykt, & Ohman, 1997; Ohman & Soares, 1998). The conditioning occurs on a non-conscious level, as individuals cannot explicitly recognise the masked visual stimuli that were previously paired with electric shocks. It has been assumed that even though individuals do not consciously perceive the conditioned masked stimuli, the autonomic response to the shock is sufficient to facilitate fear conditioning. However, Katkin, Wiens and Ohman (2001) point out that in the studies by Parra et al. and by Ohman and Soares individuals who accurately predicted the upcoming shocks did not differ in the autonomic response to the shocks associated with the masked stimuli from individuals who did not accurately predict the upcoming shocks. Consequently, Katkin and colleagues suggest that autonomic arousal is not sufficient to enable accurate prediction of shocks during masked fear conditioning.

Katkin and colleagues (2001) demonstrated that, during a masked fear conditioning task, individuals with higher discrimination accuracy were better at predicting upcoming shocks than individuals with lower heartbeat discrimination accuracy. Katkin et al.'s results suggest that it might be the ability to accurately perceive autonomic changes, associated with the unconditioned shock stimulus, that facilitate accurate prediction of upcoming shocks, rather than the autonomic changes per se. Interestingly, Raes and De Raedt (2011) observed that merely engaging in a heartbeat discrimination task prior to subliminal fear conditioning task facilitated fear conditioning. In interpreting their results, Raes and De Raedt propose that focusing attention on interoceptive autonomous signals might intensify the subsequent experience of aversive sensations associated with the unconditioned shock stimulus, as a result facilitating affective learning. Taken together, the results of the above studies implicate interoceptive accuracy in fear conditioning, demonstrating that it is the perception of bodily responses to threatening stimuli that facilitates this form of affective learning, rather than the bodily response alone.

1.9.3 Emotion Regulation

Barrett, Gross, Christensen and Benvenuto (2001) observed that the level of emotion differentiation, as assessed with experience-sampling data (daily diary

entries that were entered throughout a two-week period), was directly associated with self-reported emotion regulation. As interoceptive bodily changes are an integral part of emotional experience (Barrett & Lindquist, 2008; Barrett & Bliss-Moreau, 2009), higher accuracy in perceiving interoceptive signals could contribute to more differentiated emotional experience, consequently influencing emotion regulation (Barrett et al., 2001). Using an affective picture reappraisal paradigm, Füstös, Gramann, Herbert and Pollatos (2013) observed that heartbeat tracking accuracy scores were correlated with reappraisal-related reductions in P3 and slow wave amplitudes. The findings of Füstös et al. suggest that a more accurate perception of interoceptive signals associated with emotional reactions to affective stimuli might facilitate effective emotion regulation. Indeed, individuals with higher heartbeat tracking accuracy have been observed to report less anxiety before and after public speaking (Werner, Duschek et al., 2009a), and less negative affect after being socially excluded (Werner, Kerschreiter et al., 2013) than individuals with lower heartbeat tracking accuracy, potentially reflecting increased ability to regulate emotions in stressful situations.

However, individuals high in interoceptive accuracy do not always show behaviour consistent with the assumption that interoceptive accuracy is associated with increased ability to effectively regulate negative emotions in stressful situations. For example, in a study by Kindermann and Werner (2014), individuals with higher heartbeat tracking accuracy reported more negative affect in response to a mental stress task than individuals with lower heartbeat tracking accuracy. The results of Kindermann and Werner are in line with research showing that, in comparison to individuals with low interoceptive accuracy, highly interoceptively accurate individuals report more intense responses to emotive stimuli (Dunn et al., 2010; Pollatos et al., 2005; Pollatos, Gramann, & Schandry, 2007; Pollatos, Herbert et al., 2007; Wiens et al., 2000). Dunn, Evans, Makarova, White and Clark (2012) investigated the relationship between heartbeat tracking accuracy and emotion-related behaviour during the Ultimatum Game. It should be noted that the Ultimatum Game was developed to study economic decision-making (Güth, Schmittberger, & Schwarze, 1982). During the task, two players must agree on dividing a sum of money between them. Player 1 suggests how the

money should be divided, and Player 2 can either accept this offer (money is divided between two players according to Player 1's suggestion) or reject this offer (neither player receives any money). Negative emotions, such as anger and sadness, have been associated with rejections of unfair offers (Pillutla & Murnighan, 1996; Harle & Sanfey, 2007). As it is (financially) disadvantageous for the participant to reject an offer, even when it is low or unfair (because no subsequent offers can be made), offer rejections during the game can be interpreted as indicative of unsuccessful emotion regulation (Van 't Wout, Faught, & Menino, 2013). Dunn et al. (2012) observed that heartbeat tracking accuracy was directly associated with anger reported in response to unfair offers, and inversely related to judgments about fairness of the unfair offers. Further, heartbeat tracking accuracy was associated with larger differences in electrodermal activity associated with rejected, as compared to accepted, offers. This difference in psychophysiological arousal was associated with higher rejection rates in individuals with higher heartbeat tracking accuracy, but was not related to rejection rates in individuals with lower heartbeat tracking accuracy. Taken together, the results of the study by Dunn et al. suggest that individuals with higher interoceptive accuracy might be less able to regulate negative emotions in face of unfair offers, which are accompanied by strong physiological responses.

It might be the case that the relationship between interoceptive accuracy and emotion regulation is context-dependent. Van 't Wout et al. (2013) examined the effect of explicit emotion regulation, in the form of reappraisal, on behaviour during Ultimatum Game. The results of the study by Van 't Wout et al. indicated that individuals with higher heartbeat tracking accuracy reported feeling less emotionally involved while engaging in reappraisal during the Ultimatum Game and accepted more unfair offers following reappraisal in comparison to individuals with lower heartbeat tracking accuracy. These findings suggest that interoceptive accuracy can facilitate emotion regulation, which is contrary to the results of Dunn et al., but in line with the results of Füstös et al. (2012). Differing results of studies examining the relationship between interoceptive accuracy and emotion regulation imply that the relationship between the two might be context-

dependent, varying according to factors such as the mode of emotion regulation—for example, rejection of unfair offers during an Ultimatum Game is an implicit index of emotion regulation, whereas cued reappraisal constitutes explicit emotion regulation. Overall, future research is necessary to directly examine which factors might moderate the relationship between interoceptive accuracy and various facets of emotion regulation.

1.10 Interoception, Body Representation and Social Cognition

Interoception has been proposed to be the basis of the bodily sense of self (Craig, 2002, 2010). However, only a few studies to date have investigated the relationship between interoceptive accuracy and malleability of body representation and body ownership. Tsakiris et al. (2011) observed that individuals with higher heartbeat tracking accuracy were less susceptible to the rubber hand illusion, experiencing a lower sense of ownership of a rubber hand, following synchronous visuo-tactile stimulation, than individuals with lower heartbeat tracking accuracy. Individuals with higher heartbeat tracking accuracy have also been shown to experience the enfacement illusion to a lower extent than individuals with lower heartbeat tracking accuracy, displaying a smaller impairment in distinguishing between self and other (in a photograph recognition task) following multisensory stimulation involving the other's face (Tajadura-Jiménez & Tsakiris, 2014). Taken together, these findings suggest that self-other boundaries of individuals with higher interoceptive accuracy are less malleable and less influenced by manipulations such as interpersonal multisensory stimulation than those of individuals with lower interoceptive accuracy. Consequently, accurate perception of interoceptive signals might foster individuals' sense of self, strengthening the boundaries between self and other.

The relationship between interoceptive accuracy and self-other distinction might be context-dependent. Ainley et al. (2014) observed that individuals with higher heartbeat tracking accuracy have greater difficulty inhibiting the tendency to automatically imitate, which has been assumed to reflect individual ability to distinguish between self and other (Spengler, von Cramon, & Brass, 2009). Ainley and colleagues (2014) propose that highly interoceptively accurate

individuals may be highly sensitive to social influences and have a strong interoceptive representation of the consequences of others' actions, which can then result in an increased difficulty inhibiting the tendency to automatically imitate. Indeed, it has been shown that, in comparison to individuals with lower heartbeat tracking accuracy, individuals with higher heartbeat tracking accuracy show a higher autonomic response to social stimuli, suggestive of increased sensitivity to social factors (Ferri et al., 2013). Specifically, Ferri and colleagues (2013) found that heartbeat tracking was positively associated with RSA (respiratory sinus arrhythmia) response in a social, but not in a non-social, context. RSA has been suggested to be indicative of cardiac vagal tone, which is generally considered to be a measure of the activity of the parasympathetic nervous system. In psychological research, higher RSA amplitude has been associated with increased self-regulation and a greater social disposition (e.g. Porges, 2001, 2003, 2007). Consequently, Ferri et al. concluded that individuals with higher interoceptive accuracy might have greater social disposition, as reflected by increased RSA responses in social contexts. The link between interoception and social disposition is supported by neuroimaging evidence, which shows that directing individuals' attention to interoceptive signals is associated with an enhancement in subsequent empathy-related neural activity (Ernst, Northoff, Boker, Seifritz, & Grimm, 2013), further implicating the involvement of interoceptive processes in social functioning. Consequently, the relationship between interoceptive accuracy and the ability to control mental representations of self and of the other may be modulated by contextual factors and by inter-individual differences in affiliative motivation. Individuals high in interoceptive accuracy might selectively strengthen or attenuate representations of self and of the other, depending on environmental demands, selectively inhibiting mental representations of the self, while amplifying mental representations of the other in order to enable empathy and understanding as well as to facilitate affiliation and cooperation.

Recently, research has begun to use interoceptive information to manipulate individuals' body representation and body ownership. Suzuki et al., (2013) manipulated cardio-visual feedback projected on a virtual hand (in a

virtual reality environment) to be either synchronous or asynchronous with the participants' concurrent heart rate. Suzuki and colleagues observed that participants' subjective experience of ownership of the virtual hand was enhanced only in the synchronous cardiac feedback condition and not in the asynchronous feedback condition. Also using virtual reality, Aspell et al. (2013) found that synchronous cardio-visual feedback projected on a virtual body increased individuals' experience of ownership of the virtual body, enhancing selfidentification with the virtual body as well as affecting individuals' estimates of their location in space (shifting it towards the virtual body). The same effect of synchronicity of combined interoceptive-exteroceptive bodily information on selfidentification with a virtual body was observed using respiratory interoceptive signals (Adler et al., 2014). Adler and colleagues found that individuals selfidentified with virtual projections of their bodies when the virtual bodies flashed in synchrony, rather than asynchrony, with their concurrent breathing rate. Taken together, the results of the above studies suggest that interoceptive signals contribute to the subjective experience of body ownership and that multisensory integration of body-related information across the interoceptive and exteroceptive modalities shapes bodily self-consciousness.

1.11 Interoceptive Accuracy as a State Variable

The majority of research examining the relationship between interoception and social, cognitive and affective functioning focused on the way in which interindividual variability in interoceptive accuracy predicts various aspects of cognitive and affective processing, with very few studies investigating state-dependent fluctuations in interoceptive accuracy. This gap in the research literature is likely due to the fact that, traditionally, interoceptive accuracy has been considered to be a trait, rather than a state, variable (Cameron, 2001; Schandry, 1981). This view of interoceptive accuracy as being stable over time and not subject to change has been largely based on studies that investigated interoceptive accuracy in clinical anxiety groups and in relation to variables such as anxiety sensitivity. Studies investigating interoceptive accuracy in clinical groups were largely based on the premise that heightened interoceptive accuracy

is a maintaining factor in anxiety conditions—especially panic—and aimed to examine potential changes in interoceptive accuracy before and after psychological treatment, failing to find significant differences (Ehlers & Breuer, 1992; Ehlers et al., 1995; Antony, Meadows, Brown, & Barlow, 1994; Ehlers & Breuer, 1996; Mussgay et al., 1999). However, these studies have not considered that potential fluctuations in interoceptive accuracy might be short-lived and context-specific, rather than constituting long-term permanent changes in baseline levels of interoceptive accuracy.

There is ample evidence for cognitive, affective, and social processes modulating body perception and body representation. For example, visual attention has been found to modulate tactile perception (e.g., Tipper et al., 1998), pain (e.g., Longo, Betti, Aglioti, & Haggard, 2009) and body representation (e.g., Rubber Hand Illusion; Tsakiris & Haggard, 2005). Emotion, on the other hand, has been found to modulate pain (e.g., Roy, Piche, Chen, Peretz, & Rainville, 2009), while social factors, such as presence of other individuals, have been found to modulate pain (e.g., Krahé, Springer, Weinman, & Fotopoulou, 2013) as well as body representation (e.g., peripersonal space; Teneggi, Canzoneri, di Pellegrino, & Serino, 2013). Nevertheless, almost all of the research on factors affecting body perception has focused on exteroceptive body perception, leaving the effects of cognitive and affective states and social contexts on interoceptive perception under-examined. To date, studies that investigated context-specific changes in interoceptive accuracy suggest that interoceptive accuracy can be potentially affected by physiological states (e.g., increased cardiovascular activity, hunger), by affective states (e.g., experience of anxiety) and by cognitive states (e.g., degree of focus on one's self).

1.11.1 Effect of Physiological State on Interoceptive Accuracy

Jones and Hollandsworth (1981) and Schandry and Specht (1981) found that exercise evoked physiological arousal increases cardiac interoceptive accuracy, as measured with heartbeat discrimination, in individuals of varying levels of physical fitness. This research question was further examined using clinical samples by Antony et al. (1995), who tested whether panic patients'

heartbeat tracking accuracy would increase due to heightened cardiovascular activity, as manipulated by engaging in brief physical exercise. In order to establish whether potential changes in heartbeat tracking accuracy would be unique to panic disorder patients, Antony et al. investigated three groups: individuals diagnosed with panic disorder, individuals diagnosed with social phobia, and healthy controls. While no differences based on group were observed, neither at baseline nor following physical exercise, all participants increased in mean heartbeat tracking accuracy immediately following physical exercise. The results of the study by Antony et al. suggest that small, short-lived fluctuations in interoceptive accuracy might occur in response to contextual factors and that these fluctuations might be generally observed rather than being present only in clinical samples.

More recently, Herbert, Herbert et al. (2012) investigated whether shortterm food deprivation would affect the stability of interoceptive accuracy, as measured with the Schandry task. The results of the study indicated that heartbeat tracking accuracy increased in response to food-deprivation and that the increase in accuracy was directly associated with self-reports of experienced hunger, consequently providing evidence that interoceptive accuracy can fluctuate in a state-dependent manner. As short-term food deprivation increases the strength of interoceptive signals of hunger, a simultaneous increase in individuals' accuracy in perceiving cardiac signals might be indicative of a concurrent increased strength of cardiac interoceptive signals. However, there might be an alternative mechanism at work, and the increase in heartbeat tracking accuracy in response to food-deprivation might be reflective of increased general attention to, and consequently, more accurate perception of, interoceptive signals rather than due to an increase in the strength of the signals themselves. Overall, further research is needed to delineate the mechanisms of interoceptive accuracy fluctuations across the interoceptive modalities in response to various changes to the physiological condition of the body.

1.11.2 Effect of Cognitive State on Interoceptive Accuracy

Studies investigating the effects of cognitive state on interoceptive

accuracy have examined the way in which various modes and degrees of selffocus affect the stability of interoceptive accuracy. Weisz, Balazs and Adam (1988) found that, in a female sample, heartbeat discrimination accuracy was enhanced when individuals faced a mirror, as compared to baseline, although heartbeat tracking accuracy was not affected. Using a similar design, but including baseline heartbeat perception accuracy as a moderating variable, Ainley et al. (2012) found that, in a sample of males and females, only individuals with low baseline heartbeat tracking accuracy increased in heartbeat tracking accuracy during mirror self-observation. The results of Ainley et al. suggest that fluctuations in state interoceptive accuracy might be dependent on baseline level of interoceptive accuracy. In a follow-up study, Ainley et al. (2013) used photographs and self-referential words to further investigate the effect of selffocus on interoceptive accuracy, again revealing an increase in heartbeat tracking accuracy in response to heightened self-focus (when looking at photographs of self and when self-referential words). However, in the 2013 study by Ainley and colleagues, the enhancement in state heartbeat tracking accuracy was present in all participants, regardless of their baseline level of heartbeat tracking accuracy (it should be noted that the sample in the 2013 study was characterized by a slightly higher median heartbeat tracking accuracy, than the sample in the 2012 study, which might account for this difference). Taken together, these results suggest that cognitive states characterized by increased attention to the self can increase interoceptive accuracy. Further research is needed to determine what other cognitive states might also impact the accuracy in perceiving bodily signals of various interoceptive modalities.

1.11.3 Effect of Affective State on Interoceptive Accuracy

State changes in interoceptive accuracy in response to affective contexts have been investigated using stress-inducing manipulations, which increase negative affect. Stress affects the central representation of bodily perception (Craig, 2002). The stress hormone, cortisol has been found to amplify heartbeat evoked potentials (Schulz, Strelzyk et al., 2013), which reflect increased cortical processing of cardiovasuclar signals and have been directly associated with cardiac interoceptive accuracy (Pollatos et al., 2005; Pollatos & Schandry, 2004).

Acute stress is associated peripheral sympathetic activation and a cortisol release, with together with noradrenergic structures can influence the perception of interoceptive bodily signals (Schulz, 2015). Consequently, it can be hypothesised that stressful negative affective situations might be accompanied by an enhancement in perception accuracy of cardiovascular signals, such as heartbeats. This hypothesis is in line with evidence from neuroimaging studies, which indicate increased activation of the insula in stressful contexts (e.g., Fechir et al., 2010). Such increases in insula activity further suggest that interoceptive accuracy might be affected in emotional contexts, which elicit negative affective reactions and bring about heightened physiological arousal associated with stress. Overall, both sympathetic effects of stress-evoking manipulations on the cardiovascular system (e.g., increased stimulation of arterial baroreceptors and enhanced conduction of cardiac afferent signals) as well as the effects of stress challenges on the attentional system (e.g., increased attention to visceral signals) are likely to impact the accuracy with which individuals perceive interoceptive signals (Schulz, 2015). Stressful situations are typically associated with increases in physiological arousal and negative affect; however, stressful contexts differ from one another in character (for example, a mental arithmetic challenge differs from a respiratory challenge, which both differ from a social stress challenge). Socially stressful situations might involve the threat of negative social evaluation (e.g., public speaking challenge) or might be accompanied by negative social evaluation resulting in social rejection (e.g., social exclusion manipulation). Given the significance of interoception in cognitive-affective processes (e.g., Dunn et al., 2010; Garfinkel, Barrett, et al., 2013; Garfinkel, Tiley et al., 2013; Werner, Schweitzer et al., 2013; Werner et al., 2010; Wiens, 2005; Wiens et al., 2000), potential changes in interoceptive accuracy in stressful negative affective situations might influence emotional experience, emotion regulation, and decision making in these contexts. Only a few studies investigated state changes in interoceptive accuracy during stressful negative affective situations, focusing on clinical populations and related variables.

Increased interoceptive accuracy, as measured with heartbeat discimination accuracy, has been found in individuals after inducing emotion-

related physiological arousal with visual affective stimuli (Katkin, 1985; Katkin, Blascovich, Reed, Adamec, Jones, & Taublieb, 1982). Schandry and Specht (1981) observed an increase in heartbeat tracking accuracy after participants engaged in a public speaking challenge. Stevens et al. (2011) investigated whether highly socially anxious individuals show a larger enhancement in heartbeat tracking accuracy as a result of a public speaking manipulation, as compared to individuals low in social anxiety. Even though Stevens and colleagues failed to find changes in mean heartbeat tracking accuracy as a result of their manipulation, a marginal increase in heartbeat tracking accuracy following the speech was observed in the first post-manipulation trial for all individuals. Even though Stevens et al. concluded that their results show a lack of state-like changes in interoceptive accuracy, the results of the study, like the results of Antony et al. (1995), can be interpreted as suggestive of small, short-lived changes in state interoceptive accuracy that are likely not limited to clinical populations.

Sturges and Goetsch (1996) examined the effects of mental arithmetic stress on interoceptive accuracy in a sample of females high and low in anxiety sensitivity, observing that females high in anxiety sensitivity improved in heartbeat tracking accuracy during mental arithmetic stress, while females low in anxiety sensitivity did not. Interestingly, Fairclough and Goodwin (2007) found that females decreased in interoceptive accuracy, as measured with the heartbeat discrimination task in response to mental arithmetic stress, suggesting that the way in which stressful negative affective experiences affect interoceptive accuracy might depend on the measurement method. The importance of methodological aspects of research investigating the effect of stressful negative affective experiences on interoceptive accuracy is highlighted by Schulz, Lass-Hennemann et al. (2013), who observed that cold pressor task-induced stress increased individuals' heartbeat tracking accuracy, as measured with the Schandry task, but decreased heartbeat discrimination accuracy, as measured with the Whitehead task. Schulz, Lass-Hennemann and colleagues emphasise that the two cardiac perception tasks require different types of attention: while the Schandry task demands attention to visceral sensation, the Whitehead task demands focus on visceral sensations as well as on exteroceptive stimuli, additionally requiring a

comparison of the two to be made. Consequently, a heartbeat discrimination task might be more difficult for participants and performance on this task might be more susceptible to effects of distraction, especially in situations of increased stress.

Another line of research investigating changes in interoceptive accuracy in stressful negative affective situations focused on respiratory symptom perception. These studies (Van den Bergh et al., 2004; Bogaerts et al., 2005) measured respiratory symptom perception accuracy by calculating intra-individual correlations between the magnitude of the respiratory response and the subjective rating of the respiratory response, indicating that individuals high in negative affectivity were less accurate in judging the strength of the respiratory response during a carbon dioxide challenge (especially when the challenge is negatively framed) than individuals low in negative affectivity. Further, Bogaerts et al. (2008) observed that individuals who reported a high number of medically unexplained symptoms (high symptom reporters) became less accurate at judging the intensity of their respiratory responses to a carbon dioxide challenge than individuals who reported a low number of medically unexplained symptoms (low symptom reporters). Bogaerts et al. suggest that the observed effect might be due to high symptom reporters experiencing negative affective reactions in response to the manipulation, which in turn, can then decrease their respiratory interoceptive accuracy. It should be noted, however, that the method of assessing respiratory signal perception accuracy employed in the experiments outlined above might not necessarily gauge respiratory interoceptive accuracy, as it involves making subjective ratings of the strength of respiratory signals, not directly testing the accuracy of perception through objective standardized performance tests. While it is possible that respiratory and cardiac interoceptive accuracy are differentially affected in stressful negative affective situations, the results on respiratory symptom perception in stressful affective contexts should be interpreted with caution, serving as a platform for future research rather than constituting a basis for definite conclusion to be drawn.

Overall, research studies investigating changes in interoceptive accuracy due to stressful negative affective situations have utilised varying methods of assessing interoceptive accuracy (i.e., monitoring interoceptive sensations, comparing interoceptive and exteroceptive sensations, subjectively rating interoceptive sensations), which rely on, at least partially, distinct mechanisms, complicating the interpretation of these experimental studies. In addition to using different methods of interoceptive accuracy assessment, the experimental studies investigating the effects of stressful negative affective contexts on state interoceptive accuracy also used different manipulations, which may tap into distinct types and aspects of stress (e.g., cognitive stress versus physical threat versus social threat). Lastly, the studies outlined above have investigated both clinical and healthy samples, which may differ in their responding to stress and negative affective situations. Consequently, the use of consistent standardized methods of assessment that increase procedural comparability, and enable cross-study comparisons is needed in future investigations of the effects of stressful negative affective manipulations on state interoceptive accuracy.

1.11.4 Gaps in Research on State Interoceptive Accuracy

Because of the critical importance of interoceptive somatosensory perception to consciousness, sense of self and emotional experience (Craig, 2002, 2010; Damasio, 2010; Seth, 2013), the way in which social, cognitive and affective contexts modulate interoceptive accuracy constitutes an important topic requiring empirical investigation. The few studies to date, which have examined state changes in interoceptive accuracy, do not allow firm conclusions to be drawn with regards to the nature of state-dependent changes in interoceptive accuracy; they do, nevertheless, provide a clear indication that, in addition to being a traitlike variable, interoceptive accuracy might also function as a state variable, which can fluctuate in response to various cognitive and affective triggers. Presently, research suggests that state interoceptive accuracy might increase during heightened self-focus (Ainley et al., 2012; Ainley et al., 2013) and change in response to stressful negative affective situations (e.g., Schulz, Lass-Hennenmann et al., 2013; Sturges & Goetsch, 1996). The exact direction of the effect of stressful negative affective contexts on interoceptive accuracy is not clear, with some studies finding an increase in interoceptive accuracy in response to stress (e.g., Sturges & Goetsch, 1996) and others observing a decrease in interoceptive

accuracy in stressful negative affective situations (e.g., Van den Bergh et al., 2004; Bogaerts et al., 2005). Discrepancies in methodological aspects across studies investigating the effects of stressful negative affective states on interoceptive accuracy complicate interpretation of their results.

Overall, further research is needed to investigate state changes in interoceptive accuracy in relation to emotional experience. Interoception has been implicated in emotional experience (e.g., Wiens, 2005) and inter-individual differences in interoceptive accuracy have been correlated with trait measures of anxiety and depression, indicating direct and inverse relationships, respectively (e.g., Pollatos et al., 2009). Additionally, baseline level of interoceptive accuracy has been found to moderate emotional experience in response to emotive stimuli (e.g., Dunn et al., 2010; Pollatos, Traut-Mattausch et al., 2007), also affecting levels of negative affect in response to stressful situations such as social exclusion (Werner, Kerschreiter et al., 2013) and public speaking anticipation (Werner, Duschek et al., 2009b). State interoceptive accuracy might change in response to emotion-eliciting situations, as a function of physiological arousal, negative affect or increased self-focus. Additionally, changes in perception accuracy might be limited to the interoceptive modality, but they might also concurrently occur in exteroceptive somatosensory modalities, consequently affecting the perception of touch and/or painful exteroceptive somatosensory stimuli. While attention to, and perception of, bodily signals might be correlated across the interoceptive and exteroceptive modalities (Knapp et al., 1997), it is also possible that measures of interoceptive and exteroceptive somatosensory signal perception might be at competition with one another and consequently be inversely related (e.g., Pennebaker & Lightner, 1980). As it is not presently clear how interoceptive and exteroceptive somatosensory perception are related, research studies investigating context-dependent changes in both of these modalities are needed to establish the nature of the relationship between these two aspects of body perception: both at baseline and as modulated by environmental demands such as stressful negative affective contexts. Investigations of state changes in interoceptive and exteroceptive somatosensory signal perception accuracy can pave the way for empirical examinations of the way in which these bodily signals are integrated to

jointly influence bodily self-consciousness as well as emotion, cognition and behaviour.

1.12 Present Thesis

To date, the significance of interoceptive processing in emotional experience has been examined in an inter-individual differences context. The present thesis answers the need for further investigation of state changes in interoceptive accuracy by examining the way in which interoceptive accuracy is modulated by affective and social contexts. As studies investigating trait interoceptive accuracy and emotional experience focused on emotional states characterized by negative affect and increased self-focus, the present thesis examines the stability of interoceptive accuracy under emotional influence by utilizing stress-induction procedures which manipulate negative affect and self-focus. In order to establish whether potential changes in the interoceptive somatosensory modality, several studies comprising the present thesis investigate changes in both of these body perception modalities.

The studies in this thesis manipulate social anxiety (Experiment 1), social awareness of the self (Experiment 2), social inclusion/exclusion (Experiments 3 and 4) and pain anticipation (Experiment 5), examining the effects of these contexts on cardiac interoceptive accuracy (all experiments) as well as on exteroceptive tactile perception that is painful (Experiment 4) or not (Experiment 2). Additionally, the relationship between cardiac interoceptive accuracy and tactile processing that is painful (Experiments 4 and 5) and not (Experiment 2) is examined.

Throughout the thesis, interoceptive accuracy is indexed with heartbeat tracking accuracy, measured according to the Schandry Mental Tracking Method (1981), in which individuals silently count, and later report, the number of heartbeats they feel within a given time interval. As outlined at the beginning of the introductory chapter, this procedure is a widely-used method used to assess interoceptive accuracy (e.g., Herbert & Pollatos, 2014; Ferri et al., 2013; Furman et al., 2013; Füstös et al., 2013; Koch & Pollatos, 2014; Krautwurst et al., 2014;

Michal et al., 2014; Penton, Thierry, & Davis, 2014; Pollatos, et al., 2008; Pollatos et al., 2012; Schaefer, Egloff, Gerlach, & Witthoft, 2014). In the present thesis, the heartbeat tracking method was chosen over the heartbeat discrimination accuracy method (e.g., Brener & Kluvitse, 1988; Katkin et al., 1983; Whitehead et al., 1977), as the heartbeat discrimination task requires individuals to judge whether a heartbeat stimulus (tone) they are presented with matches their own heart rhythm, which, it can be argued, engages not only interoceptive, but also exteroceptive processing, requiring simultaneous processing of both types of information and their comparison. Heartbeat tracking and heartbeat discrimination may be reliant on shared, but largely distinct underlying mechanisms, in that heartbeat tracking is reliant on internal monitoring, whereas heartbeat discrimination also requires internal and external information to simultaneously integrated. Consequently, as proposed at the beginning of the introductory chapter, the mental tracking method likely constitutes a more pure measure of interoceptive processing. The Schandry method of assessing interoceptive accuracy was used in all experiments in the thesis. Exteroceptive somatosensory perception was assessed via perception of electrical tactile stimuli. The aspect of tactile processing measured (e.g., detection of threshold stimuli or pain thresholds) differed across experiments. Experiment 2 employed the Somatosensory Signal Detection Task (Lloyd et al., 2008), in which signal detection analysis is used to index the accuracy in perceiving exteroceptive tactile stimuli of threshold intensity. Experiments 4 and Experiment 5 measured pain thresholds and pain intensity and unpleasantness ratings.

To summarise, Experiment 1 investigated the effect of public speaking anticipation on heartbeat tracking accuracy; Experiment 2 investigated the effect of enhanced public self-focus on heartbeat tracking accuracy, and on threshold-tactile stimulus perception accuracy. Experiment 2 also investigated the relationship between heartbeat tracking accuracy and tactile perception accuracy. Experiment 3 investigated the effect of social exclusion on heartbeat tracking accuracy, while Experiment 4 investigated the effect of social exclusion on both heartbeat tracking accuracy and on exteroceptive tactile pain thresholds and pain intensity and pain unpleasantness ratings. Experiment 5 investigated the effect of

pain anticipation on heartbeat tracking accuracy, also examining the relationship between heartbeat tracking accuracy and pain perception.

Overall, the studies comprising this thesis aim to further the current understanding of the way in which cardiac interoceptive perception functions as a state variable that is subject to modulation by social and affective contexts. This investigation will provide novel evidence as for the existence of a bi-directional relationship between interoception and emotion, in which in addition to interoceptive accuracy influencing emotional experience in a trait-like manner, emotional experience also influences interoceptive accuracy as a state-variable. Additionally, the studies aim to further the current understanding of the way in which cardiac interoceptive perception accuracy is related to other modes of body perception, such as noxious and neutral tactile perception. Consequently, the approach employed in the current theses allows for an investigation of:

- 1) Which aspects of stress might affect state interoceptive accuracy (e.g., physiological arousal, negative affect, self-focus)?
- 2) What kind of stress affects state interoceptive accuracy (e.g., social threat, physical threat)?
- 3) How general/specific is the effect of stress on state interoceptive accuracy? Does it extend to exteroceptive somatosensory perception accuracy or is it restricted to interoceptive bodily signal processing?

Chapter 2: Stability of Interoceptive Accuracy During Public Speaking Anticipation¹

2.1 Introduction

Interoceptive information constitutes a basic building block of emotion (Barrett & Bliss-Moreau, 2009; Barrett & Lindquist, 2008) and interoceptive perception is central to emotional experience (Damasio, 2010). Several lines of investigation, including behavioural and neuroimaging studies, suggest that emotional experience is mediated by the accuracy with which interoceptive bodily signals, involved in emotion responses, are perceived (Critchley et al., 2004; Gray et al., 2012; Katkin et al., 2001; Pollatos, Herbert et al., 2007; e.g., Pollatos, Gramann, & Schandry, 2007). Not surprisingly, emotional experiences engage the insula (e.g., Zaki et al., 2012)—the central brain region associated with interoception (e.g., Critchley et al., 2004). Moreover, interoceptive accuracy has been found to directly relate to the perceived intensity of emotional experience, as measured with subjective ratings of arousal (e.g., Barrett et al., 2004; Dunn et al., 2010; Pollatos, Traut-Mattausch et al., 2007). Interoceptive accuracy has been observed to positively correlate with anxiety (Schandry, 1981; Critchley et al., 2004; Pollatos, Herbert et al., 2007), anxiety sensitivity (i.e., fear of anxietyrelated autonomic arousal (Reiss, 1991)) (Stewart et al., 2001) and emotional lability (i.e., emotional instability) (Schandry, 1981). Because interoceptive accuracy has been directly associated with anxiety and because interoceptive signals are inherently linked to the physiological experience of anxiety (e.g., McLeod, Hoehn-Saric, & Stefan, 1986), it might be the case that interoceptive accuracy increases when an individual experiences heightened state anxiety via heightened self-focus. Self-focus or "objective self-awareness" (Duval & Wicklund, 1972) involves the individual taking an observer's perspective and considering one's self an object of own and others' thoughts. According to Silvia

¹ Experiment 1 has been published as Durlik, C., Brown, G., & Tsakiris, M. (2014). Enhanced interoceptive awareness during anticipation of public speaking is associated with fear of negative evaluation. *Cognition & Emotion*, 28(3), 530-540. doi: 10.1080/02699931.2013.832654

and Gendolla's (2001) "perceptual accuracy hypothesis", focusing the attention on one's self increases the accuracy of self-related judgments, however, further research is needed to ascertain this hypothesis. Until now, the link between body awareness and self-focus has been only studied using self-report measures (Mehling et al., 2009) and the relationship between interoceptive accuracy and self-focus has not been examined, with the exception of Ainley et al. (2012?), who found that increasing self-focus via mirror self-observation increases interoceptive accuracy. Consequently, further investigation of the relationship between selffocus and interoceptive accuracy is required. The hypothesis that interoceptive accuracy would increase due to anticipatory anxiety is supported by evidence indicating that anxiety is associated with increased self-focus (Mor & Winquist, 2002), whereas heightened self-focus has been found to increase state interoceptive accuracy (Ainley et al., 2011, 2012). As state anxiety has been effectively elicited in experimental settings using public speaking anticipation manipulations (e.g., Hinrichsen & Clark, 2003; Moscovitch, Suvak, & Hofmann, 2010; Stevens et al., 2011), Experiment 1 investigated the stability of interoceptive accuracy under emotional influence by examining the effect of public speaking anticipation on heartbeat tracking accuracy.

One study to date has examined the effect of public speaking anticipation on heartbeat tracking accuracy. Stevens et al. (2011) measured heartbeat tracking accuracy before and during public speaking anticipation in individuals high and low in social anxiety. Contrary to their predictions, Stevens and colleagues failed to find significant differences in heartbeat tracking accuracy from baseline to anticipation in either group; although they did observe an increase in accuracy from baseline to the first heartbeat tracking trial of the anticipation phase in both groups. Because this result was not observed when analysing all heartbeat tracking trials of the anticipation phase and because a control condition was not used in the study, it is not clear whether the enhancement in heartbeat tracking accuracy observed by Stevens et al. in the first heartbeat tracking trial of the anticipation phase represented a statistical artefact or a meaningful difference reflecting a very short-lived change in state interoceptive accuracy brought about by the manipulation. Importantly, because the focus of Stevens et al.'s

investigation was solely on individuals high and low in social anxiety—those who either feared negative evaluation significantly more, or significantly less than an average individual—the results cannot be generalised to the normal population of individuals falling on a continuum with regard to their social fears.

Stevens et al. investigated the effect of public speaking anticipation on heartbeat tracking accuracy without taking into consideration individual differences in baseline heartbeat tracking accuracy, leaving unexamined the possibility of heartbeat tracking accuracy increasing during speech anticipation only in participants with low baseline heartbeat tracking accuracy and not in participants with high baseline heartbeat tracking accuracy. A moderating effect of baseline heartbeat tracking accuracy on state changes in heartbeat tracking accuracy was observed by Ainley and colleagues (2012). Ainley and colleagues investigated state changes in heartbeat tracking accuracy due to enhanced selffocus, as manipulated by mirror self-observation, observing that only individuals with low baseline heartbeat perception accuracy showed a change (an increase) in heartbeat perception accuracy during mirror self-observation. Tsakiris et al. (2011) suggest that individuals with high interoceptive accuracy might show lower malleability of body representation than individuals with lower interoceptive accuracy. This lower malleability of body representation might, in turn, result in individuals with high interoceptive accuracy being less susceptible to state changes in their perception of bodily signals.

In line with neuroimagining evidence of increased insula activation during anticipation of emotionally aversive stimuli (Simmons, Matthews, Stein, & Paulus, 2004; Simmons et al., 2011; Simmons, Strigo, Matthews, Paulus, & Stein, 2006) and findings of Stevens et al., indicating heightened heartbeat tracking accuracy in the first trial of speech anticipation, it was hypothesised that speech anticipation would enhance state heartbeat tracking accuracy. More specifically, it was predicted that participants in the experimental group only would show higher accuracy on the heartbeat tracking task during speech anticipation, as compared to baseline and that this enhancement would be stronger for participants with higher fear of negative evaluation, who are likely to be more affected by the speech anticipation manipulation. In line with findings of Ainley et al. (2012), it was

further hypothesised that the speech anticipation manipulation would enhance heartbeat tracking accuracy more, if not only, in individuals with low baseline heartbeat tracking accuracy. The heartbeat tracking task was performed in the absence of mirrors, video-cameras and any other tools that may increase selffocus and consequently enhance heartbeat tracking accuracy (e.g., Ainley et al., 2012), in order to ensure any effect on heartbeat tracking accuracy observed would be due to the speech anticipation manipulation and not due to otherwise increased self-focus. A between-subjects design was employed to ensure that any observed change in heartbeat tracking accuracy would be due to the experimental manipulation and not due to another factor such as training. Self-report measures of trait and state anxiety, anxiety sensitivity and depression were administered before the experiment to ensure that the experimental and control groups did not differ on variables that could potentially affect their interoceptive accuracy. As Werner, Duschek et al. (2009a) observed that individuals with higher heartbeat tracking accuracy experienced less anxiety before and after a public speaking challenge, Experiment 1 examined for potential differences in anxiety evoked by the public speaking manipulation based on individuals' level of baseline heartbeat tracking accuracy. Lastly, as sex differences have been observed in interoceptive accuracy, with males being more accurate than females (Cameron, 2001), sex was included as a between-subjects factor in the analyses of heartbeat tracking accuracy.

2.2 Methods

2.2.1 Experimental Design

The study employed a mixed design with a within-subjects factor of Time (baseline, anticipation) and between-subjects factor of Condition (experimental, control). Subjects were randomly assigned to one of two conditions. In the experimental condition, participants prepared a short speech about the pros and cons of animal use in research, and anticipated presenting the speech it in front of a small audience. In the control condition, participants prepared by reading a list of pros and cons of animal use in research (see Appendix 7.1), and anticipated sharing their general impressions of the arguments they had read. The dependent

measures of heartbeat tracking accuracy (HTA) and mood were taken at baseline and during the anticipation phase (following the preparation phase) in each condition.

2.2.2 Measures

2.2.2.1 Self-Reported Measures

Participants provided demographic information, and completed a range of self-reported questionnaires the State-Trait Inventory of Cognitive and Somatic Anxiety Scale (STICSA; Ree, French, MacLeod, & Locke, 2008), Anxiety Sensitivity Index-3 (ASI-3; Taylor et al., 2007). Brief Fear of Negative Evaluation-Straightforward Items (BFNE-S; Rodebaugh et al., 2004), Liebowitz Social Anxiety Scale (LSAS; Liebowitz, 1987), and Depression Anxiety and Stress Scale-Depression subscale (DASS-Depression; Lovibond & Lovibond, 1995). Participants reported their momentary anxiety and calmness levels on a Visual Analogue Scale (VAS) ranging from 0 (not at all anxious, not at all calm) to 100 (extremely anxious, extremely calm).

2.2.2.2 Behavioural Measures: Heartbeat Tracking Accuracy

HTA was assessed at baseline and during the period of anticipation via heartbeat perception, using the Mental Tracking Method (Schandry, 1981). Participants were instructed to mentally count their heartbeats from the moment they received an audiovisual computer-generated cue: "Go!" until they received an otherwise identical cue: "Stop!" and then to type the number of heartbeats they had counted into the computer program. The heartbeat counting task consisted of a four-trial block: 25-second, 35-second, 45-second, and 100-second trials, presented in a random order. The single four-trial block was administered at baseline, and during anticipation. In the baseline HTA assessment, a 10-second training trial was also administered prior to the four trials constituting the heartbeat counting task in order to familiarise participants with the task. Heartbeat signals were acquired with a piezo-electric pulse transducer, fitted to the participant's left index finger and connected to a physiological data unit (26T PowerLab, AD Instruments), sampling at 1 kHz, which recorded the derived

electrical signal onto a second PC running LabChart 6 software (AD Instruments). Throughout the assessment, participants were not permitted to take their pulse, nor was information regarding the length of individual trials or feedback regarding participants' performance given. The task was programmed using Presentation software (Neurobehavioural Systems: www.neurobs.com).

2.2.3 Procedure

Prior to in-lab participation, participants provided online their demographic information, STICSA-Trait, BFNE-S, LSAS, and DASS-Depression. Before the questionnaire commenced, participants were given basic information about the study that was essential to provide informed consent to participate, yet that did not disclose any details that could affect the effectiveness of the main manipulation itself. All participants were informed they will have to "engage in a brief behavioural task" once in-lab, but they will be free to withdraw at any point in time, if they wish to, without penalty. Further, participants were informed that they did not have to answer any questions that they felt uncomfortable with, and that the information they would provide will be kept completely confidential and anonymous. Participants in both conditions were given the exact same information, and instructions.

Upon arrival to the lab, participants were given a hard copy of the information sheet, and have signed the informed consent form. In-lab, each participant completed STICSA-State, and ASI followed by the first HTA assessment, counterbalanced with Time 1 VAS mood ratings. Then, by way of a distracter, participants answered five questions about Britain in the context of European Union, afterwards providing Time 2 VAS mood ratings (aimed at verifying that no change took place in mood prior to the main manipulation). Up until this point, the all details of the procedure were exactly the same for participants in both experimental and control conditions. Subsequently, in the experimental group, the experimenter told participants that they would be given three minutes to prepare a 10-minute speech on the pros and cons of animal use in research, to present in front of a small audience and videocamera in a nearby room right after completion of remaining computer-administered tasks. Participants

were then given scrap paper and a pen in order to prepare the speech. Instead, in the control group, the experimenter gave participants a list of arguments for and against the use of animals in research, and instructed them to read the arguments for three minutes, without worrying about getting through all of the points (see Appendix for a list of arguments that was provided to the control group). The control participants were told that they would share their general impressions of the arguments with the experimenter, after having completed the remaining computer-administered tasks. After the manipulation, each participant was asked to perform one more HTA assessment, counterbalanced with Time 3 VAS mood ratings. It is important to note that the two HTA assessments were administered in a counterbalanced order with the VAS mood ratings in order to account for possible short-lived effect of the manipulation on HTA, at the same time ensuring that the measure of mood change due to the manipulation was not confounded by the administration of the HTA task before the VAS ratings. See Figure 2-1 for a graphical depiction of the procedure. After the experiment, each participant was informed that the study had come to an end, and the deception was explained to each participant. Participants were then asked to reiterate their consent for their data to be retained and used in the study.

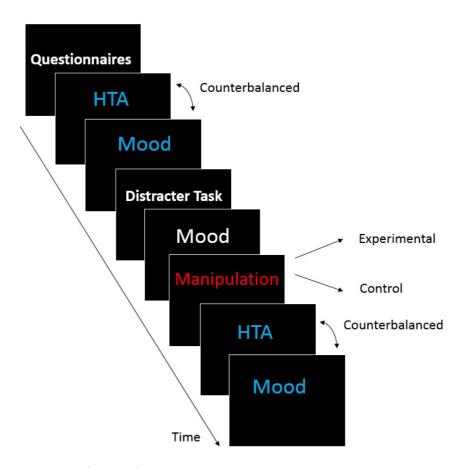


Figure 2-1. Experimental procedure.

2.2.4 Data Analysis

2.2.4.1 Heartbeat Tracking Accuracy Scores

Heartbeat tracking accuracy scores were calculated according to the following formula:

 $1/4 \Sigma$ (1 - (| actual heartbeats – reported heartbeats |) / actual heartbeats).

The resulting scores varied between 0 and 1, with higher scores indicating better heartbeat tracking accuracy, reflecting a smaller difference between perceived and actual heartbeats. Individuals were categorized as high or low in HTA using a median split on the baseline HTA score (Mdn = .637). The sample consisted of 28 low HTA individuals (mean HTA = .515, SD = .089), and 28 high HTA individuals (mean HTA = .754, SD = .101). HTA scores were normally distributed, as indicated by a Shapiro-Wilk test of normality (W = .987, p = .816).

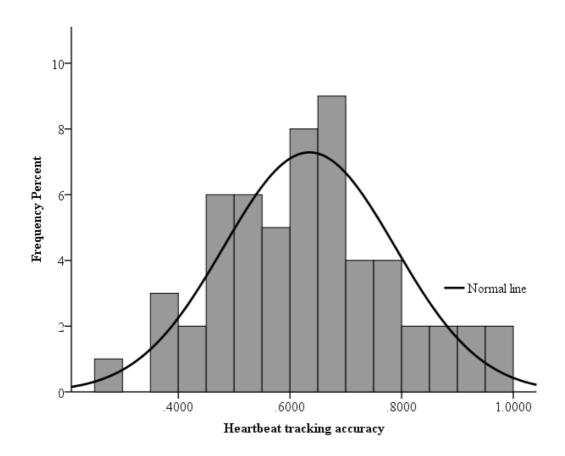


Figure 2-2. Frequency distribution of HTA baseline scores in Experiment 1.

2.2.4.2 Average Heart Rate

Average heart rate was calculated according to the following formula:

 $1/4~\Sigma$ ((actual heartbeats / length of time interval in seconds) * 60 seconds)

2.2.4.3 Self-Reported Data

Self-reported anxiety and calmness VAS scores were stable between Time 1 and 2 and so were averaged, yielding baseline anxiety score and baseline calmness score. VAS scores at Time 3 were used as the post-manipulation scores. Baseline and post-manipulation anxiety and (reverse-scored) calmness scores were averaged into overall baseline and post-manipulation mood scores, with higher values indicating a more anxious mood. Difference scores for the

dependent variables were calculated by subtracting the baseline scores for HTA, heart rate (HR), and self-rated anxious mood from the post-manipulation scores for the same variables. Where the assumption of compound symmetry was violated, degrees of freedom were adjusted using the Greenhouse-Geisser correction. Also, where variables were found to be non-normally distributed, transformations were used to normalize the data.

2.2.4.4 Data Analysis Overview

Effects of the experimental manipulation on the dependent variables were compared using mixed analyses of variance (ANOVAs) with Time (baseline and anticipation) as the within-subject factor and Condition (experimental vs. control), Counterbalancing Order (HTA before VAS vs. HTA after VAS), HTA group (low, high) and Sex (male, female) as between-subject factors. Then, hierarchical multiple regression analyses were conducted to test for predictors of change in dependent variables and for potential moderation of the observed effects.

2.2.5 Participants

Sixty-two (42 females; mean age = 20.35, SD = 2.34) undergraduate students took part in the experiment voluntarily, provided informed consent to participate in this study, and in compensation, received first year psychology course credit or entered a cash prize draw. The study was approved by the Departmental Ethics Committee at Royal Holloway, University of London. Participants were randomly assigned to either the experimental (N = 32) or control condition (N = 30).

2.2.<u>5.1 Outliers</u>

Outliers were excluded if the z-score for the dependent variable (change in: HTA, HR, and self-rated anxious mood) by condition was $> \pm 2.58$. Six outliers were excluded on this basis, leaving a final sample of 28 in the experimental condition (8 males, and 20 females) and 28 in the control condition (10 males and 18 females).

2.2.5.2 Sample Characteristics Between Groups

The groups did not differ significantly on variables such as age, gender, body mass index, baseline HTA, HR, and self-report measures of anxiety and depression (see Table 2-1).

Table 2-1. Sample characteristics: means (with standard deviations) and t-test statistics (with degrees of freedom) for group comparisons.

	Experimental	Control		
	(N=28)	(N=28)	<i>t</i> (df)*	
	Mean (SD)	Mean (SD)		
Age	20.04 (2.07)	20.64 (2.58)	-0.958 (53)	
BMI ^a	21.51 (2.89)	22.73 (2.93)	-1.505 (50)	
HR baseline	79.29 (10.35)	79.10 (13.89)	059 (54)	
HTA baseline	0.62 (0.15)	0.65 (0.15)	-0.883 (54)	
Mood baseline	31.43 (16.73)	35.44 (16.68)	0.898 (54)	
BFNE-S ^b	11.36 (8.12)	12.93 (7.04)	0.774 (54)	
DASS-D ^c	3.86 (3.69)	4.64 (3.86)	0.779 (54)	
ASI ^d	16.52 (10.15)	21.96 (12.00)	-1.814 (53)	
LSAS ^e	35.79 (19.19)	42.07 (23.39)	-1.099 (54)	
STICSA-S ^f	33.59 (8.41)	38.96 (11.62)	-1.970 (49.22)	
STICSA-T ^g	36.61 (8.05)	36.50 (10.93)	0.042 (54)	

^{*}None of the t-test statistics were significant at $\alpha = .05$ level (2-tailed)

^a Body Mass Index; ^b Brief Fear of Negative Evaluation-Straightforward Items; ^c Depression Anxiety and Stress Scale-Depression subscale; ^d Anxiety Sensitivity Index; ^e Liebowitz Social Anxiety Scale; ^f State-Trait Inventory of Cognitive and

Somatic Anxiety Scale- State subscale; f State-Trait Inventory of Cognitive and Somatic Anxiety Scale-Trait subscale

2.3 Results

2.3.1 Self-Reported Anxious Mood

As average self-rated anxious mood was normally distributed both preand post-manipulation (W = .981, p = .504; W = .977, p = .368, respectively) and all of the assumptions for normality tests were met, average self-rated anxious mood was analysed in a 2 x 2 x 2 x 2 x 2 mixed ANOVA with Time (baseline and anticipation) as the within-subjects factor, and Condition (experimental or control), Counterbalancing order (HTA task before VAS versus HTA task after VAS), HTA group (lower HTA, higher HTA) and Sex (male, female) as between-subjects factors. As there were no main effects of Counterbalancing order (F (1, 41) < .000, p = .991), of HTA group (F (1, 41) = 1.031, p = .316), or of Sex (F (1, 41) = .320, p = .575) on mood, and no interaction effects of Counterbalancing order and Condition (F (1, 41) = .951, p = .335), of HTA group and Condition (F (1, 41) = .106, p = .747), or of Sex and Condition (F (1, 41) = .054, p = .818) on mood, the between-subjects factors of Counterbalancing order, HTA group, and Sex were removed from the analysis.

The 2 x 2 ANOVA with the within-subjects factor of Time (baseline and anticipation) and between-subjects factor of Condition (experimental or control), revealed no main effect of Condition ($F(1, 54) = 3.321, p = .074, \eta_p^2 = .058$) on mood. There was a main effect of Time ($F(1, 54) = 27.827, p < .001, \eta_p^2 = .340$) and an interaction effect of Condition and Time ($F(1, 54) = 54.145, p < .001, \eta_p^2 = .501$) on mood. Pairwise t-tests revealed a significant increase in self-rated anxious mood from baseline to speech anticipation found only in the experimental (t(27) = -1.854, p < .001, Cohen's d = -.714) but not in the control condition (t(27) = 1.647, p = .111), confirming that the manipulation was successful in inducing anxiety. See Figure 2-3 for a graphical depiction of these results and Table 2-2 for anxious mood means and standard deviations at baseline and during anticipation in the two groups.

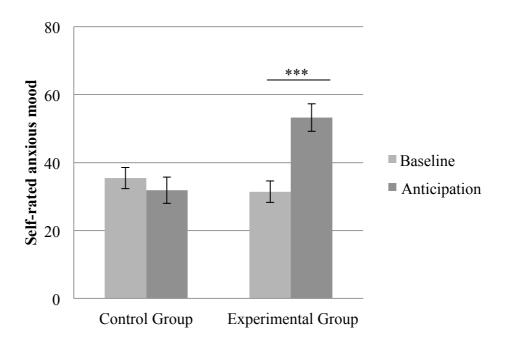


Figure 2-3. Self-rated anxious mood at baseline and during anticipation in control and experimental groups. Error bars represent standard errors of mean. Note: ***: p < .001.

In order to investigate predictors of change in mood in the experimental group, a moderated regression model (see Table 2-2) predicted mood during anticipation from HTA at baseline, Fear of negative evaluation and their product (along with mood at baseline as a covariate). The overall model predicted 65% of the variance in anxious mood during anticipation (F(4, 23) = 10.676, p < .0001, $R^2 = .6500$). Multicollinearity diagnostics were assessed and were within an acceptable range. In the first step, baseline mood, Fear of negative evaluation, and baseline HTA values were included. These variables accounted for a significant amount of variance in mood scores during anticipation ($R^2 = .650$, F(3, 24) =14.840, p < .001). Fear of negative evaluation was a significant predictor of anxious mood scores during anticipation ($\beta = .311$, t (27) = 2.345, p = .028). Baseline HTA was not a significant predictor of anxious mood at anticipation (β = .182, t(27) = 1.359, p = .187). The interaction term of Fear of negative evaluation and baseline HTA was entered in the second step to test for moderation, but did not significantly add to the amount of variance accounted for $(\Delta R^2 < .001, \Delta F(1,$ 23) = .015, p = .905, $\beta = -.019$) indicating that the association between Fear of negative evaluation and anxious mood during the anticipation in the experimental condition was not dependent on baseline HTA.

Table 2-2. Hierarchical multiple regression analysis predicting anxious mood during anticipation in the experimental group from Fear of Negative Evaluation, baseline HTA and interaction of Fear of Negative Evaluation and baseline HTA, while controlling for anxious mood at baseline.

		ΔR^2	β	Correlations		
Predictor				Zero- order	Partial	Part
Step 1		.650***				
	Mood 1		.738***	.752	.771	.717
	BFNE-S		.311*	.365	.432	.283
	HTA 1		.182	102	.267	.164
Step 2		<.001				
	BFNE-S * HTA 1		121	253	025	015
Total R ²		.650***				

Note: N=28. Mood 1: anxious mood at baseline, HTA 1: baseline heartbeat perception accuracy, BFNE-S: Fear of negative evaluation; $^{\dagger}p<.1,^{*}p<.05,^{***}p<.001$.

2.3.2 Heartbeat Tracking Accuracy

As HTA scores were normally distributed both pre- and post-manipulation (W = .987, p = .816; W = .974, p = .265, respectively) and all of the assumptions for normality tests were met, they were analysed in a 2 x 2 x 2 x 2 x 2 x 2 ANOVA with the within-subjects factor of Time (baseline, anticipation) and between-

subjects factors of Condition (experimental or control), Counterbalancing order (HTA before VAS versus HTA after VAS), HTA group (lower baseline HTA, higher baseline HTA) and Sex (male, female). As there was no main effect of Counterbalancing order on HTA (F(1, 41) = .183, p = .671), and no interaction of Counterbalancing order and Condition on HTA (F(1, 41) = .812, p = .373), as well as no main effect of Sex on HTA (F(1, 41) = .364, p = .550) and no interaction effect of Sex and Condition on HTA (F(1, 41) = .879, p = .354) the between-subjects factors of Counterbalancing order and Sex were removed from the analysis. The resulting 2 x 2 x 2 ANOVA consisted of the within-subjects factor of Time (baseline, anticipation) and between-subjects factors of Condition (experimental or control) and HTA group (lower baseline HTA, higher baseline HTA). This analysis revealed a main effect of Time on HTA (F(1, 52) = 4.496, p)= .039, η_p^2 = .080), with individuals increasing in HTA from baseline to anticipation, and interaction effect of Time and Condition on HTA (F(1, 52))9.9119, p = .004, $\eta_p^2 = .149$). There was no interaction effect of Baseline HTA group with Time and Condition on HTA (F(1, 52) = 1.939, p = .170). Pairwise ttests revealed that HTA changed significantly from baseline to anticipation only in the experimental group (t(27) = 4.536, p < .001, Cohen's d = -0.856) and not in the control group (t(27) = .461, p = .649). See Figure 2-4 for a graphical depiction of these results and Table 2-2 for HTA means and standard deviations at baseline and during anticipation in the two groups.

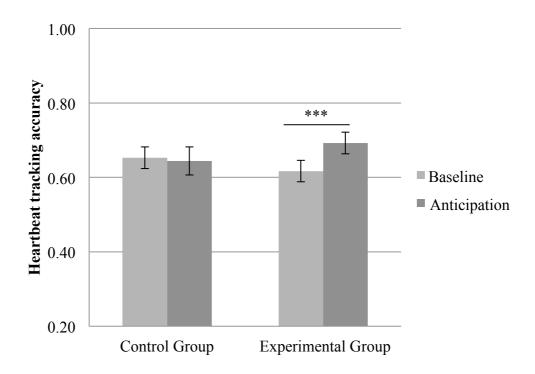


Figure 2-4. Heartbeat tracking accuracy at baseline and during anticipation in control and experimental groups. Error bars represent standard errors of mean. Note: ***: p < .001.

To ensure the increase in HTA from baseline to anticipation in the experimental, and not control, group was not due to change in heart rate (HR), HR was investigated in a 2 x 2 ANOVA with Time (baseline and anticipation) as the within-subjects factor and Condition (experimental or control) as the between-subjects factor. There was no main effect of Time (F (1, 54) = .892, p = .349) on HR, nor interaction effect between the Condition and Time (F (1, 54) = .990, p = .326) on HR. See Table 2-3 for HR means and standard deviations at baseline and during anticipation in the two groups.

Table 2-3. Changes in dependent measures from baseline to anticipation in experimental (N = 28) and control (N = 28) conditions

	Experi	mental	Control		
	Baseline	Anticipation	Baseline	Anticipation	
HR	79.29 (10.35)	80.13 (9.34)	79.10 (13.89)	79.07 (13.16)	
НТА	0.62 (0.15)	0.69 (.15)	0.65 (0.15)	.64 (.15)	
Anxious Mood	31.43 (16.73)	53.25 (21.47)	35.44 (16.68)	31.84 (20.61)	

Potential moderation of the effect of Condition on HTA during anticipation by Fear of negative evaluation was investigated using a hierarchical multiple regression analysis. The model (see Table 2-4) predicted HTA during anticipation from Condition, Fear of negative evaluation and their product (along with HTA at baseline as a covariate). The overall model was significant and predicted 73.8% of the variance in HTA during anticipation (F(4, 51) = 35.844, p) $< .0001, R^2 = .7376$). Multicollinearity diagnostics were assessed and were within an acceptable range. In the first step, baseline HTA, Condition, and Fear of negative evaluation values were included. These variables accounted for a significant amount of variance in anticipation HTA scores $(R^2 = .736, F(3, 52) =$ 48.268, p < .001). Fear of negative evaluation marginally predicted HTA scores during anticipation ($\beta = .311$, t (54) = 1.896, p = .064). The interaction term of Condition and Fear of negative evaluation was entered in the second step to test for moderation, but did not significantly add to the amount of variance accounted for $(\Delta R^2 = .0018, \Delta F (1, 51) = .359, p = .552, \beta = .044)$ indicating that the effect of Condition on HTA during anticipation was not dependent on level of Fear of negative evaluation.

Table 2-4. Hierarchical multiple regression analysis predicting HTA during anticipation from Condition, Fear of negative evaluation and interaction of Condition and Fear of negative evaluation, while controlling for baseline HTA.

		ΔR^2	β	Correlations		
Predictor				Zero- order	Partial	Part
Step 1		.736***				
	HTA 1		.866***	.814	.855	.847
	Condition		.255***	.137	.439	.251
	BFNE-S		.138 [†]	027	.254	.135
Step 2		.002				
	Condition * BFNE-S		.044	152	.084	.043
Total R ²		.738***				

Note: N = 56. HTA 1: baseline heartbeat tracking accuracy, BFNE-S: Fear of negative evaluation; $^{\dagger}p < .1$, $^{***}p < .001$.

2.4 Discussion

The current study investigated changes in heartbeat tracking accuracy in response to an anxiety-provoking situation, using a public speaking anticipation paradigm. As hypothesised, participants in the experimental condition who completed a second heartbeat tracking task while anticipating giving a speech were significantly more accurate during anticipation than individuals in the control condition. This result supports the prediction that a state anxiety manipulation would bring about heightened cardiac interoceptive accuracy. Even though heart rate did not significantly differ from baseline to anticipation, it can be assumed the manipulation did not fail, as indicated by self-rated mood of

participants in the experimental condition. Moreover, there is evidence from research showing the possibility of a lack of correspondence between objective and subjective measures of arousal (Miers, Blote, Sumter, Kallen, & Westenberg, 2011) or anxiety (Bacow, May, Choate-Summers, Pincus, & Mattis, 2010). Perhaps individuals in the current study were more anxious cognitively, as indicated by self-rated mood, rather than physiologically, as reflected by lack of heart rate response. Since the present manipulation had an effect on self-rated anxious mood, and on the dependent variable of heartbeat tracking accuracy, the lack of change in heart rate was not assumed to be an index of manipulation failure. The increase in anxious mood and increase in heartbeat tracking accuracy in the experimental condition were both positively correlated with the fear of negative evaluation scores. There were no moderating effects of sex and baseline heartbeat tracking accuracy present in the data. Fear of negative evaluation did not moderate the effect of condition on heartbeat tracking accuracy and individuals with differing levels of fear of negative evaluation experienced change in heartbeat tracking accuracy to the same degree as the result of the experimental manipulation. Fear of negative evaluation predicted self-rated anxiety during speech anticipation in individuals of differing baseline heartbeat tracking accuracy.

Overall, the results of the current study indicate that cardiac interoceptive accuracy, although a stable individual difference variable is subject to state-dependent fluctuations in response to emotional states, such as anticipatory anxiety. These findings extend on the results of the study by Stevens et al. (2011), which found an increase in heartbeat tracking accuracy in the first trial of speech anticipation. Unlike in the study by Stevens et al., in the present study a significant difference in heartbeat tracking accuracy was observed when all trials of the anticipation phase were analysed. This discrepancy might perhaps be due to differences in sample characteristics of Stevens et al. and the current study. While Stevens et al. sampled only two groups: high social anxiety (high fear of negative evaluation) and low social anxiety (low fear of negative evaluation), the current study sampled a non-anxious population (as indicated by LSAS scores) falling on a continuum of fear of negative evaluation. Therefore, it is possible that the very

high in anxiety and very low in anxiety participants in the study by Stevens et al. were, respectively, more and less affected by the manipulation than an average individual. Secondly, the speech manipulation procedure was slightly different in the current study. Participants in Stevens et al. were asked to rate how they thought they would appear during the speech in order to elicit anxiety, while participants in the present study were not asked to provide such ratings, instead just being given three minutes to prepare the content of the speech prior to the second heartbeat counting task. Further, unlike the study by Stevens et al., in the current study the order of the post-manipulation heartbeat tracking task and momentary mood ratings was counterbalanced in order to account for the potentially short-lived effect of enhanced cardiac interoceptive accuracy immediately after the manipulation, as reported by Antony et al. (1995) in the context of interoception and physical exercise, and as suggested by Stevens et al. (2011) in their interpretation of their results.

Even though no moderation of the manipulation effect on heartbeat tracking accuracy by fear of negative evaluation was observed in the present study, the results of the current study suggest that the higher the fear of negative evaluation, the higher heartbeat tracking accuracy during speech anticipation. This would explain why Stevens et al. failed to find a significant difference in heartbeat tracking accuracy from baseline to anticipation in the low social anxiety group with low fear of negative evaluation group (as a smaller increase in heartbeat tracking accuracy would be expected in these participants). Further, as the present study sampled non-anxious individuals, the relationship that was found between fear of negative evaluation and heartbeat tracking accuracy change might not hold for individuals on the upper extreme of fear of negative evaluation (the other group investigated by Stevens et al.), for whom perhaps it might be more difficult to deploy required attentional resources to the heartbeat counting task in the stressful situation of speech anticipation, or who, alternatively, might be already quite high in cardiac interoceptive accuracy (as suggested by Stevens et al., and the literature on cardiac interoceptive accuracy and anxiety (see Domschke et al., 2010 for a review)), and thus might face a ceiling effect with regards to enhancement in state cardiac interoceptive accuracy (as suggested by results of Ainley et al., 2012). Overall, it is important to note that the results of the present study may not generalise to the clinical population of individuals with social anxiety.

Taken together, the results of the current study show that the speech anticipation manipulation brought about heightened cardiac interoceptive accuracy and participants became more accurate at tracking their heartbeats when in the anxiety provoking situation. The fact that higher fear of negative evaluation was associated with a larger increase in heartbeat tracking accuracy in the anxiety-provoking situation could be explained by a number of factors, one being increased self-focused attention, as suggested by cognitive theories of social anxiety (Clark & Wells, 1995). The present speech anticipation manipulation likely increased self-focused attention, which then, independently, increased anxiety (see Jakymin & Harris, 2012 for review) and heartbeat tracking accuracy (as suggested by Ainley et al., 2012) in the individuals anticipating the speech, with the degree of the increase in self-focused attention being directly related to the degree of fear of negative evaluation.

At first glance, the relationship between fear of negative evaluation and heartbeat tracking accuracy during speech anticipation provides support for cognitive models of social anxiety (e.g. Clark & Wells, 1995), which suggest that higher fear of negative evaluation is associated with increased self-focus when entering a social situation. These theories imply that better detection of heartbeats might lead to their misinterpretation as symptoms of anxiety and arousal, visible to external observers, consequently, bringing about an increase in anxiety (e.g. Wild et al., 2008). However, the results of the current study did not indicate a significant association between enhancement in heartbeat tracking accuracy and increase in anxious mood, contradicting the above model. Moreover, the fact that heartbeat tracking accuracy increased in all participants, including those with low fear of negative evaluation suggests that the observed enhancement in heartbeat tracking accuracy might be reflective of a general strategy of the organism to deal with uncertainty (such as experience of anxiety). Indeed, the somatic marker hypothesis (Damasio, 1994, 1999) proposes that more accurate perception of

somatic signals under uncertainty might enable more efficient information processing, in this way guiding emotional, behavioural and cognitive processes, optimising the individual's responses in effectively dealing with the faced situation. For example, increased interoceptive accuracy during speech anticipation might help the individual downregulate anxious mood when later giving the speech (Werner et al., 2009). It should be kept in mind though that the current design does not allow conclusions to be drawn pertaining to whether the observed enhancement in heartbeat tracking accuracy would indeed be associated with altered information processing and cognitive and behavioural responses in the anxiety-provoking situation.

To conclude, the evidence from Experiment 1 indicates that individual level of cardiac interoceptive accuracy can change as a function of the emotional state of an individual, increasing during the experience of social anxiety, perhaps by means of heightened self-focused attention. However, as the current study focused only on anticipatory social anxiety, it remains to be ascertained how specific and/or how general this effect is. Even though fear of negative evaluation scores were directly associated with interoceptive accuracy scores during anticipation (suggesting that interoceptive accuracy increased due to higher social anxiety in the situation), it is a possibility that interoceptive accuracy is increased by the experience of anxiety, in general, rather than by the experience of social anxiety, specifically. The experiments to follow manipulate emotional experiences other than anticipatory social anxiety and also measure exteroceptive somatosensory perception accuracy, consequently, exploring whether emotions other than anticipatory social anxiety can also affect cardiac interoceptive accuracy, and whether the experience of anxiety (and potentially other emotions) can also influence modes of body perception other than cardiac interoceptive signals. First, testing the hypothesis that self-focused attention in a social context increases interoceptive accuracy, Experiment 2 investigated the effect of social self-focus, without an anxiety manipulation, on cardiac interoceptive accuracy, as well as on tactile body perception.

Chapter 3: Stability of Interoceptive and Exteroceptive Somatosensory Perception Accuracy During Heightened Social Self-Focus²

3.1 Introduction

The results of Experiment 1 suggest that the experience of social anxiety increases cardiac interoceptive accuracy. Specifically, in Experiment 1, heartbeat tracking accuracy increased from baseline to anticipation in individuals who were anticipating giving a public speech. The enhancement in heartbeat tracking accuracy in the experimental group was directly associated with fear of negative evaluation. Heartbeat tracking accuracy might increase in situations that evoke social anxiety due to increased social self-focus in these contexts. This hypothesis is in line with cognitive theories of anxiety (Clark & Wells, 1995), which suggest that higher fear of negative evaluation is associated with increased self-focus in social situations. Heartbeat tracking accuracy has been found to increase due to self-focus evoked by mirror self-observation (Ainley et al., 2012; Weisz et al., 1988), however, the effect self-focus that is more social in nature (as elicited by public speaking anticipation) on heartbeat tracking accuracy has not been examined.

Distinct modes of self-focus enhance aspects of the self-relevant to the given focus-mode—for example, mirrors have been found to elicit private self-focus, by directing individuals' attention to inner aspects of the self, whereas video cameras have been found to elicit social self-focus, by drawing individuals' attention to the external, observable to others aspects of the self (Carver & Scheier, 1981; Davies, 2005). Private self-focus has been found to enhance cardiac interoceptive accuracy, as reflected by higher heartbeat tracking accuracy

² Experiment 2 has been published as Durlik, C., Cardini, F., & Tsakiris, M. (2014). Being watched: The effect of social self-focus on interoceptive and exteroceptive somatosensory perception. *Consciousness & Cognition*, 25, 42-50. doi: 10.1016/j.concog.2014.01.010

when attending to pictures of self, self-referential words (Ainley et al., 2013) or to the reflection of one's self in a mirror (Ainley et al., 2012; Weisz et al., 1988). Baltazar et al. (2014) found that social self-focus (manipulated using a photograph of a face with a direct gaze) increased the correspondence between skin conductance responses and individuals' ratings of the intensity of their emotional responses to affective visual stimuli. It might be the case that in the study by Baltazar et al. social self-focus increased correspondence between objective and subjective measures of emotional arousal by increasing interoceptive accuracy. However, the effect of social self-focus on interoceptive accuracy remains to be empirically investigated. As there is evidence that private self-focus and social self-focus might impact body perception accuracy in a different manner than private self-focus.

Interoceptive and exteroceptive signals are integrated to jointly shape body awareness and perception (Neisser, 1993). Combined interoceptive-exteroceptive somatosensory signals can significantly alter ownership of a virtual hand (Suzuki et al., 2013), as well as awareness of one's body in space (Adler et al., 2014; Aspell et al., 2013). Because online integration of sensory signals across the interoceptive and exteroceptive modalities is a dynamic process that is strongly modulated by attention (e.g., Talsma & Woldorff, 2005), state-dependent fluctuations in both interoceptive and exteroceptive somatosensory perception as a function of various modes of attention to the self could be expected. The effect of bodily self-focus on exteroceptive somatosensory perception was examined by Mirams et al. (2012), who found that interoceptive attention to the body (as opposed to exteroceptive bodily attention) was followed by a higher propensity to report feeling a tactile stimulus regardless of whether it has occurred or not. In a follow-up study, Mirams, Poliakoff, Brown and Lloyd (2013) observed that bodily self-focus in the form of body-scan meditation practice (in which participants were trained to attend to selective areas of the body, one at a time, while taking the time to notice any somatic sensations in a non-evaluative manner) increased sensitivity and decreased false alarm rates on a tactile perception task. Mirams and colleagues (2013) concluded that bodily self-focus

might have differential effects on exteroceptive somatosensory processing depending on the mode of attention to the body.

Despite several studies having investigated the effects of various modes of self-focus on somatosensory perception accuracy, no study to date has directly examined the way in which interoceptive accuracy and exteroceptive perception accuracy are affected by social self-focus. Social self-focus has been successfully elicited in experimental settings with a turned on video camera facing the participant, as if s/he is being filmed (e.g., Burgio, Merluzzi, & Pryor, 1986; Duval & Lalwani, 1999). The aim of the present study (Experiment 2) was to investigate whether social self-focus evoked by a turned on video camera (selffocus condition: camera turned on and facing the participant; non self-focus condition: camera turned off and facing away from the participant) would affect interoceptive and/or exteroceptive somatosensory processing, as measured with heartbeat tracking accuracy and tactile perception accuracy. Heartbeat tracking accuracy was measured using the Mental Tracking Task (Schandry, 1981), while tactile perception accuracy was measured using a modified Somatic Signal Detection Task (SSDT; Lloyd et al., 2008). The SSDT has been used by Mirams et al. (2012, 2013) to examine the effects of bodily self-focus on exteroceptive somatosensory perception accuracy. The SSDT involves detecting the presence of a near-threshold tactile stimulus presented on 50% of the trials, while a simultaneous visual stimulus, such as an LED, also flashes on 50% of the trials, resulting in an increase in participants' hit rate and false alarm rate due to the flashing LED (Lloyd et al., 2008). A signal detection analysis is used to establish whether any observed change in responses is due to an effect of the manipulation on tactile sensitivity (i.e., ability to tell apart signal from noise), response criterion (i.e., propensity to report feeling a tactile stimulus), or both. Overall, higher sensitivity, higher hit rate, and lower false alarm rate suggest a more accurate exteroceptive/tactile perception of the body.

It was hypothesised that, in Experiment 2, social self-focus would enhance somatosensory processing in both, interoceptive and exteroceptive, modalities: cardiac interoceptive accuracy would be higher in the self-focus condition, as

opposed to the non-self-focus condition, as reflected by better heartbeat tracking accuracy in the "camera on" as opposed to "camera off" condition; the "camera on" condition would also be associated with improved tactile perception, as reflected by increased hit rate and decreased false alarm rate (i.e., higher sensitivity) on the SSDT in the "camera on" as opposed to the "camera off" condition. As significant differences in emotional and cognitive processing based on individuals' interoceptive accuracy level have been found—for example, in regards to emotional experience (e.g., Pollatos, Herbert et al., 2007), decisionmaking (e.g., Werner, Jung et al., 2009), and memory performance (e.g., Werner et al., 2010)—the potential modulation of SSDT performance by general cardiac interoceptive accuracy level was investigated. It was hypothesised that individuals with high heartbeat tracking accuracy are highly aware of their bodies, and hence, would display accurate tactile perception. This hypothesis is in line with the results of Knapp et al., (1997), which indicated a positive correlation between heartbeat discrimination accuracy and vibrotactile perception accuracy, suggesting that general somatosensory perception acuity might span across the interoceptive and exteroceptive modalities. Consequently, it was hypothesised that in the current study (Experiment 2) individuals with higher heartbeat tracking accuracy would display higher sensitivity, higher hit rate, and lower false alarm rate on the SSDT than individuals with lower heartbeat tracking accuracy. Lastly, general interoceptive ability was examined as a potential moderator of the effect of social self-focus on interoceptive and/or exteroceptive somatosensory processing; as sex differences have been observed in interoceptive accuracy, with males being more accurate than females (Cameron, 2001), sex was included as a between-subjects factor in the analyses of heartbeat tracking accuracy.

3.2 Methods

3.2.1 Experimental Design

The experiment was a fully counterbalanced within-subject design. Participants completed the heartbeat tracking accuracy (HTA) task and the Somatic Signal Detection Task (SSDT) two times each—one time with the video camera turned on and facing the participant (i.e., social self-focus condition), and

one time with the video camera turned off and facing away from the participant (i.e., non-self-focus condition). The order of "camera on"/"camera off" conditions was counterbalanced across participants. The order of HTA task and SSDT within each condition ("camera on", and "camera off") was also counterbalanced across participants. Together, there were 8 possible orders. The order in which a given participant completed the tasks was randomised.

3.2.2 Measures

3.2.2.1 Heartbeat Tracking Accuracy

HTA was assessed using the Mental Tracking Method (Schandry, 1981) outlined in Chapter 2. In this experiment, the assessment consisted of a three-trial block: 25-second, 35-second, and 45-second, trials, presented in a random order. Four trials of HTA assessment (as used in Experiment 1) were no longer used; the 100-second trial was excluded in order to minimise potential measurement error, as participants might potentially find it difficult to focus their attention on continuously tracking their heartbeats over a long 100-second trial. Even though numerous experiments have used a four-trial version of the task (Pollatos et al., 2008; Tsakiris et al., 2011; Tajadura-Jimenez, Longo, Coleman, & Tsakiris, 2012), a three-trial version of the task is also used (e.g., Ainley et al., 2012; Furman et al., 2013; Pollatos, Herbert et al., 2007; Werner, Schweitzer et al., 2013). Inter-trial reliability was increased by using a three-trial version of the task. In Experiment 1, Cronbach's $\alpha = .87$ for Time 1, and $\alpha = .90$ for Time 2; in the present study, Cronbach's $\alpha = .94$ for the no camera condition, and $\alpha = .95$ for the camera condition. Prior to the first HTA assessment, a 10-second training trial was administered in order to familiarise participants with the task.

3.2.2.2 Somatic Signal Detection Task

The Somatic Signal Detection Task (SSDT; Lloyd et al., 2008) measures somatic sensitivity and response bias in detecting whether a tactile stimulus at threshold intensity is present or absent, while an irrelevant LED flashes (at the same time as the occurrence of tactile stimulation) or not. The dependent variable is the participant's response: "definitely yes," "maybe yes," "maybe no,"

"definitely no". It should be noted that in order to adapt the SSDT paradigm to the present investigation, some aspects of the procedure were modified in the present study. Specifically, tactile stimuli were delivered to the cheek, and not to the hand, as in the original paradigm. This adjustment was made to ensure that tactile stimulation occurred at a body-site that is the focus of attention during the video-camera manipulation—the face—as opposed to the hand, which is peripheral to the focus of attention during the manipulation. As the site of tactile stimulation was moved, the location of the LED also needed to be adjusted accordingly. The light was positioned on eye-level, a meter away from the participant, in his or her central visual field, and slightly behind the video-camera to ensure that the light remained close enough to be salient, yet not too close as to interfere with the salience of the camera manipulation.

Tactile stimuli were delivered through a constant current electrical stimulator (DS7A, Digitimer). One couple of surface electrodes, placed on the participants' right cheek approximately 1 cm apart, delivered a single constant current rectangular monophasic pulse. The beginning of each trial was signalled by two brief audio tones. Then, a stimulus period of 1020 ms followed. In the tactile-present trials a 0.05 ms tactile stimulus was presented after 500 ms. In tactile-absent trials an empty 1020 ms period took place. A single audio tone signaled the end of the trial, at which point participants were asked to report whether they perceived a tactile stimulus on their cheek or not. First, a staircase procedure was used to establish a threshold for each participant—the point at which participant reported feeling the tactile stimulus on 40-60% of the tactilepresent trials. The threshold protocol consisted of 5 tactile-present and 5 tactileabsent trials, and the participant was asked to give a verbal response of "yes" or "no" to each trial. The thresholding procedure was repeated as many times as needed in order to establish the threshold, before the main experimental trials could take place.

The main experiment consisted of 2 blocks of 80 trials, with 20 trials for each of the four conditions (tactile present-light present, tactile present-light absent, tactile absent-light present, tactile absent-light present per block

in a random order. In the light-present trials the LED was illuminated for 20 ms with a delay of 500 ms on either side. The light was either simultaneous with the tactile pulse (in the tactile present-light present trials) or occurred on its own (in the tactile absent-light present trials). Participants had to report whether they felt the tactile stimulus during the trial period by pressing one of four buttons on the response pad: 'definitely yes,' 'maybe yes,' 'maybe no,' 'definitely no' (the order of the response buttons was also reversed and random half of the participants responded in the above order, while the other half responded in the reverse order of: 'definitely no,' 'maybe no,' 'maybe yes,' 'definitely yes'). Participants were unaware of the significance of the light stimulus and were asked to report solely whether they felt a tactile stimulus. The stimuli were controlled via a PC running NI LabVIEW 2011 software, which was also used to record the responses. In between the two blocks, the thresholding procedure was repeated in order to reestablish the threshold before the second experimental block.

3.2.3 Procedure

Upon arrival to the lab participants were given information about the study that was essential to provide informed consent, but that did not reveal the real objectives of the experiment. Participants were told that part of the task was going to be video-recorded for procedure monitoring purposes. After participants signed the informed consent form the experiment begun. Each participant was seated at a desk-chair about 1 m away from the wall. A black screen with a 10 mm red LED in the middle was attached directly to the wall. The LED was at eye-level of the seated participant and directly in front of him or her. A video camera was mounted on a tripod and placed about 75 cm directly in front of the participant. The LED was about 25 cm behind the video camera. The camera was slightly below eye-level of the participant in order not to interfere with the participant's vision of the LED. However, when turned on and facing the participant, the camera lens was turned slightly upwards in order to capture participant's face. When the camera was turned off and the lens was facing away from the participant, the tripod and the camera remained in the same position in front of the participant. See Figure 3-1 for an illustration of the experimental set up.

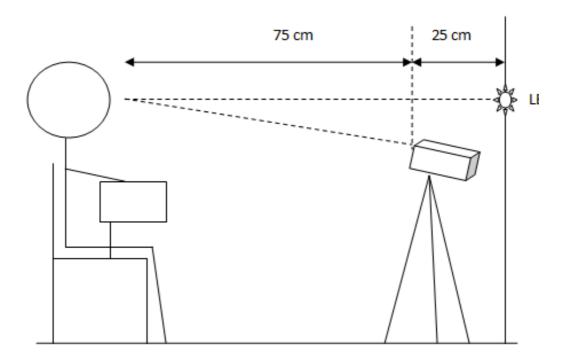


Figure 3-1. Experimental set-up.

During the experiment, the lab was dark; a spotlight placed above the participant illuminated the area in which the participant was seated. The spotlight did not directly illuminate the wall on which the LED was situated in order not to reduce visibility of the flashing light during the SSDT. Two electrodes were attached to participant's right cheek with the use of surgical tape, and a piezo-electric pulse transducer was attached to participant's right index finger. Participants then completed the HTA task and the SSDT in the "camera on" and "camera off" conditions (see 'Experimental design' section for information on counterbalancing of task order). Upon completion of the experiment participants were fully debriefed and informed about the real purpose of the study. See Figure 3-2 for a graphical depiction of the procedure.

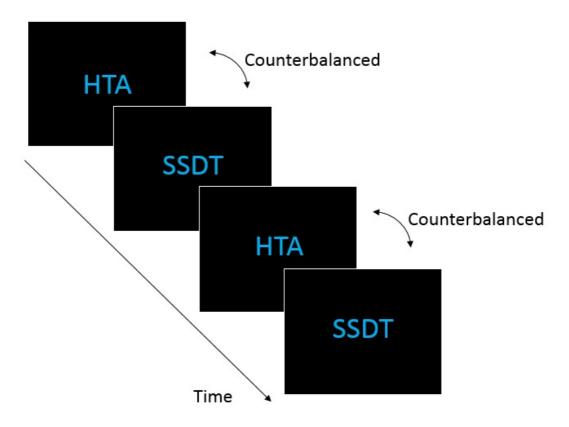


Figure 3-2. Experimental procedure.

3.2.4 Data Analysis

3.2.4.1 Heartbeat Tracking Accuracy Scores

HTA scores were calculated according to the following formula:

 $1/3 \Sigma (1-(|actual heartbeats - reported heartbeats |) / actual heartbeats).$

Individuals were categorized as high or low in HTA using a median split on the "camera off" HTA score (Mdn = .590). The sample consisted of 29 low HTA individuals (mean HTA = .487, SD = .078), and 28 high HPA individuals (mean HTA = .794, SD = .125). HTA was not normally distributed, as indicated by a Shapiro-Wilk test of normality (W = .952, p = .023). See Figure 3-3 for a frequency distribution plot.

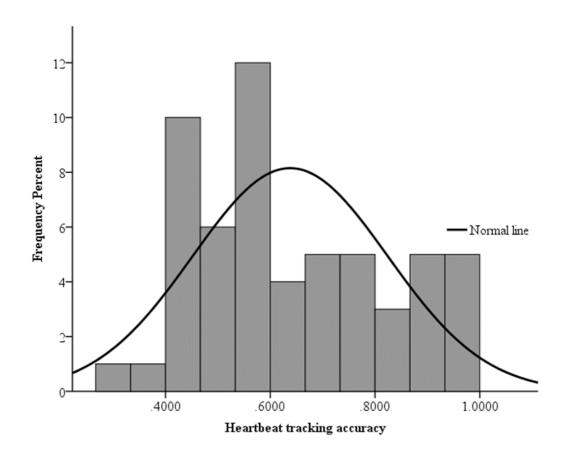


Figure 3-3. Frequency distribution of HTA scores in the "camera off" condition in Experiment 2.

3.2.4.2 Average Heart Rate

Average heart rate was calculated according to the following formula:

1/3 Σ ((actual heartbeats / length of time interval in seconds) * 60 seconds)

3.2.4.3 Somatic Signal Detection Task Data

In accordance with the original SSDT paradigm (Lloyd et al., 2008), responses "definitely" and "maybe" were combined, and grouped into 'yes' and 'no' responses, which were then categorized as hits, misses, false alarms and correct rejections. Hit rate and false alarm rate were calculated using the following formulas:

 $Hit\ rate = hits / (hits + misses)$

Sensitivity (d') and response criterion (c) statistics were calculated using Statilite software (Version 1.05 developed by Chris Rorden: http://www.mccauslandcenter.sc.edu/mricro/stats/index.html). Where false alarms were equal to zero, 1 was added to both false alarms and to correct rejections to calculate d' and c values. This correction was applied as it was necessary for the Statilite software to accurately perform the associated calculations. For a closer analysis of the statistical issues surrounding extreme signal detection values and multiple ways of resolving them, refer to Stanislaw and Todorov (1999).

3.2.4.4 Data Analysis Overview

Correlation analyses were conducted to test for association between HTA and SSDT outcome measures. The effects of experimental manipulation on HTA and HR were examined using a Wilcoxon Signed Rank Test and a mixed ANOVA with Condition ("camera on", "camera off") as the within-subjects factor and HTA group (low, high) and Sex (male, female) as between subjects-factors, respectively. The effect of the experimental manipulation on SSDT outcome measures was investigated using a mixed ANOVA with within-subject factors of Light (present or absent) and Camera (on or off) and between subjects factors of Camera order (camera first or camera second), Task order (4 possible orders) and HTA group (higher HTA, lower HTA) and with Wilcoxon Signed Rank Tests in the case of non-normal distribution of data.

3.2.5 Participants

Seventy-nine (64 females; mean age = 18.73, SD = .90) undergraduate psychology students at Royal Holloway, University of London took part in the experiment in compensation for course credit. Table 3-1 lists demographic characteristics of the sample.

Table 3-1. Experiment 2 sample characteristics: means (with standard deviations).

	Mean (SD)
Age	18.73 (.90)
BMI ^a	21.84 (3.84)
HR camera off ^b	81.90 (10.04)
HTA camera off ^c	.64 (.18)
BFNE-S ^d	26.96 (7.72)
STICSA-S ^e	34.95 (8.82)
STICSA-T ^f	44.10 (9.21)

^a Body Mass Index; ^b Heart rate in the "camera off" condition; ^c Heartbeat tracking accuracy in the "camera off" condition; ^d Brief Fear of Negative Evaluation-Straightforward Items; ^e State-Trait Inventory of Cognitive and Somatic Anxiety Scale- State subscale; ^f State-Trait Inventory of Cognitive and Somatic Anxiety Scale-Trait subscale

3.2.5.1 Data Exclusion

On the SSDT, participants who completed 16 or less trials out of 20 trials of each condition per block on, or who displayed a hit rate, and/or false alarm rate over or under 1.5 standard deviations from the mean (means were calculated for all participants, separately for all 4 conditions, light (present or absent)/camera (present or absent)), respectively, due to measurement error were excluded from the sample. This exclusion criterion ensured that the hit rate remained between 40 and 60% and that the tactile stimulus was indeed of the intensity corresponding to the perceptual threshold. Eighteen participants were excluded from the sample based on these criteria. Four more participants were excluded from the sample due to heartbeat data measurement error. The final sample consisted of 57 participants (48 female; mean age = 18.67; SD = .93).

3.3 Results

3.3.1 Association Between Heartbeat Tracking Accuracy and Somatic Signal Detection Task Measures

Correlational analyses were performed for HTA scores (across all participants) and SSDT outcome variables of hit rate, false alarm rate, sensitivity, and response criterion for the non-self-focus condition. As HTA scores in this condition were not normally distributed, Spearman's rho (r_s) correlation coefficients were computed. HTA scores were positively correlated with overall false alarm rate in the "camera off" condition (r_s = .299, p = .024, 95% CI [.042, .519]). Bonferroni correction for multiple comparisons resulted in this correlation being significant at α = .1, but not at α = .05 level. HTA scores were not significantly correlated with hit rate (r_s = .075, p = .578, 95% CI [-.189, .329]), sensitivity (d') (r_s = -.060, p = .659, 95% CI [-.315, .203]) or response criterion (c) (r_s = -.146, p = .277, 95% CI [-.391, .119]) in the "camera off" condition.

3.3.2 Heartbeat Tracking Accuracy

As HTA scores in the non-self-focus condition were not normally distributed, non-parametric test statistics were used to investigate whether the camera manipulation had an effect on HTA. A Wilcoxon Signed Rank Test revealed that HTA scores did not differ between self-focus ("camera on"; Mdn = .63, range = .77) and non-self-focus ("camera off"; Mdn = .59, range = .72) conditions (Z = -1.148, p = .251). No effect of camera remained when separately examining the low HTA group (Z = -.876, p = .381) and the high HTA group (Z = -.638, p = .524), and when separately examining males (Z = -.533, p = .652) and females (Z = -.985, p = .330).

Average heart rate was analysed in a 2 x 2 x 2 ANOVA with a withinsubjects factor of Condition ("camera on", "camera off") and between-subjects factors of HTA group (lower HTA, higher HTA), and Sex (male, female). There was no main effect of Condition (F(1, 53) = .167, p = .685), no interaction effect of Condition and HTA group on heart rate (F(1, 53) = .048, p = .828), and no interaction effect of Condition and Sex on heart rate (F(1, 53) = .320, p = .574).

3.3.3 Somatic Signal Detection Task

Sensitivity (d'), hit rate, and response criterion (c) were each submitted to a 2 x 2 x 2 x 4 x 2 ANOVA with within subject factors of Light (present or absent) and Camera (on or off), and between subjects factors of Camera order (camera first or camera second), Task order (4 possible orders) and HTA group (higher HTA, lower HTA). As there were no main effects of Camera order on sensitivity (F(1, 41) = .095, p = .760), hit rate (F(1, 41) = .012, p = .913), or response criterion (F(1, 41) = .004, p = .950), and of Task order on sensitivity (F(3, 41) = .990, p = .407), hit rate (F(3, 41) = .678, p = .571), or response criterion (F(3, 41) = .286, p = .835) these factors were removed from final analyses, and the dependent variables were analysed in 2 (Light) x 2 (Camera) x 2 (HTA group) ANOVAs. As false alarms were not normally distributed, non-parametric test statistics were used to test for differences between groups and within conditions based on factors of Camera order and Task order. A series of Mann-Whitney U tests and Kruskal-Wallis H tests revealed no group differences in any of the false alarm measures based on Camera order and Task order, respectively—all values were above the significance level of $\alpha = .05$. Table 3-2 contains descriptive statistics for each outcome measure in each Light condition.

Table 3-2. Means of hit rates, false alarm rates, d, and c in each camera and light condition. Standard deviations in parentheses.

	Light condition	Camera condition	
Variable		Camera off (NSF)	Camera on (SF)
Hits (%)	No light	49.46 (17.65)	56.14 (16.18)
	Light	62.71 (14.59)	64.73 (15.30)
	Overall	56.09 (15.00)	60.43 (14.56)
False Alarms (%)	No light	2.56 (3.72)	2.50 (4.72)
	Light	4.08 (5.08)	3.60 (5.47)
	Overall	3.34 (3.93)	3.05 (4.22)
d'	No light	1.72 (.51)	2.01 (.50)
	Light	1.91 (.50)	2.13 (.52)
	Overall	1.86 (.46)	2.02 (.47)
c	No light	.87 (.28)	.66 (.26)
	Light	.78 (.26)	.65 (.27)
	Overall	.77 (.24)	.72 (.24)

Note: $NSF = non \ self-focus$; SF = self-focus; d' = sensitivity, $c = response \ criterion$.

Sensitivity (*d'*) was higher in the self-focus condition than in the non-self-focus condition ($F(1, 55) = 5.866 p = .019, \eta_p^2 = .096$). There was a significant main effect of Light on sensitivity ($F(1, 55) = 34.430 p < .001, \eta_p^2 = .385$) with *d'* being significantly higher in light-present trials than in light-absent trials. There

was no interaction effect of Camera and Light on d'(F(1, 55) = 1.036, p = .313). There was no main effect of HTA group on d'(F(1, 55) = .878, p = .353), nor interaction of HTA group with Camera (F(1, 55) = .717, p = .401) or Light (F(1, 55) = .277, p = .601) on d'. In order to investigate the components of the increase in sensitivity, hit rate and false alarms across conditions were examined next.

Hit rate was significantly affected by Light (F(1, 55) = 87.801, p < .001, $\eta_p^2 = .615$) — being higher in light-present than in light-absent trials—and by Camera (F (1, 55) = 4.276, p = .043, $\eta_p^2 = .072$)—being significantly higher in camera-present trials than in camera-absent trials. There was a significant interaction of Light and Camera on hit rate $(F(1, 55) = 4.304, p = .043, \eta_p^2 =$.073). In order to probe the interaction, pairwise t-tests comparing hit rate in both Camera conditions were conducted for each of the Light conditions separately. Bonferroni corrections were applied throughout, adjusting the alpha level to .025 (.05/2) in order to correct for multiple comparisons. The results revealed that the effect of Camera on hit rate was driven by the difference in hit rate across Camera conditions in light-absent trials (t (56) = -2.816, p = .007, Cohen's d = -.753), as there was no difference in hit rate across Camera conditions in light-present trials (t(56) = 2.096, p = .400). To see whether Light had a smaller effect on hit rate in the self-focus condition—when the camera was on—than in the non-self-focus condition—when the camera was off—difference scores (hit rate light-present – hit rate light-absent) in each condition were compared in a single pairwise t-test. Light had a significantly smaller effect on hit rate in the self-focus condition (mean difference = 8.59 (SD = 12.01)) than in the non-self-focus condition (mean difference = 13.25 (SD = 12.21)), t(56) = 2.096, p = .041, Cohen's d = .56. Figure 3-4 illustrates the effect of Light and Camera on hit rate. There was no main effect of HTA group on hit rate (F(1, 55) = .020, p = .887), nor interaction of HTA group with Camera (F(1, 55) = .278, p = .600) or Light (F(1, 55) = .004, p = .004).947) on hit rate.

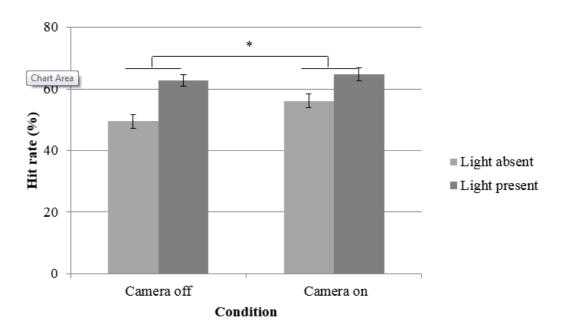


Figure 3-4. The effect of camera and light on hit rate. Note: *p < .05.

As false alarms were not normally distributed, non-parametric test statistics were used to examine for significant differences in false alarms between conditions. A Wilcoxon Signed Rank Test showed a main effect of Light on false alarm rates (Z = -2.739, p = .006) with false alarm rates being higher in lightpresent than in light-absent trials, but no main effect of Camera on false alarm rates (Z = -1.001, p = .317)—Bonferroni correction for multiple comparisons applied and alpha level adjusted to .025 (.05/2). The main effect of Light on false alarms was driven by the "camera off" condition where false alarms were higher in light-present trials (Z = -2.557, p = .011), as opposed to the "camera on" condition where false alarms did not significantly differ between light-present and light-absent trials (Z = -1.699, p = .089)—Bonferroni correction for multiple comparisons applied and alpha level adjusted to .025 (.05/2). However, the effect of Light on false alarm rate in each condition, as compared using a single pairwise comparison on mean difference scores (false alarm rate light-present – false alarm rate light-absent) was not significant (Z = -.436, p = .663). Figure 3-5 illustrates the effect of Light and Camera on false alarm rate. Although the number of false alarms was higher in the high HTA group than in the low HTA group, the effect of HTA group on false alarm rate was not statistically significant indicated by significance level values above .05 on a series of Mann-Whitney U tests investigating group differences in false alarm rates based on the between-subjects factor of HTA group.

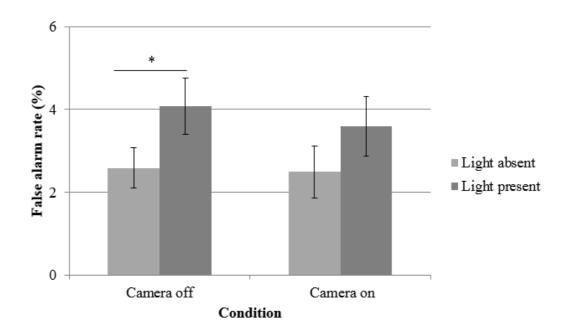


Figure 3-5. The effect of camera and light on false alarm rate. Note: *p < .05.

Response criterion (*c*) was not affected by Camera (F(1, 55) = 2.076, p = .155), and there was only a main effect of Light ($F(1, 55) = 87.990 \, p < .001$, $\eta_p^2 = .615$), with a significantly more liberal response criterion in light-present trials as opposed to light-absent trials. There was no interaction effect of Camera and Light on the response criterion (F(1, 55) = 3.2634, p = .078). There was no main effect of HTA group (F(1, 55) = .372, p = .544), nor interaction of HTA group with Camera (F(1, 55) = .000, p = .996) or Light (F(1, 55) = .271, p = .605) on the response criterion.

3.4 Discussion

Experiment 2 investigated interoceptive and exteroceptive somatosensory perception accuracy in two conditions: self-focus and non-self-focus, as manipulated with a video camera being turned on or turned off, respectively.

Contrary to the predictions made at the beginning of the experiment, interoceptive somatosensation, as measured with a heartbeat tracking accuracy task, was not significantly affected by the self-focus manipulation. However, exteroceptive somatosensation, measured with the Somatic Signal Detection Task (SSDT), differed significantly between the two self-focus conditions. It should be noted that certain aspects of the SSDT paradigm were modified for purposes of investigating this research question—namely, the site of tactile stimulation, and respective position of the light in relation to the stimulated body part. Due to strong automatic integration of visual and tactile sensory modalities, the light in this modified version of the SSDT, which, importantly, was in the central visual field of the participant, retained its salience, and as expected, and in accordance with the SSDT paradigm, in both conditions the light's occurrence enhanced tactile perception, as reflected by increased sensitivity and hit rate in light-present trials. Light presence also increased false alarm rate in the "camera off" condition, increasing the likelihood of participants reporting feeling a stimulus (as reflected by a more liberal response criterion in light-present as opposed to lightabsent trials). Importantly, the presence of a switched on camera also enhanced tactile perception, as reflected by increased sensitivity and higher hit rate in the "camera on", as opposed to "camera off" condition. Further, in the "camera on" condition, the light did not have an effect on false alarm rate as it did in the "camera off" condition, nor did the light increase hit rate as much in the "camera on" condition as it did in the "camera off" condition. Heartbeat tracking accuracy was not a significant moderator of SSDT performance. The only significant association between heartbeat tracking accuracy and SSDT measures was observed between heartbeat tracking accuracy and false alarm rate in the "camera off", non-self-focus condition.

To summarise, when the video camera was turned on, tactile perception was enhanced, as reflected by increased sensitivity and hit rate. Moreover, when it was turned on and recording, there was a lesser impact of light presence on hit rate and no effect of light on false alarm rate. The fact that the presence of the light improved hit rate to a larger degree when the camera was off than when the camera was on, as well as significantly increased false alarm rate only when the

camera was off and not when it was on, suggests that the self-focus condition during which the camera was on was powerful enough to override the effect of light on tactile perception. Importantly, the self-focus condition with the camera turned on did not affect the response criterion, consequently eliminating the possibility of differences in SSDT performance being due to mere change in tendency to report feeling a tactile stimulus, instead likely reflecting an actual change in sensitivity due to the camera manipulation. It should be noted that the "camera on" condition might have diminished the effect of the light more easily as a result of an already weakened link between the visual and tactile sensory modalities (as compared to the original SSDT paradigm) brought about by a greater spatial distance between the sources of tactile and visual stimulation. As false alarm rates were lower in the present study than in the original SSDT paradigm, it is indeed likely that the magnitude of the light effect on tactile perception was smaller in the present study than in the original SSDT study by Lloyd et al. (2008). Nevertheless, it should be noted that multisensory integration is not narrowly constrained by spatial correspondence and there is a large body of research demonstrating cross-modal integration also when the sensory stimulation from the two modalities occurs in distinct locations (see Spence, 2013 for a review). Overall, the light in the current manipulation elicited the expected effect on tactile perception and the fact that this effect was diminished in the presence of the camera can be explained by the increase in tactile sensitivity due to heightened self-focus brought about by the turned on video camera. In interpreting these results, it can be suggested that the "camera on" condition evoked a cognitive shift from first to third person perspective in participants who, as a result of the "camera on" manipulation, were primed with a third person representation of the self as if one sees oneself from the outside, and particularly their face (which was the focus of the camera), which, consequently, might have contributed to the enhancement of tactile perception on the face. The visual enhancement of touch (VET) effect is a well-studied phenomenon, which demonstrates that viewing a given body region improves tactile perception in that skin region (e.g., Kennett, Taylor-Clarke, & Haggard, 2001), by influencing processing in the early somatosensory cortex (e.g., Fiorio & Haggard, 2005). While participants in the

present study did not actually view their face, the video-camera being turned on might have primed thoughts of the face being viewed from the third person perspective (being previously told that the video recording of them performing the task could be watched by a third party), consequently, increasing sensitivity in detecting tactile stimuli in the "camera on", but not the "camera off" condition through a mental imagery effect analogous to the VET.

Contrary to the predictions made at the beginning of the study, the videocamera manipulation did not affect interoceptive accuracy, as there was no difference in heartbeat tracking accuracy between the "camera on" and "camera off" conditions. As past research experiments by Ainley et al. (2012, 2013) found an increase in heartbeat tracking accuracy during mirror and still photograph selfobservation—also used to increase self-focus—the finding that camera induced self-focus did not affect heartbeat perception accuracy is surprising. It could be argued that the lack of an observed effect of the camera manipulation on heartbeat tracking accuracy could be due to the mode of self-focus elicited by the manipulation, which was social rather than private in nature. While mirror presence has been found to direct individual's attention to inner aspects of the self, video camera manipulations have been found to draw attention to external, or social aspects of one's self that are observable to others (Carver & Scheier, 1981). Accordingly, while mirror presence can enhance an individual's perception of his or her inner body—a very private aspect of the self—a turned on video camera, on the other hand, might more selectively enhance tactile perception, which is the sensory modality through which individuals interact with the external world, hence, a sensory modality that is given a stronger weighting in the context of the social self-focus manipulation, thereby enhancing information processing associated with that modality. Even though the results of Baltazar et al. (2014) could be taken to suggest that social self-focus might increase correspondence between physiological arousal and subjective emotional experience by increasing interoceptive accuracy, it should be noted that the study by Baltazar et al. did not directly measure interoceptive accuracy, and consequently does not provide evidence for social self-focus increasing interoceptive accuracy. Of course, it is possible that cardiac interoceptive accuracy was affected by mere presence of the

video camera, which automatically enhanced self-focus, without much further difference between "camera on" and "camera off" conditions. The design of the present study, however, limits the conclusions that can be drawn from the data, as there was no third condition present in the design, in which the camera would be absent, or an independent baseline measure, which would allow such a comparison to be made. Another possibility might be that the video camera manipulation did not elicit self-focus sufficiently to increase cardiac interoceptive accuracy. A limitation of the current experiment is that the actual extent to which the camera manipulation increased self-focus was not explicitly measured. Individuals were not asked to report on whether they felt more focused on themselves, because the aim of the experiment was not necessarily to evoke a conscious increase in self-focus, and because the video camera is likely to increase self-focus in a way that the individual is not explicitly conscious of. Nevertheless, as cameras have been successfully used to elicit self-focus in past research (e.g., Burgio et al., 1986; Duval & Lalwani, 1999) and because the current manipulation did have a significant effect on tactile perception, as anticipated, it can be assumed that the manipulation was successful. In addition to investigating the effects of social self-focus on body perception, Experiment 2 also examined the relationship between interoceptive and exteroceptive somatosensory perception. The data was analysed for potential moderating effects of heartbeat tracking accuracy on SSDT performance, after splitting the participants into two groups: higher and lower heartbeat tracking accuracy groups based on the sample median in the "camera off" condition. While there was no modulation of tactile perceptual performance present based on heartbeat tracking accuracy being higher or lower, it should be noted that the sample median was rather low, hence the two groups did not represent individuals truly high and low in cardiac interoceptive accuracy. Interestingly, a positive correlation between heartbeat tracking accuracy and false alarm rates in the "camera off" condition was observed. This relationship was not reflected in the independent sample comparison results—most likely due to the heavily skewed distribution of false alarms, which included many values of zero, necessitating the use of nonparametric statistical tests, which likely lacked in power to detect the difference.

As Knapp et al. (1997) found a direct association between heartbeat discrimination accuracy and vibrotactile perception accuracy, the hypotheses set out at the beginning of this chapter predicted a positive relationship between heartbeat tracking accuracy and tactile perception accuracy. It was hypothesised that individuals with higher heartbeat tracking accuracy would display higher sensitivity, higher hit rate, and lower false alarm rate on the SSDT than individuals with lower heartbeat tracking accuracy. However, heartbeat tracking accuracy was not related to sensitivity in detecting threshold tactile stimuli or to hit rate. Instead, heartbeat tracking accuracy was inversely related to the rate of false alarms on the SSDT. It has been proposed that increased attention to interoceptive stimuli might contribute to the occurrence of false alarms by increasing sensory noise, thereby making it more difficult for an individual to distinguish between signal and noise (sensations originating outside and inside the body, respectively) when detecting a tactile stimulus (Mirams et al., 2013; Silvia & Gendolla, 2001). Mirams et al. (2012) found that directing individuals' attention to pulse sensations in the fingertip increased individual propensity to report feeling a threshold tactile stimulus, nevertheless did not significantly affect sensitivity measures. Consequently, the results of that study suggest that interoceptive attention might bias individuals toward reporting tactile sensations in their absence, but do not entirely support the hypothesis that interoceptive attention contributes to individuals being less able to distinguish sensory noise from signal. It should be considered that in their experiment, Mirams et al. utilized an untypical interoceptive attention task in which they asked participants to focus their attention on pulse sensations in their fingertip. This methodology might account for an increased propensity to report having felt a tactile stimulus on the fingertip when completing the SSDT afterwards. Notably, in the present study, where a classic version of the task was employed, there was no effect of engaging in the heartbeat tracking task on SSDT performance, as indicated by a lack of task order effects in the data. Importantly, while Mirams et al. investigated overall effects of interoceptive attention on SSDT performance, they left unexamined the question of whether inter-individual variability in baseline interoceptive accuracy was related to tactile perception. While the results of the current study show that individuals with higher heartbeat tracking accuracy made more false alarms on the SSDT during the "camera off" condition, there was no association present between heartbeat tracking accuracy and sensitivity measures which would be more directly indicative of diminished ability to tell apart sensory signal from sensory noise.

Even though false alarms on the SSDT have been associated with activity in the right insula and the anterior cingulate cortex (Poliakoff et al., in preparation, as cited in Mirams et al., 2013)—regions central to bodily attention and interoception (Craig, 2003; Critchley et al., 2004)—more empirical evidence is needed to test whether increased interoceptive accuracy interferes with exteroceptive processing of bodily signals—especially, given the evidence for the contrary, where individuals with higher cardiac interoceptive accuracy have been shown to be less susceptible to the Rubber Hand Illusion (Tsakiris et al., 2011). The Tsakiris et al. study suggests that individuals with higher cardiac interoceptive accuracy are less susceptible to interference from exteroceptive signals in their perceptual experience. Nevertheless, individuals with higher cardiac interoceptive accuracy would then be expected to show enhanced exteroceptive somatosensory perception, and more specifically, increased sensitivity on the SSDT, which is also not supported by the current study's data inasmuch as there was no relationship observed between heartbeat tracking accuracy and tactile sensitivity measures. Consequently, further research is needed to establish the exact nature of the relationship between interoceptive and exteroceptive somatosensory processing, especially under various top-down influences—an empirical question that will be addressed in the studies that will be described in the following chapters of this thesis.

To conclude, Experiment 2 investigated the effect of social self-focus on cardiac interoceptive accuracy, as measured with a heartbeat tracking accuracy task, and on exteroceptive somatosensory processing, as measured with the Somatic Signal Detection Task. The results show that heartbeat tracking accuracy was not affected by the video camera being turned on, relative to the "camera off" condition, which enhanced only tactile perception. Essentially, it can be

concluded that social self-focus, as manipulated with a video camera being turned on or turned off, enhanced bodily perception in the exteroceptive tactile modality. Unlike mirrors, which have been found to evoke private self-focus by directing attention to private aspects of the self, video cameras have been found to direct attention to social aspects of the self that are external and observable to others (Davies, 2005). Therefore, the effect of social self-focus on tactile perception, and not on heartbeat perception, could be perhaps attributed to the inherently social aspect of tactile processing. Even though the effect of the switched on video camera on exteroceptive somatosensory processing was not modulated by cardiac interoceptive accuracy, heartbeat tracking accuracy was positively correlated with false alarms in the "camera off" condition. This finding is consistent with recent research showing that false alarm responses on the SSDT are associated with activity in the interoceptive centres of the brain—the right insula and the ACC (Poliakoff, in preparation, as cited in Mirams et al., 2013), nevertheless, these results do not shed further light on the nature of the relationship between cardiac interoceptive accuracy and exteroceptive somatosensory processing such as tactile processing, as there were no significant correlations between heartbeat perception accuracy and any of the other SSDT outcome measures present in the data. Consequently, further research is necessary to determine the nature of the relationship between interoceptive and exteroceptive somatosensory perception accuracy. Chapter 4 describes two studies: Experiment 3, investigating the effect of social exclusion on heartbeat tracking accuracy and Experiment 4 examining both non-painful and painful tactile perception after social exclusion, as it related to heartbeat tracking accuracy. Chapter 4 investigates stability of heartbeat tracking accuracy under another negative affect-inducing social evaluative experience—one in which an individual experiences social exclusion. Experiment 3 thereby examines an emotional context that is different from anticipatory social anxiety, but at the same time retains the negative affective quality as well as a social evaluative component.

Chapter 4: Stability of Interoceptive Accuracy After Social Exclusion—the Relationship Between Social and Physical Pain³

4.1 Introduction

The need for social affiliation is one of the most important and fundamental human needs. Evolutionarily, belonging to social groups carried several advantages in terms of survival and reproductive opportunities and success (Brewer, 2004). Consequently, it is not surprising that humans display strong negative reactions to social exclusion and rejection. Long-term social isolation and loneliness have been associated with depression and other negative health outcomes such as increased mortality (e.g., Steptoe, Shankar, Demakakos, & Wardle, 2013) and enhanced risk of immune dysregulation (e.g., Jaremka et al., 2013). Even small-scale social rejection in a computerised ball-tossing game, Cyberball (Williams, Cheung, & Choi, 2000; Williams & Jarvis, 2006)—a paradigm developed to study social ostracism in an experimental setting—can impact individual's psychological and physiological state. A few minutes of being Cyber-ostracised can significantly increase negative affect and lower one's sense of belonging, control, meaningful existence and self-esteem (see Williams, 2009 for a review)—independently of factors such as monetary gains and costs associated with ball possession (Van Beest & Williams, 2006) or the desirability of the ostracisers (Gonsalkorale & Williams, 2007). Social exclusion has also been found to bring about a significant drop in skin temperature (IJzerman et al., 2012), while both, heart rate deceleration (Gunther Moor, Crone, & Van der Molen, 2010) and acceleration (Iffland, Sansen, Catani, & Neuner, 2014) have been observed in response to exclusion.

The dorsal anterior cingulate cortex (dACC) and the anterior insula (see

³ Experiment 3 has been published as Durlik, C. & Tsakiris, M. (2015). Decreased interoceptive accuracy following social exclusion. *International Journal of Psychophysiology*, *96*, 57-63. doi:10.1016/j.ijpsycho.2015.02.020.

Eisenberger, 2012a, 2012b)—brain regions associated with interoception (Craig, 2009) and with the affectively distressing component of physical pain (Rainville, 2002)—have been shown to be activated in individuals experiencing Cyberball exclusion. The fact that insula activity has been linked to the affective component of physical pain as well as to emotional pain evoked by social rejection (see Eisenberger, 2012a, 2012b for a review) suggests that interoceptive processes might be crucial in linking physical and emotional pain systems. Pollatos, Füstös and Critchley (2012) observed that individuals with higher heartbeat tracking accuracy displayed higher sensitivity and lower tolerance to cutaneous pressure pain than individuals with lower heartbeat tracking accuracy (cf. Werner, Duschek et al., 2009b). Moreover, Pollatos and colleagues found that individuals with higher heartbeat tracking accuracy exhibited more autonomic reactivity in response to pain, and rated the painful sensations as significantly more unpleasant than individuals with lower heartbeat tracking accuracy. The results of Pollatos et al. suggest that high interoceptive accuracy is associated with higher sensitivity to pain and an increased affective (as opposed to sensory) response to pain, which is in line with neuroimaging evidence linking the insular and anterior cingulate cortices to the affective-motivational dimension of pain (Rainville, 2002).

Importantly, sensitivity to physical pain has been observed to predict self-reports of distress in response to social exclusion, while social exclusion has been found to predict unpleasantness ratings of subsequently delivered physically painful stimuli (Eisenberger, Jarcho, Lieberman, & Naliboff, 2006). DeWall and colleagues (2010) found that the impact of social rejection can be reduced by acetaminophen—a chemical agent used to alleviate physical pain—as reflected by reduced dACC and anterior insula activation in response to Cyberball rejection in individuals taking the analgesic. However, social exclusion has also been associated with a numbing response where there is a decrease in physical pain. DeWall and Baumeister (2006) observed that anticipated aloneness can bring about decreased sensitivity to physical pain, as reflected by higher pain thresholds and higher pain tolerance in the experimental condition (Experiment 1-4). The body typically undergoes changes in response to a physical threat, which enable the body to carry out an appropriate action—for example, when faced with severe

physical threat the body might release analgesics numbing the body, aiding in flight from attack despite any sustained injuries (MacDonald, Kingsbury, & Shaw, 2005). Considering the significant overlap of neural networks involved in social and physical pain, it seems likely that a system capable of detecting and responding to social pain evolved by piggybacking onto the pre-existing physical pain system, utilising the pain signal to mark the threat of social disconnection and to prompt social reconnection (Panksepp, 1998).

4.2 Experiment 3

4.2.1 Introduction

Because Experiment 1 observed that heartbeat tracking accuracy increased in response to a stressful negative affective experience of public speaking anticipation, Experiment 3 investigated whether heartbeat tracking accuracy would be affected by the stressful negative affective experience of social exclusion. Because social exclusion has been found to bring about increased activity in the anterior insula (Cacioppo et al., 2013; Eisenberger 2012a, 2012b), which, in turn, has been associated with enhanced interoceptive accuracy (e.g., Critchley et al., 2004) and because previous research has found interoceptive accuracy to be directly associated with the intensity of emotional experience (e.g., Pollatos, Traut-Mattausch et al., 2007), it was hypothesised that social exclusion during the Cyberball game would bring about increased interoceptive accuracy as reflected by an increase in heartbeat perception accuracy from pre- to post-Cyberball in excluded, but not in included individuals. It was hypothesised that the increase in heartbeat tracking accuracy from pre- to post-Cyberball in excluded individuals would be positively correlated with self-reported distress following the exclusion. Previous research has found that individuals with lower baseline heartbeat perception accuracy, categorised with median splits, experienced greater subjective reactions to social exclusion (Werner, Kerschreiter et al., 2013), consequently, HTA group was included as a potential moderator when analysing the results. Additionally, as males and females have been sometimes observed to display reactions to Cyberball exclusion that were of differing magnitudes (e.g., Benenson et al., 2013; Bolling, Pelphrey, & Vander

Wyk, 2012; Iffland et al., 2014), the potential moderating effect of sex was examined.

4.2.2 Methods

4.2.2.1 Experimental Design

The study utilised a mixed design with a within-subjects factor of Time (baseline, post-Cyberball) and between-subjects factor of Condition (excluded, included). Subjects were randomly assigned to one of two conditions: Cyberball inclusion or Cyberball exclusion (see below description of Cyberball for details regarding the excluded and included conditions). The dependent measure of heartbeat tracking accuracy (HTA) was taken at baseline and post-Cyberball. The post-Cyberball Questionnaire, assessing the effectiveness of the manipulation, was administered after the Cyberball game.

4.2.2.1.1 Cyberball

The computerised ball tossing game (Williams et al., 2000) consisted of 30 ball tosses in total, between the participant and 2 computerised players. Participants were asked to pose for a photograph to be taken. They were told the photograph would be displayed in a box beside their avatar, while they played the game, for the other participants to see. Photographs of the computerised players: Player 1 and Player 3 were taken from The Center for Vital Longevity Face Database (Minear from: Park, 2004; obtained http://agingmind.utdallas.edu/stimuli/facedb/). Player 2 was the participant and the photograph of the participant was not visible on the screen during the game in order not to increase self-focus, which has been found to enhance heartbeat perception accuracy (Ainley et al., 2012, 2013). In the included condition the tosses were distributed equally among the three players, with the participant receiving the ball on one third of the tosses (10 tosses in total), while in the excluded condition the participant received the ball 2 times, at the very beginning of the game (once from Player 1 and once from Player 3), after which the participant was excluded from the game while the ball was passed only between Player 1 and Player 3 for the remainder of tosses (28 tosses). Cyberball 4.0

(Williams, Yeager, Cheung, & Choi, 2012) was administered through the online survey software Qualtrics (www.qualtrics.com), using the script obtained on www.cyberball.wikispaces.com

4.2.2.2 Measures

4.2.2.2.1 Heartbeat Tracking Accuracy

HTA was assessed using the Mental Tracking Method (Schandry, 1981), as outlined in Chapter 2. As in Experiment 2 the HTA assessment consisted of a three-trial block: 25-second, 35-second and 45-second trials. In the current experiment (Experiment 3), the POLAR RS800CX heart rate monitor was used (Polar Electro Oy, Kempele, Finland; sampling rate of 1000 Hz). Signals were analysed by the Polar ProTrainer 5 software (version 5.40.172), which relies on the HRV analysis software of the University of Kuopio, Finland (Niskanen, Tarvainen, Ranta-aho, & Karjalainen, 2004). POLAR products have excellent construct validity and instrument reliability, measuring heart rate and R-R interval data on par with electrocardiogram recorded data (e.g., Kingsley, Lewis, & Marson, 2005; Nunan et al., 2008; Quintana, Heathers, & Kemp, 2012; Weippert et al., 2010). Participants were instructed to lightly place the heels of their hands on the heart rate sensor that was attached to the desk in front of them and mentally count their heartbeats from the moment they received an audio cue signalling the start of the trial until they received an otherwise identical cue signalling the end of the trial and then to verbally report to the experimenter the number of heartbeats they have counted. Every participant was first presented with a 10-second training trial (during the first assessment only) and then with a pseudo-randomized block of 35-second, 25-second, and 45-second trials, with 20-second pauses in between the trials. During the whole duration of the task, participants' true heart rate was monitored using the POLAR RS800CX. Throughout the task, participants were not permitted to take their pulse or to use any other strategy such as holding their breath. No information regarding the length of the individual trials or feedback regarding participants' performance was given. All participants performed the heartbeat tracking task twice: at baseline and after the Cyberball game.

4.2.2.2.2 Post-Cyberball Questionnaire

The post-Cyberball questionnaire was based on previous studies utilising the Cyberball paradigm (e.g., Williams et al., 2002; Zadro, Boland, & Richardson, 2006) and assessed four fundamental needs (with five items per need): Belonging (e.g., "I felt like an outsider during the game", reverse scored), Control (e.g., "I felt I had control over the course of the game"), Meaningful existence (e.g., "I felt meaningless", reverse scored) and Self-esteem (e.g., ""I felt good about myself"). Eight items, retrospectively, assessed positive affect during the game: feeling "good," "friendly," "pleasant" and "happy", and negative affect during the game: feeling "bad," "unfriendly," "angry" and "sad". Additionally, three manipulation check questions were asked: participants reported how "ignored" and "excluded" they felt during the game, as well as estimated the percentage of total throws they think they have received during the game. All items, except for the last one, were rated on a continuous 5-point scale ranging from 'not at all' to 'extremely'. Additionally, at the end of the experiment participants were asked two debriefing questions about whether they thought, and felt like, they were playing against the computer or against real players.

4.2.2.3 Procedure

Upon arrival to the lab, participants were given information about the study that was essential to provide informed consent, but that did not disclose the real objectives of the experiment. After the participants signed an informed consent form the experiment begun. Participants were seated at a desk in front of a computer with an attached web-camera (the web-camera was used to take a photograph of the participant and was facing away from the participants during the remainder of the experiment) and begun by providing basic demographic information. Then, participants completed the first heartbeat tracking accuracy task (approximately 3 minutes prior to playing Cyberball), which served as a baseline interoceptive accuracy measure. Afterwards, participants were asked if they agree for the experimenter to take a photograph of them, which they were told would be displayed to other players with whom they would be playing a computerised ball-throwing game (Cyberball). After a photograph of the

participant was taken using a web-camera connected to the computer, participants read the standard Cyberball instructions (see Williams & Jarvis, 2006). Participants were told that they would be playing the game with other students currently online on the University of London network. Participants then played the game for about 2-3 minutes, during which they were either included or excluded by the other two players. Once the game came to an end, participants started the heartbeat tracking accuracy task for the second time (within 1 minute after finishing the Cyberball game). Then, participants completed the post-Cyberball questionnaire and answered 2 questions assessing whether they believed they were playing against real players. The heartbeat tracking accuracy task was administered before the post-Cyberball questionnaire, due to a potentially short-lived fluctuation in heartbeat perception accuracy (e.g., Antony et al., 1995). The entire experiment was administered using the online survey software Qualtrics (www.qualtrics.com). Upon completion of the experiment, participants were fully debriefed and informed about the real purpose of the study, and provided second-informed consent agreeing to let their data be used in the experiment after they have found out about the deception. See Figure 4-1 for a graphical depiction of the procedure.

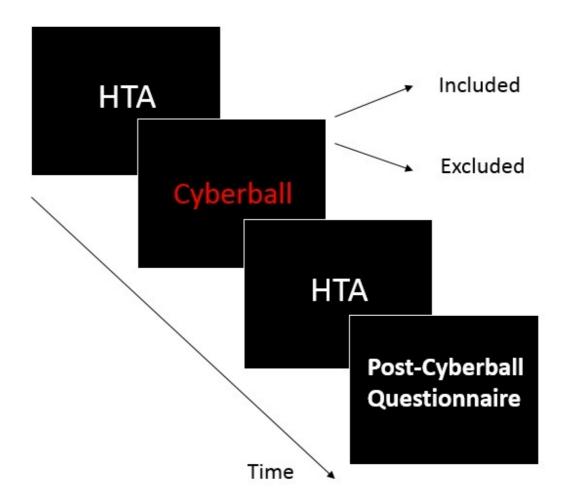


Figure 4-1. Experimental procedure.

4.2.2.4 Data Analysis

4.2.2.4.1 Heartbeat Tracking Accuracy Scores

Heartbeat tracking accuracy (HTA) scores were calculated according to the standard formula:

 $1/3 \Sigma$ (1-(| actual heartbeats – reported heartbeats |) / actual heartbeats).

In the present study, Cronbach's α for the HTA task (based on the tracking accuracy scores of the three intervals) was $\alpha = .94$ for the first assessment and $\alpha = .93$ for the second assessment. Participants were categorised into two HTA groups, consisting of 30 persons with lower baseline HTA (M = .44, SD = .09) and 29 persons with higher baseline HTA (M = .76, SD = .12), using a

median split on the baseline HTA score (Mdn = .57). HTA scores were normally distributed, as indicated by a Shapiro-Wilk test of normality (W = .962, p = .066). See Figure 4-2 for a frequency distribution plot.

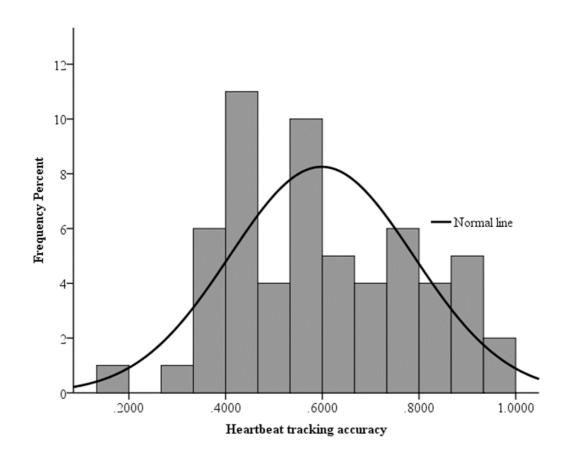


Figure 4-2. Frequency distribution of pre-Cyberball HTA scores in Experiment 3.

4.2.2.4.2 Average Heart Rate

Average heart rate was calculated according to the following formula:

1/3 Σ ((actual heartbeats / length of time interval in seconds) * 60 seconds)

4.2.2.4.3 Post-Cyberball Questionnaire

Items belonging to each of the four need subscales were summed (negative items were first reverse scored) to create four total scores of Belonging, Control,

Meaningful existence, and Self-esteem. Items assessing positive affect and items assessing negative affect were summed to create total positive affect and negative affect scores, respectively. The two items assessing how ignored and how excluded the participants felt were summed.

4.2.2.4.4 Data Analysis Overview

Manipulation check analyses tested for differences in post-Cyberball questionnaire scores between the included and excluded groups. Where the scores were normally distributed, independent samples t-tests were computed and where the scores were not normally distributed, Mann–Whitney U tests were computed. The effect of social exclusion versus inclusion on HTA scores and on HR was examined using two mixed ANOVAs, each with a within-subjects factor of Time (baseline, post-Cyberball) and between-subjects factors of Condition (excluded or included), Sex (male, female) and HTA group (lower HTA, higher HTA). Pearson's r (where both variables were normally distributed) and Spearman's rho (where one or both variables were not normally distributed) correlation coefficients were computed to examine the associations between changes in HTA, changes in HR and post-Cyberball questionnaire subscales.

4.2.2.5 Participants

Sixty-four (43 females; *Mean age* = 21.31; SD = 2.86) students at Royal Holloway, University of London took part in the experiment in compensation for £5. Participants were randomly assigned to one of two conditions so that half of the participants were in the experimental condition (N = 32) where they were excluded while playing Cyberball and the other half of the participants were in the control condition (N = 32) where they were included while playing Cyberball. All participants were non-psychology students who were naïve to the Cyberball paradigm.

4.2.2.5.1 Data Exclusion

In order to ensure that individuals experienced the manipulation as intended, an outlier analysis was performed on manipulation check scores—i.e., retrospective reports of exclusion and mood (positive and negative affect) during

the game. Cases with scores 2 standard deviations above/below group mean on either exclusion or total mood scores were excluded from the main analysis, as they reported experiencing the game in an atypical manner in comparison to the vast majority of the sample (for example, reporting feeling highly included in the excluded condition, or reporting feeling highly excluded in the included condition). Three cases were excluded from the excluded group (reports of exclusion 2 standard deviations below the condition mean) and 2 cases were excluded from the included group (negative mood 2 standard deviations above the condition mean) with 59 cases remaining in total (29 in the excluded condition and 30 in the included condition).

4.2.3 Results

4.2.3.1 Post-Cyberball Questionnaire

Average need subscale scores (Belonging, Control, Meaningful Excistence and Self-esteem) were significantly lower in the excluded group (mean = 10.81, SD = 2.83) than in the included group (mean = 17.32, SD = 2.33) (t (57) = -9.656, p < .001). Mann-Whitney U tests were conducted to test for differences in the specific post-Cyberball questrionnaire subscales, as they were not normally distributed across all participants (with the exception of the Self-esteem and positive affect subscales, which were normally distributed across all participants, allowing for the use of independent samples t-tests). Bonferroni corrections for multiple comparisons were applied throughout the analysis. Participants in the exclusion condition reported significantly lower sense of Belonging (U = 39.000, Z = -6.018, p < .001), Control (U = 109.000, Z = -4.956, p < .001), Meaningful existence (U = 76.000, Z = -5.462, p < .001) and Self-esteem (t = .001.001) after the Cyberball game than participants in the inclusion condition. Moreover, participants in the exclusion condition reported feeling significantly more negative affect (U = 100.500, Z = -5.103, p < .001) and significantly less positive affect (t (57) = -6.053, p < .001) during the game than participants in the inclusion condition. Lastly, participants in the exclusion condition reported feeling significantly more excluded during the game (U = 10.500, Z = -6.549, p <.001) than participants in the inclusion condition, and estimated that they received a significantly lower percentage of total throws during the game (U = .000, Z = -6.639, p < .001) than participants in the inclusion condition. Overall, the included and excluded groups differed significantly on all of the self-reported measures (see Table 4-1), confirming that the Cyberball manipulation was successful. Note that there were no significant differences between excluded male and female individuals, and between excluded individuals who had lower baseline HTA and higher baseline HTA, as indicated by p-values above .05 on a series of Mann-Whitney U tests, and independent sample t-tests.

Table 4-1. Means (and standard deviations) and medians (and ranges) of the post-Cyberball questionnaire scores in the two conditions.

	Excluded gr	roup (N = 29)	Included group $(N=30)$		
	Mean (SD)	Median (range)	Mean (SD)	Median (range)	
Belonging	9.86 (3.56)	9.00 (14.00)	18.93 (3.44)	20.00 (12.00)	
Control	8.76 (3.23)	13.00 (13.00)	14.30 (3.40)	17.00 (12.00)	
Meaningful existence	12.10 (4.03)	13.00 (17.00)	19.17 (2.82)	20.00 (10.00)	
Self-esteem	12.52 (3.16)	8.00 (10.00)	16.87 (3.03)	14.50 (14.00)	
Negative affect	10.86 (3.50)	9.00 (12.00)	5.93 (2.05)	13.50 (10.00)	
Positive affect	9.17 (3.02)	11.00 (12.00)	13.50 (2.45)	6.00 (8.00)	
Feeling excluded	8.28 (1.60)	8.00 (6.00)	3.1 (1.16)	3.00 (4.00)	
Percentage of throws	7.62 (3.5)	8.00 (13.00)	31.10 (6.49)	30.00 (26.00)	

Note: The two groups differed significantly on all scores at $\alpha = .001$ (2-tailed).

4.2.3.2 Heartbeat Tracking Accuracy

HTA scores at baseline were not significantly different in the included and excluded groups (t (57) = 1.235, p = .222). Baseline and post-Cyberball HTA scores were both normally distributed and were analysed in a 2 x 2 x 2 x 2 mixed ANOVA with a within-subjects factor of Time (pre-Cyberball, post-Cyberball) and between-subjects factors of Condition (excluded or included), Sex (male, female) and HTA group (lower HTA, higher HTA). The results revealed a significant interaction effect of Time and Condition on HTA scores (F (1, 51) = 7.017, p = .011, η^2_p = .121). Pairwise t-tests revealed a significant difference in HTA from pre- to post-Cyberball only in the excluded group, where HTA decreased significantly from pre- to post-Cyberball (t (28) = 2.468, p = .020, Cohen's d = .203) and no significant difference in HTA from pre- to post-Cyberball in the included group (t (29) = -.466, p = .644). The effect of Time on HTA in the excluded group remained significant after applying the Bonferroni correction for multiple comparisons (p = .05/2 = .025). See Figure 4-3 for a graphical depiction of the interaction effect of Time and Condition on HTA.

There was no main effect of Sex on HTA (F(1, 51) = .018, p = .895) and Sex did not moderate the interaction effect of Time and Condition on HTA (F(1, 51) = 1.475, p = .230). HTA group also did not moderate the interaction effect of Time and Condition on HTA (F(1, 51) = .987, p = .325).

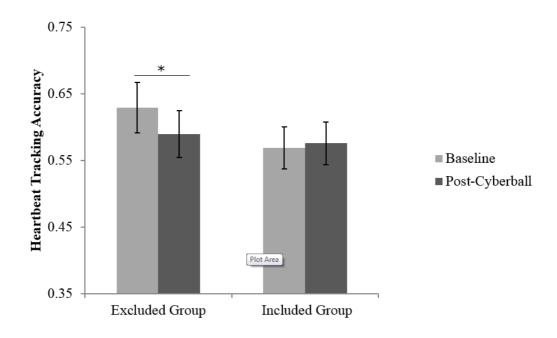


Figure 4-3. Mean heartbeat tracking accuracy scores at baseline and post-Cyberball in the excluded and the included groups along with respective standard errors of means. Note: *p < .05.

In order to ensure that the decrease in HTA from pre- to post-Cyberball observed in the excluded group was not due to change in average heart rate (HR), HR was analysed in a 2 x 2 x 2 x 2 mixed ANOVA with a within-subjects factor of Time (pre-Cyberball, post-Cyberball) and between-subjects factors of Condition (excluded or included), Sex (male, female) and HTA group (lower HTA, higher HTA). The results revealed a significant effect of Time on HR (F(1,51) = 7.049, p = .011, $\eta_p^2 = .121$), as participants decreased in HR from baseline to post-Cyberball. Importantly, there was no significant interaction effect of Time and Condition on HR (F(1, 51) = 2.067, p = .157), indicating that all participants' HR decreased by a comparable degree, suggesting that HR decrease was not due to the manipulation, but rather was brought about by a habituation to the lab setting. There was no main effect of Sex (F(1, 51) = .178, p = .675) and no interaction effect of Time, Condition and Sex (F(1, 51) = 2.040, p = .159) on HR. Although there was a significant main effect of HTA group on HR (F(1, 51) =16.591, p < .001, $\eta^2_p = .245$), there was no interaction effect of Time, Condition and HTA group (F(1, 51) = .569, p = .454) on HR. See Table 4-2 for means of HTA and HR pre- and post-Cyberball in both groups.

Table 4-2. Means (and standard deviations) of average heart rate (HR) in the excluded and in the included groups pre- and post-Cyberball.

		HR Time 1	HR Time 2
Excluded	Low HTA (<i>N</i> = 14)	79.83 (9.22)	79.09 (9.77)
group (N=	High HTA $(N = 15)$	71.08 (11.67)	70.71 (11.57)
29)	Overall	75.30 (11.29)	74.75 (11.38)
Included	Low HTA (<i>N</i> = 16)	91.39 (11.49)	89.62 (10.44)
group (N=	High HTA $(N = 14)$	74.76 (13.80)	73.86 (12.88)
30)	Overall	83.63 (15.00)	82.26 (13.95)

Note: Time 1: pre-Cyberball, Time 2: post-Cyberball.

4.2.3.3 Relationship Between Heartbeat Tracking Accuracy and Other Dependent Measures

In order to examine whether the decrease in HTA from pre- to post-Cyberball in the excluded group was associated with change in HR or with post-Cyberball questionnaire measures, Pearson's r correlation coefficients were computed for analyses where both variables were normally distributed, and Spearman's rho correlation coefficients were computed for analyses where one or both variables were not normally distributed. Variables, which were not normally distributed within the excluded group, included the Control subscale, self-reported exclusion and the perceived percentage of throws received. Baseline HTA scores in excluded participants were not correlated with any of the need subscales, nor mood or exclusion measures. Baseline HTA scores were, however, negatively correlated with change in HTA (HTA post-exclusion — HTA baseline) with individuals with higher baseline HTA experiencing a bigger decrease in HTA from baseline to post-exclusion. Even though baseline HTA and baseline heart

rate (HR) were negatively associated, change in HTA was not significantly correlated with baseline HR, or with change in HR (HR post-exclusion – HR baseline), or with any of the need subscales, nor mood, or exclusion measures. See Table 4-3 for correlation coefficients.

Table 4-3. Correlation coefficients between baseline heartbeat tracking accuracy (baseline HTA) and change in heartbeat tracking accuracy (change in HTA) and other dependent variables in participants in the exclusion condition.

Variable 1	Variable 2				
_	Baseline HTA	Change in HTA			
Baseline HTA		376 [*]			
Change in HTA	376*				
Baseline HR	493**	.171			
Change in HR	018	248			
Belonging	074	.014			
Control	155	.015			
Meaningful existence	113	.054			
Self-esteem	021	.075			
Negative affect	.138	.262			
Positive affect	073	045			
Feeling excluded	.187	204			
Percentage of throws	.264	132			

Note: * correlation is significant at $\alpha = .05$ level, ** correlation is significant at $\alpha = .01$ level (2-tailed). Also, note that Spearman's rho non-parametric correlations

were calculated for Control, Negative affect, Feeling excluded and Percentage of throws as these were not normally distributed. The remaining correlation coefficients are Pearson's r coefficients. N = 29.

4.2.4 Discussion

Experiment 3 utilised the Cyberball paradigm to investigate the effect of a stressful negative affective experience of social exclusion on interoceptive accuracy, measured via heartbeat tracking accuracy (HTA). Because previous research found that social exclusion increases activity in the anterior insula (Cacioppo et al., 2013; Eisenberger 2012a, 2012b) and because anterior insula activation has been associated with enhanced interoceptive accuracy (e.g., Critchley et al., 2004), it was hypothesised that HTA would increase from pre- to post-Cyberball in individuals who were excluded, but not in individuals who were included, during the game. The results of Experiment 3 indicate that HTA remained unchanged in individuals who were included during the game, however, contrary to the hypothesis, HTA decreased from baseline to post-Cyberball in individuals who were excluded. Neither sex, nor HTA group moderated the effect of condition on change in HTA. Nevertheless, change in HTA in the socially excluded individuals was related to baseline HTA, with those higher in baseline HTA showing a greater decrease in HTA after the exclusion. Change in HTA was not due to change in heart rate—included and excluded individuals decreased in heart rate to the same extent, whereas HTA changed only in the excluded group. The change in heart rate, therefore, can be attributed to habituation to the lab setting. It should be noted that there was an effect of HTA group on heart rate and individuals with higher baseline HTA had lower heart rates, overall, than individuals with lower baseline HTA. This finding is in line with past research indicating a negative association between heart rate and heartbeat perception accuracy (Ainley et al., 2012; Fairclough & Goodwin, 2007; Knapp-Kline & Kline, 2005; Stevens et al., 2011), likely due to decreasing stroke volume of individual heartbeats with increasing heart rate (Schandry et al., 1993). Also, the change in HTA was not significantly associated with any of the post-Cyberball questionnaire subscales. It should be noted that it was essential to administer the post-Cyberball questionnaire after the heartbeat counting task due to a potentially

short lived effect of social exclusion on HTA, in comparison to the established robust effect of social exclusion on the post-Cyberball questionnaire measures. However, a limitation of the study is that due to the delay in the administration of the post-Cyberball questionnaire, the self-reports were more reflective rather than reflexive, which could, in turn, potentially account for the lack of a correlation between changes in HTA and self-reported affect after the game. Lastly, baseline HTA was not significantly associated with outcome variables measured post-exclusion, which is contrary to previous findings (e.g., Werner et al., 2009b), and is likely due to the fact that the current sample did not include a sufficient number of individuals on the opposite ends of the spectrum with regards to their interoceptive accuracy scores. Taken together, these results suggest that social exclusion can decrease individual ability to accurately perceive cardiac interoceptive signals, such as heartbeats.

The decrease in HTA observed in Experiment 3 contradicts studies indicating increased activity in the insula—the interoceptive centre of the brain (Craig, 2009)—in response to social exclusion (see Cacioppo et al., 2013). However, the HTA decrease observed in Experiment 3 can be explained using previous research on the nature of social exclusion and its physiological and behavioural effects. One possibility is that decreased accuracy in detecting interoceptive signals might reflect a numbing response to social exclusion. Evidence for numbing effects of socially painful experiences comes from a series of experiments by DeWall and Baumeister (2006) who found that anticipated aloneness can bring about decreased sensitivity to physical pain, as reflected by higher pain thresholds, and higher pain tolerance in the experimental condition, lesser emotional sensitivity, as reflected by lesser empathising with another person's physical and social pain, as well as decreased affective forecasting. In line with these results, it could be suggested that, in Experiment 3, individuals experienced social pain during the game, which then induced a pain-induced analgesic response. This hypothesis would also be in line with studies showing an inverse relationship between HTA and pain thresholds or pain tolerance levels (Pollatos et al., 2012). Nevertheless, it should be considered that DeWall and Baumeister used a different social exclusion paradigm than Experiment 3, and studies investigating the effect of Cyberball exclusion on physical pain perception suggest that there is a heightening, rather than numbing, of physical pain following social pain (Eisenberger et al., 2006). Bernstein and Claypool (2012) suggest that exclusion severity might determine whether hyper- or hyposensitivity to physical pain follows, with pain sensitization being associated with exclusion of lesser severity, and pain numbing being associated with highly severe exclusion. As there was no measure of physical pain in Experiment 3, it cannot be ascertained whether the participants experienced physical pain numbing or heightening following social exclusion. Consequently, the following experiment (Experiment 4) investigates the relationship between interoceptive and pain processing changes following social exclusion.

4.3 Experiment 4

4.3.1 Introduction

Experiment 3 found that heartbeat tracking accuracy decreased from preto post-Cyberball in individuals who were excluded, but not in individuals who were included, during the game. This decrease in heartbeat tracking accuracy can be interpreted in the context of the pain overlap theory (Eisenberger et al., 2006), potentially constituting a form of an analgesic response that is a consequence of the socially painful experience of being socially excluded. Research evidence indicates that social exclusion can be followed by a numbing response reflected by decreased sensitivity to physical pain (e.g., DeWall & Baumeister, 2006). Even though heartbeat tracking accuracy has been found to be negatively correlated with pain thresholds and pain tolerance at rest (Pollatos et al., 2012), the relationship between changes in heartbeat tracking accuracy and changes in pain perception in response to a stressful negative affective experience has not been examined. The present study (Experiment 4) investigated heartbeat tracking accuracy and a pain perception both before and after a Cyberball game, during which participants were included or excluded. It was hypothesised that, as in Experiment 3, heartbeat tracking accuracy would decrease from pre- to post-Cyberball in excluded individuals, but would remain unchanged in included individuals. It was hypothesised that pain thresholds would increase, while pain Cyberball in excluded individuals, but would remain unchanged in included individuals. Lastly, it was hypothesised that in the excluded group, the change in heartbeat tracking accuracy from pre- to post-Cyberball would be inversely related to change in pain thresholds and directly associated with change in pain intensity and pain unpleasantness ratings from pre- to post-exclusion. Both painful and non-painful electrical stimuli were delivered during the pain assessment task in order to determine whether the potential effect of exclusion on pain sensitivity would be specific to the perception of painful exteroceptive signals, or whether it would generalise to the perception of exteroceptive signals that are both painful and not.

4.3.2 Methods

4.3.2.1 Experimental Design

The study utilised a mixed design with a within-subjects factor of Time (pre-Cyberball, post-Cyberball) and between-subjects factor of Condition (excluded, included). Participants were randomly assigned to one of two conditions: included or excluded. See section 4.2.2.1.1 for a description of Cyberball and for details regarding the excluded and included conditions. The dependent measures of HTA, pain threshold and shock ratings were taken pre-Cyberball and post-Cyberball. The post-Cyberball questionnaire was administered post-Cyberball. The order of the HTA task and the pain assessment task (pain threshold measurement and shock intensity and unpleasantness ratings) was counterbalanced across all participants both pre- and post-Cyberball (four possible task orders).

4.3.2.2 Measures

4.3.2.2.1 Post-Cyberball Questionnaire

See section 4.2.2.2.2 for description of the Post-Cyberball Questionnaire.

4.3.2.2.2 Heartbeat Tracking Accuracy

HTA was assessed using the Mental Tracking Method (Schandry, 1981)

outlined in Chapter 2. In this experiment, the assessment consisted of a three-trial block: 25-second, 35-second, and 45-second, trials, presented in a random order. As Experiment 3 used the POLAR RS800CX heart rate monitor during the HTA assessment, Experiment 4 aimed to replicate the effect found in Experiment 3 using the piezo-electric pulse transducer (PowerLab 26T, AD Instruments, UK) to monitor participants' true heart rate.

4.3.2.2.3 Electrical Stimulation

Electric shocks were delivered through two constant current electrical stimulators (DS7A, Digitimer) via two couples of surface electrodes placed in close proximity on the participants' left inner wrist. The shocks were single constant current rectangular monophasic pulses with duration of 2-ms. Each pair of electrodes was connected to one constant current electrical stimulator. One stimulator delivered low intensity shocks and the other stimulator delivered high intensity shocks. The two pairs of electrodes were placed in close proximity so that the shocks from both stimulators occurred in locations on the wrist that were indiscriminable to the participant. Shock intensities were based on individual pain thresholds obtained during the threshold procedure at the beginning of each pain perception assessment (see section 4.3.2.2.3.1 below). Based on the procedure of Sawamoto et al. (2000), low intensity shocks were set to an intensity of 70% of the pain threshold intensity and high intensity shocks were set to an intensity of 170% of the pain threshold intensity so that the high intensity shocks were below pain tolerance level and the low intensity shock were below pain threshold level, but above perceptual threshold level. During the pain perception task, 5 low intensity shocks and 5 high intensity shocks were delivered in random order. Participants were not informed about the intensity of each upcoming shock. One second after shock delivery, the participant was asked to rate shock intensity on a scale from 0 (not at all strong) to 10 (very strong) and shock unpleasantness also on a scale from 0 (not at all unpleasant) to 10 (very unpleasant). Each question, along with the rating scale, was displayed on the screen in front of the participant, one at a time. Participant was asked to answer each question verbally and the answers were recorded by the experimenter. The order in which the two shock

rating questions were administered was counterbalanced across participants. In every trial, a white fixation cross was displayed on the screen from the beginning of the trial until the shock rating questions were displayed. The stimuli were controlled and presented with Matlab software.

4.3.2.2.3.1 Establishing the Pain Threshold

The pain threshold was set through a staircase procedure. Participants received 2-ms shocks on the inner left wrist also in non-fixed time intervals and were asked to verbally report whether the stimulus was painful: 'yes' or 'no'. Once a pain threshold was found, 5 shocks of the pain threshold intensity and 5 shocks of an intensity below the pain threshold intensity were delivered in random order, and participants were asked to verbally report whether each shock was painful: 'yes' or 'no'. In case participant's responses did not indicate that the shocks of the pain threshold intensity were painful and that the shocks of the intensity below pain threshold intensity were not painful, the thresholding procedure, as described above, was resumed. The pain threshold was always calibrated using the same electrical current stimulator, within and across participants.

4.3.2.3 Procedure

Upon completion of demographic information reports, participants were connected to the electrodes and the pulse-transducer by the experimenter. The procedure followed the procedure of Experiment 3, with the exception of also including a pain assessment task before and after the Cyberball game (see section 4.3.2.1 for details of counterbalancing order). During each pain assessment task (both pre- and post-Cyberball), the experimenter calibrated the pain threshold and set the low and high shock intensities accordingly. Then 5 high and 5 low intensity shocks were delivered uncued and in random order (see section 4.3.2.2.3 for details). The entire experiment was administered using Qualtrics online survey software (www.qualtrics.com). As in Experiment 3, participants were fully debriefed and informed about the real purpose of the study upon completion of the study and provided second-informed consent agreeing to let their data be used in the experiment after they have found out about the deception. See Figure 4-4 for a

graphical depiction of the procedure.

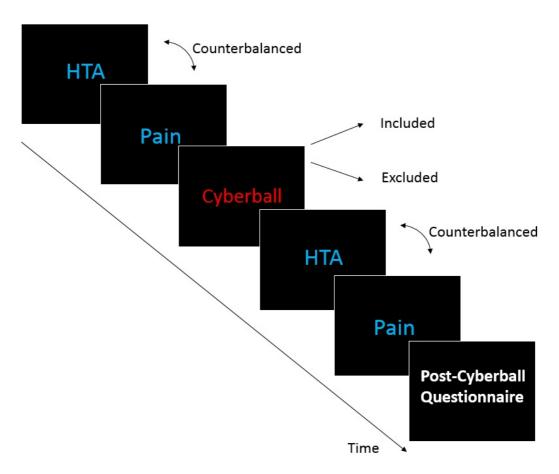


Figure 4-4. Experimental procedure.

4.3.2.4 Data Analysis

4.3.2.4.1 Heartbeat Tracking Accuracy Scores

Heartbeat tracking accuracy (HTA) scores were calculated using the standard formula:

 $1/3 \Sigma$ (1-(| actual heartbeats – reported heartbeats |) / actual heartbeats).

Participants were categorised into two groups, consisting of 30 persons with lower baseline HTA (M = .54, SD = .09) and 29 persons with higher baseline HTA (M = .89, SD = .08), using a median split on the baseline HTA score (Mdn = .72). HTA scores were not normally distributed, as indicated by a Shapiro-Wilk test of normality (W = .925, p = .001). See Figure 4-5 for a frequency distribution

plot.

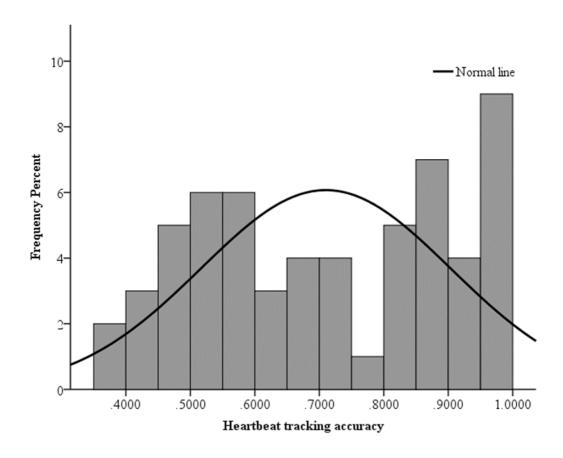


Figure 4-5. Frquency distribution of pre-Cyberball HTA scores in Experiment 4.

4.3.2.4.2 Average Heart Rate

Average heart rate was calculated according to the following formula:

1/3 Σ ((actual heartbeats / length of time interval in seconds) * 60 seconds)

4.3.2.4.3 Shock Intensity and Unpleasantness Ratings

Mean scores were calculated for the intensity ratings of low intensity shocks, for the intensity ratings of high intensity shocks, for the unpleasantness ratings of low intensity and for the unpleasantness ratings of high intensity shocks.

4.3.2.4.4 Post-Cyberball Questionnaire

As in Experiment 3, items belonging to each of the four need subscales were summed (negative items were first reverse scored) to create four total scores of Belonging, Control, Meaningful existence, and Self-esteem. Items assessing positive affect and items assessing negative affect were summed to create total positive affect and negative affect scores, respectively. The two items assessing how ignored and how excluded the participants felt were summed.

4.3.2.4.5 Data Analysis Overview

Manipulation check analyses tested for differences in post-Cyberball questionnaire scores between the included and excluded groups. Where the scores were normally distributed, independent samples t-tests were computed and where the scores were not normally distributed, Mann–Whitney U tests were computed. Correlation analyses were conducted to test for association between dependent variables (HTA, pain perception and post-Cyberball questionnaire scores). The effect of social exclusion versus inclusion on HTA scores, HR and pain perception was examined using mixed ANOVAs with within-subjects factors of Time (baseline, post-Cyberball) and between-subjects factors of Condition (excluded or included), Sex (male, female) and HTA group (lower HTA, higher HTA).

4.3.2.5 Participants

Sixty-three (42 females; mean age = 24.51, SD = 6.21) students at Royal Holloway, University of London took part in the experiment in compensation for £10. Participants were randomly assigned to one of two conditions so that half of the participants were in the experimental condition (N = 32) where they were excluded while playing Cyberball and the other half of the participants were in the control condition (N = 31) where they were included while playing Cyberball. All participants were non-psychology students who were naïve to the Cyberball paradigm.

4.3.2.5.1 Data Exclusion

As in Experiment 3, participants whose manipulation check measures (reports of exclusion and mood during the game) were 2 standard deviations above/below their group mean were excluded from the main analysis. Three cases were excluded from the excluded group (exclusion scores and negative affect scores over 2 standard deviations below the condition mean), and one case was excluded from the included group (negative affect score over 2 standard deviations above the condition mean) with 59 cases remaining in total (29 in the excluded condition and 30 in the included condition).

4.3.3 Results

4.3.3.1 Post-Cyberball Questionnaire

Mann-Whitney U tests were conducted to test for differences in the post-Cyberball questrionnaire subscales, as they were not normally distributed across all participants (with the exception of the Self-esteem and positive affect subscales, which were normally distributed across all participants, allowing for the use of independent samples t-tests). Bonferroni corrections for multiple comparisons were applied throughout the analysis. Participants in the exclusion condition reported significantly lower sense of Belonging (U = 41.500, Z = -5.984, p < .001), Control (U = 102.500, Z = -5.064, p < .001), Meaningful existence (U = 137.000, Z = -4.535, p < .001), and Self-esteem (t (57) = 5.053, p < .001) .001) after the Cyberball game than participants in the inclusion condition Moreover, participants in the exclusion condition reported feeling significantly more negative affect (U = 108.500, Z = -4.982, p < .001) and significantly less positive affect (t (57) = 5.457, p < .001) during the game than participants in the inclusion condition. Lastly, participants in the exclusion condition reported feeling significantly more excluded during the game (U = 44.000, Z = -6.003, p <.001) than participants in the inclusion condition, and estimated that they received a significantly lower percentage of total throws during the game (U = 36.500, Z =- 5.937, p < .001) than participants in the inclusion condition. Overall, the included and excluded groups differed significantly on all of the self-reported measures (see Table 4-3 for means and standard deviations), confirming that the

Cyberball manipulation was successful. Note that there were no significant differences between excluded male and female individuals, and between excluded individuals who had lower baseline HTA and higher baseline HTA, as indicated by *p*-values above .05 on a series of Mann-Whitney U tests, and independent sample t-tests.

Table 4-4. Means (with standard deviations) and medians (with ranges) for self-reported scores in the excluded and included conditions.

	Excluded g	roup (N = 29)	Included group $(N=30)$		
	Mean (SD)	Median (range)	Mean (SD)	Median (range)	
Belonging	9.76 (2.44)	10.00 (12.00)	18.33 (3.99)	18.50 (16.00)	
Control	8.07 (2.75)	10.00 (15.00)	14.07 (4.03)	16.00 (14.00)	
Meaningful existence	11.97 (3.64)	12.00 (12.00)	17.47 (3.99)	17.50 (16.00)	
Self-esteem	11.17 (3.99)	7.00 (9.00)	16.33 (3.85)	15.00 (15.00)	
Negative affect	12.55 (3.87)	9.00 (11.00)	6.90 (2.44)	14.00 (14.00)	
Positive affect	8.65 (2.57)	13.00 (16.00)	13.13 (3.63)	6.00 (8.00)	
Feeling excluded	8.31 (1.42)	8.00 (5.00)	4.17 (1.78)	4.00 (6.00)	
Percentage of throws	10.48 (6.53)	10.00 (29.00)	31.25 (10.63)	30.00 (60.00)	

Note: The two groups differed significantly on all scores at $\alpha = .001$ (2-tailed).

4.3.3.2 Relationship Between Heartbeat Tracking Accuracy and Pain Perception

Baseline heartbeat perception accuracy was not significantly correlated with pain thresholds or with the intensity and unpleasantness ratings of high and low intensity shocks (in all participants and pre-Cyberball). Spearman's rho correlation coefficients (all of the variables were not normally distributed) are listed in Table 4-5.

Table 4-5. Spearman's rho correlation coefficients between heartbeat tracking acuracy (HTA), pain thresholds, intensity and unpleasantness ratings of high and low intensity shocks pre-Cyberball in all participants.

	1.	2.	3.	4.	5.	6.
1. HTA	-					
2. Pain threshold	037	-				
3. Intensity HS	026	.193	-			
4. Unpleasantness HS	228	.228	.721***	-		
5. Intensity LS	.000	.137	.415**	.176	-	
6. Unpleasantness LS	111	.196	.349**	.416**	.749***	-

Note: ***: correlation is significant at p < .001 (2-tailed), **: correlation is significant at p < .01 (2-tailed). HS: high intensity shocks; LS: low intensity shocks. N = 56.

4.3.3.3 Relationship Between Heartbeat Tracking Accuracy, Pain Thresholds and Post-Cyberball Questionnaire Measures

Baseline heartbeat tracking accuracy did not significantly correlate with self-reported measures of exclusion, as measured with the post-Cyberball questionnaire (see Table 4-6). However, baseline pain threshold was significantly

correlated with several post-Cyberball questionnaire scores post-exclusion. Specifically, higher baseline pain thresholds were associated with higher sense of Belonging (as a trend), Meaningful existence and Self-esteem following exclusion in the Cyberball game. Additionally, higher baseline pain threshold was associated with lower level of Negative affect and higher level of Positive affect following the exclusion (see Table 4-6).

Table 4-6. Correlation coefficients between post-Cyberball questionnaire measures and baseline pain thresholds, and baseline heartbeat tracking accuracy (baseline HTA) in the excluded group.

Variable 1	Variable 2			
	Baseline pain threshold	Baseline HTA		
Belonging	.330 ⁺	142		
Control	.283	.125		
Meaningful existence	.507**	.049		
Self-esteem	.579**	.005		
Negative affect	531**	.031		
Positive affect	.523**	114		
Feeling excluded	092	213		
Percentage of throws	092	.118		

Note: ** correlation is significant at p < .01 (2-tailed), + correlation is significant at p < .10 (2-tailed). Also, note that Spearman's rho non-parametric correlations were calculated for Baseline pain threshold, Control, Meaningful existence, Self-esteem, Feeling excluded and Percentage of throws as these were not normally distributed. The remaining correlation coefficients are Pearson's r coefficients. N = 28.

4.3.3.4 Heartbeat Tracking Accuracy

HTA scores pre-Cyberball were not significantly different in the included and excluded groups as revealed by a Mann-Whitney U test (U = 385.000, Z = .758, p = .456) (note that baseline and and post-Cyberball HTA scores were nonnormally distributed). The Kruskal-Wallis test revealed no significant effect of Task order on HTA pre-Cyberball (χ^2 (3, 59) = 1.448, p = .694) and post Cyberball (χ^2 (3, 59) = 1.668, p = .644). Because the pre- and post-Cyberball HTA scores were non-normally distributed, and the baseline scores were not significantly different between the included and excluded conditions, normally distributed HTA change (HTA post-Cyberball – HTA pre-Cyberball) scores were used in subsequent analyses of HTA. A 2 x 4 ANOVA with the between-subjects factors of Condition and Task order was used to analyse change in HTA (HTA post-Cyberball – HTA baseline), revealing no significant effect of Task order on HTA change (F (3, 51) = .104, p = .958) and no significant interaction effect of Task order and Condition on HTA change (F (3, 51) = .818, p = .490).

HTA change scores were analysed in a 2 x 2 x 2 between-subjects ANOVA with factors of Condition (included or excluded), HTA group (lower HTA, higher HTA) and Sex (male, female). The results revealed no effect of Condition on HTA change (F(1, 51) = .449, p = .506). There was no main effect of Sex on HTA change (F(1, 51) = 1.011, p = .320), no interaction effect of Condition and Sex on HTA change (F(1, 51) = .199, p = .657), and no interaction effect of Condition and HTA group on HTA change (F(1, 51) = .974, p = .328). In order to test for the effect of Time (pre-Cyberball, post-Cyberball) on HTA, Wilcoxon Signed Ranks Tests were conducted on HTA scores pre- and post-Cyberball in the included and excluded groups. The Wilcoxon Signed Ranks Test indicated no significant difference in HTA from baseline to post-Cyberball in included individuals (Z = -.195, p = .855) and in excluded individuals (Z = -1.027, p = .314).

Average heart rate (HR) scores were square root transformed in order to normalise the data, and were subsequently analysed in a 2 x 2 x 2 x 2 x 4 mixed ANOVA with within-subjects factor of Time (pre-Cyberball, post-Cyberball) and

between-subjects factors of Condition (excluded or included), Sex (male, female), HTA group (lower HTA, higher HTA) and Task order (4 possible orders). There was no main effect of Task order (F(3, 31) = .048, p = .986), no main effect of Sex (F(1, 31) = .471, p = .498), no interaction effect of Task order and Condition (F(3,31) = 1.732, p = .181) and no interaction effect of Sex and Condition (F(1,31) = .129, p = .722) on HR so the factors of Task order and Sex were removed from the analysis. The resultant 2 x 2 x 2 mixed ANOVA revealed a significant effect of Time on HR $(F(1, 55) = 10.093, p = .002, \eta_p^2 = .155)$ with participants decreasing in HR from pre- to post-Cyberball. There was no significant interaction effect of Time and Condition on HR (F(1, 55) = .002, p = .966)indicating that HR in both groups decreased by a comparable degree, suggesting the decrease was not due to the manipulation, but rather habituating to the lab setting. There was a significant main effect of HTA group on HR (F(1, 55)).983, p = .011, $\eta_p^2 = .112$), with individuals with lower HTA displaying higher HR than individuals with higher HTA. There was a significant interaction effect of Time, Condition and HTA group on HR $(F(1, 55) = 6.119, p = .016, \eta_p^2 =$.100). After splitting the data by Condition, there was a significant interaction of Time and HTA group on HR in the excluded group (F(1, 27) = 8.862, p = .006, $\eta_p^2 = .247$) and not in the included group (F (1, 28) = 1.992, p = .169). Pairwise ttests revealed a significant decrease in HR from pre- to post-Cyberball only in excluded individuals with lower HTA (t (14) = 4.115, p < .001) and not in excluded individuals with higher HTA (t(13) = .871, p = .399). See Table 4-7 for means and standard deviations of HTA and HR pre- and post-Cyberball in both groups. See Table 4-7 for means and standard deviations of heartbeat tracking accuracy scores and average heart rate pre- and post-Cyberball in both conditions.

Table 4-7. Means (with standard deviations) and medians (with ranges) of the heartbeat tracking accuracy (HTA) and average heart rate (HR) in the excluded and in the included groups pre- and post-Cyberball.

	Excluded group (N = 29)		Included group $(N=30)$		
	Mean (SD) Median (range)		Mean (SD)	Median (range)	
HTA Time 1	.69 (.19)	.68 (.60)	.73 (.20)	.76 (.58)	
HTA Time 2	.71 (.19)	.75 (.60)	.73 (.20)	.74 (.64)	
HR Time 1	77.72 (14.89)	76.20 (63.22)	76.90 (10.38)	75.57 (44.72)	
HR Time 2	75.52 (12.49)	75.49 (58.63)	74.93 (11.15)	73.66 (52.20)	

Note: Time 1: pre-Cyberball, Time 2: post-Cyberball.

4.3.3.5 Pain Perception

4.3.3.5.1 Pain Thresholds

Three outliers were identified with scores over 3.5 standard deviations above sample mean on both threshold values and were excluded from this analysis (2 in the included condition and 1 in the excluded condition) resulting in a total of 56 cases being included in this analysis. The scores were transformed to normality using a square root transformation. Pain thresholds at baseline were not significantly different in the included and excluded groups as indicated by an independent samples t-test (t (54) = -.893, p = .376). The threshold values were entered into a 2 x 2 x 4 x 2 x 2 mixed ANOVA with within-subjects factor of Time (baseline, post-Cyberball) and between-subjects factors of Condition (included, excluded), Task order (4 possible orders), Sex (male, female) and HTA group (lower HTA, higher HTA). As there was no significant effect of Task order (F (3, 30) = .384, P = .766) and no significant interaction effect of Task order and Condition (F (3, 30) = 2.813, P = .056) on thresholds, the factor of Task order was removed from the analysis. The resulting 2 x 2 x 2 x 2 mixed ANOVA revealed

no significant effect of Time (F (1, 48) = .014, p = .905) and no significant interaction of Time and Condition (F (1, 48) = .820, p = .370) on pain thresholds. There was no main effect of Sex (F (1, 48) = 3.209, p = .080), no interaction of Sex and Condition (F (1, 48) = .009, p = .924) and no interaction of Sex, Condition and Time (F (1, 48) = .064, p = .802) on pain thresholds. There was no main effect of HTA group (F (1, 48) = .765, p = .386), no interaction of HTA group and Condition (F (1, 48) = .979, p = .327) and no interaction of HTA group, Condition and Time (F (1, 48) = .825, p = .368) on pain thresholds. See Figure 4-7 for a graphical depiction of the results.

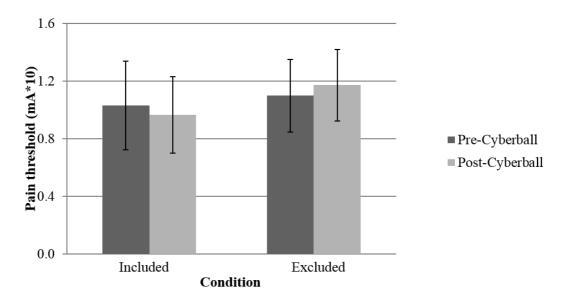


Figure 4-6. Pain thresholds pre- and post-Cyberball in the included and excluded groups along with respective standard errors of means.

4.3.3.5.2 Shock Intensity and Unpleasantness Ratings

Both intensity and unpleasantness ratings of the high intensity shocks pre-Cyberball were not significantly different between the included and excluded groups (Z = -.788, p = .438 and t (42) = .870, p = .389, respectively), as well shock intensity and unpleasantness ratings of the low intensity shocks pre-Cyberball were not significantly different between the included and excluded groups (Z = -.165, p = .875 and Z = -.436, p = .670, respectively). Note that both pre- and post-Cyberball high and low intensity shock intensity ratings were nonnormally distributed and pre- and post-Cyberball low intensity shock unpleasantness ratings were non-normally distributed.

4.3.3.5.2.1 High Intensity Shocks

Intensity ratings of high intensity shocks (squared, in order to transform the scores to normality) were analysed in a 2 x 2 x 2 x 2 mixed ANOVA with a within-subjects factor of Time (pre-Cyberball, post-Cyberball) and between-subjects factors of Condition (included or excluded), Sex (male, female) and HTA group (lower HTA, higher HTA). The results revealed no main effect of Time (F (1, 48) = 3.085, p = .085), no interaction of Time and Condition (F (1, 48) = .441, p = .510), no interaction of Time, Condition and Sex (F (1, 48) = 1.074, p = .305) and no interaction of Time, Condition and HTA group (F (1, 48) = .000, p = .996) on the intensity ratings of high intensity shocks. Also, there was no main effect of Sex (F (1, 48) = .334, p = .566) and no main effect of HTA group (F (1, 48) = .743, F = .393) on the intensity ratings of high intensity shocks. See Table 4-8 for means and standard deviations of the intensity ratings of high intensity shocks across conditions.

Unpleasantness ratings of high intensity shocks were analysed in a 2 x 2 x 2 mixed ANOVA with the same factors as above, revealing a main effect of Time (F (1, 48) = 4.141, p = .047, η_p^2 = .079), with unpleasantness ratings of high intensity shocks increasing from pre- to post-Cyberball in all participants, regardless of participants' group. There was no interaction of Time and Condition (F (1, 48) = .008, p = .928), no interaction of Time, Condition and Sex (F (1, 48) = .258, p = .614) and no interaction of Time, Condition and HTA group (F (1, 48) = .192, p = .663) on the unpleasantness ratings of high intensity shocks. Also, there was no main effect of Sex (F (1, 48) = 1.197, p = .279) and no main effect of HTA group (F (1, 48) = 1.400, p = .243) on the unpleasantness ratings of high intensity shocks. See Table 4-8 for means and standard deviations of the unpleasantness ratings of high intensity shocks across conditions.

Table 4-8. Mean intensity ratings (and standard deviations) and mean unpleasantness ratings (and standard deviations) of low intensity shocks and of high intensity shocks pre- and post-Cyberball in included and excluded groups.

		Low	Shock	High Shock		
		Intense	Unpleasant	Intense	Unpleasant	
Included group	Pre- Cyberball	2.42 (1.58)	2.00 (1.50)	7.06 (1.45)	6.49 (1.49)	
(N=28)	Post- Cyberball	2.46 (1.79)	2.19 (1.67)	7.33 (1.55)	7.02 (1.43)	
Excluded group	Pre- Cyberball	2.15 (1.11)	1.76 (1.21)	6.62 (2.04)	6.25 (1.72)	
(N=28)	Post- Cyberball	2.56 (1.25)	1.91 (1.25)	6.97 (2.13)	6.69 (1.80)	

4.3.3.5.2.2 Low Intensity Shocks

Intensity ratings of low intensity shocks (square root transformed to normality) were analysed in a 2 x 2 x 2 x 2 mixed ANOVA with a within-subjects factor of Time (pre-Cyberball, post-Cyberball) and between-subjects factors of Condition (included or excluded), Sex (male, female) and HTA group (lower HTA, higher HTA). The results revealed no main effect of Time (F (1, 48) = .790, p = .379), no interaction of Time and Condition (F (1, 48) = 3.061, p = .087), no interaction of Time, Condition and Sex (F (1, 48) = 2.207, p = .144) and no interaction of Time, Condition and HTA group (F (1, 48) = .119, p = .731) on the intensity ratings of low intensity shocks. Also, there was no main effect of Sex (F (1, 48) = .205, p = .653) and no main effect of HTA group (F (1, 48) = .515, p =

.476) on the intensity ratings of low intensity shocks. See Table 4-6 for means and standard deviations of the intensity ratings of low intensity shocks across conditions.

Unpleasantness ratings of low intensity shocks (also square root transformed to normality) were analysed in a 2 x 2 x 2 x 2 mixed ANOVA with the same factors as above, revealing no main effect of Time (F(1, 48) = .741, p = .394), no interaction of Time and Condition (F(1, 48) = .647, p = .425), no interaction of Time, Condition and Sex (F(1, 48) = 2.753, p = .104) and no interaction of Time, Condition and HTA group (F(1, 48) = .439, p = .511) on the unpleasantness ratings of low intensity shocks. Also, there was no main effect of Sex (F(1, 48) = .196, p = .660) and no main effect of HTA group (F(1, 48) = .648, p = .425) on the unpleasantness ratings of low intensity shocks. See Table 4-6 for means and standard deviations of the unpleasantness ratings of low intensity shocks across conditions.

4.3.4 Discussion

Experiment 4 investigated the effect of a stressful negative affective experience of social exclusion on interoceptive accuracy (measured via heartbeat tracking accuracy) and on pain perception (measured via pain thresholds and intensity and unpleasantness ratings of high and low intensity shocks). As Experiment 3 found that heartbeat tracking accuracy decreased from pre- to postexclusion, it was hypothesised that the same effect of social exclusion on heartbeat tracking accuracy would be observed in Experiment 4. Experiment 4 tested the hypothesis that the decrease in heartbeat tracking accuracy from pre- to post-exclusion observed in Experiment 3 was due to a numbing effect of social exclusion. This hypothesis was based on the findings of DeWall and Baumeister (2006), who observed a decrease in physical pain following social exclusion and on the results of Pollatos et al. (2012), indicating an inverse relationship between heartbeat tracking accuracy and sensitivity to pain. Consequently, it was predicted that, in Experiment 4, a decrease in heartbeat tracking accuracy and a decrease in pain sensitivity (as reflected by increased pain thresholds and decreased pain intensity and pain unpleasantness ratings) would be observed from pre- to postCyberball in the excluded, but not in the included individuals. It was hypothesised that change in heartbeat tracking accuracy and pain sensitivity in the excluded participants would be inversely related.

Contrary to the predictions set out at the beginning of Experiment 4, social exclusion during the Cyberball game did not decrease heartbeat tracking accuracy. Social exclusion, furthermore, did not decrease pain sensitivity, as evidenced by unchanged pain thresholds and the intensity and unpleasantness ratings of high intensity shocks. Unpleasantness ratings of high intensity shocks increased from pre- to post-Cyberball in all individuals, regardless of inclusion/exclusion, likely reflecting time-related sensitisation to pain. This results of sensitisation to pain unpleasantness is in line with findings of Meulders, Vansteenwegen and Vlaeyen (2012) indicating sensitisation to electrocutaneous pain unpleasantness (and not pain intensity) occurring in females during pain conditioning. Meulders and colleagues suggest that this sensitisation effect might be due to increases in conditioned fear of pain throughout the experiment. As the present study (Experiment 4) also used a conditioning paradigm and electrocutaneous stimulation to induce pain (while the sample was predominantly female), it is likely that increased pain unpleasantness ratings in included and excluded participants reflect the pain unpleasantness sensitisation effect observed by Meulders et al.

Interestingly, average heart rate decreased in individuals with low baseline heartbeat tracking accuracy from pre- to post-exclusion, but not in individuals with high baseline heartbeat tracking accuracy. Heart rate was unchanged in individuals who were included during the Cyberball game. The decrease in average heart rate from pre- to post-Cyberball in the excluded individuals might be a manifestation of heart rate deceleration in response to social exclusion that has been previously observed in research on the topic (e.g., Gunther Moor et al., 2010). As individuals with higher heartbeat tracking accuracy had average heart rates significantly lower than individuals with lower heartbeat tracking accuracy—in line with past research (e.g., Ainley et al., 2012; Stevens et al., 2011)—it might be the case that individuals with high heartbeat tracking accuracy faced a 'floor effect', with their heart rates not decreasing as much following the

exclusion due to already being relatively low. It should be noted, however, that Experiment 4 did not aim to investigate the effect of social exclusion on heart rate, and consequently heart rate was not monitored during the Cyberball game, limiting the conclusions that can be drawn from the data.

The results of Experiment 4 indicated that heartbeat tracking accuracy was not significantly correlated with sensitivity to pain at rest, as reflected by lack of significant associations between heartbeat tracking accuracy scores and pain thresholds as well as intensity and unpleasantness ratings of high and low intensity shocks. The lack of a relationship between heartbeat tracking accuracy and pain sensitivity observed in Experiment 4 is contrary to the results of Pollatos et al. (2012) who found a significant negative correlation between heartbeat tracking accuracy scores and pressure pain thresholds and pressure pain tolerance. However, it should be noted that an association between interoceptive accuracy and pain perception has not always been observed. For example, Werner et al. (2009b) failed to observe a significant relationship between cardiac interoceptive accuracy and the perception of heat pain. A potential reason for the disparate results of the present study, of the results of Pollatos et al. and of the results of Werner et al. might be the use of varying methods of pain assessment (electrocutaneous pain, pressure pain and heat pain, respectively). Even though it has been suggested that pain thresholds to different types of stimuli (i.e., heat, electric, pressure) measure the same phenomenon of general pain sensitivity (e.g., Neddermeyer, Flühr, & Lötsch, 2008), it might be the case that different pain modalities tap into distinct dimensions of nociception (Neziri et al., 2011). Consequently, consistent methodology in pain assessment and interoceptive accuracy assessment across experiments is necessary in order to establish the nature of the relationship between interoceptive accuracy and pain perception.

As previous research found that the experience of social exclusion can activate an endogenous opioid system (Hsu et al., 2013) as well as be followed by decreased sensitivity to physical pain (DeWall & Baumeister, 2006), it was hypothesised that excluded, but not included, individuals in Experiment 4 would show increased pain thresholds and decreased intensity and unpleasantness ratings of high intensity shocks following the Cyberball game. The results of Experiment

4 indicated no effect of social exclusion on pain sensitivity. However, baseline pain thresholds were inversely related to the severity of the psychological response to social exclusion, as measured by the self-reported outcomes reported on the post-Cyberball questionnaire. This relationship between physical pain sensitivity and social pain sensitivity has been previously observed by Eisenberger et al. (2006), and likely is the manifestation of common mechanisms being involved in social and physical pain processing (Eisenberger & Lieberman, 2004). The findings of Experiment 4 indicating no effect of social exclusion on physical pain are contrary to the results of DeWall and Baumeister (2006), but also to other research evidence indicating pain sensitisation following social exclusion (e.g., Eisenberger, Lieberman, & Williams, 2003). Bernstein and Claypool (2012) suggest that whether social exclusion leads to pain heightening or pain numbing might depend on the severity of the exclusion, observing that a more severe version of an exclusion manipulation led to higher pressure pain thresholds and tolerance levels, while a less severe version of the exclusion manipulation led to lower pressure pain thresholds and tolerance levels. While the exclusion paradigm might influence the effect of social exclusion on pain perception, other aspects of the methodology, such as pain modality measured, might account for disparate results across experiments investigating the effect of social exclusion on pain. Importantly, there might be a limit to social and physical pain overlap. More specifically, Riva et al. (2014) have observed that fear of physical pain and fear of social pain selectively affect the experience of physical and social pain, respectively, failing to find an effect of fear of physical pain on the experience social pain and vice versa. Additionally, a recent meta-analysis by Cacioppo et al. (2013) did not indicate a full overlap in the neural networks activated by social rejection and by physical pain, suggesting that the connection between social and physical pain systems might be more complex than previously thought. Consequently, Cacioppo and colleagues suggest that the neural network activated by social exclusion - reliably involving the anterior insula and the anterior cingulate – might be more reflective of "social uncertainty, rumination, distress, and craving rather than social pain per se" (p. 2). For further discussion of the limitations of the pain overlap theory, see Iannetti, Salomons, Moayedi, Mouraux

and Davis (2013).

Finally, several inter-individual difference variables might moderate the effect of social exclusion on pain perception. For example, pain perception can be directly influenced by individual levels of pain catastrophising (Weissman-Fogel, Sprecher, & Pud, 2008) and fear of pain (Hirsh, George, Bialosky, & Robinson, 2008), and therefore might also influence the way in which social exclusion affects pain perception. Moreover, as the way in which an individual relates to others (i.e., their attachment style) may influence his or her predictions about safety and threat (Krahé et al., 2013), attachment style might be a key factor moderating the effect of social exclusion on pain perception. Frías and Shaver (2014) found that attachment anxiety and attachment avoidance predicted pain sensitivity during a cold pressor task following exclusion in a Cyberball game, suggesting that the effect of exclusion on pain perception might be moderated by attachment style. Consequently, the fact that social exclusion did not affect pain sensitivity in Experiment 4 might be explained by unmeasured individual difference characteristics of the tested sample.

4.4 General Discussion

Experiment 3 examined the effect of social exclusion on heartbeat tracking accuracy, finding that individuals who were socially excluded while playing the Cyberball game displayed decreased heartbeat tracking accuracy following the game as compared to baseline. As social exclusion has been previously observed to bring about a numbing of physical pain, it was hypothesised that the decrease in heartbeat tracking accuracy after the exclusion might be reflective of bodily numbing induced by the experience of social pain. Experiment 4 aimed to test this hypothesis by measuring both heartbeat tracking accuracy and pain perception before and after social exclusion. However, Experiment 4 failed to replicate the decrease in heartbeat tracking accuracy from pre- to post-exclusion. Further, the results of Experiment 4 did not show a physical numbing effect in socially excluded individuals.

It must be considered that Experiment 4 was not a direct replication of Experiment 3 and the lack of an effect of social exclusion on heartbeat tracking

accuracy in Experiment 4 does not invalidate the results of Experiment 3. Considering pain anticipation is inherently anxiety provoking, it could have increased heartbeat tracking accuracy, thereby cancelling out the decrease in heartbeat tracking accuracy evoked by social exclusion. The hypothesis that pain anticipation would impact heartbeat tracking accuracy is supported by evidence from brain imaging studies showing increased insula activity during pain anticipation (Chua et al., 1999; Ploghaus et al., 1999), and is explored in Experiment 5 described in the following chapter. Additionally, is possible that pain perception was affected by engaging in the cardiac interoceptive accuracy task. Pain is a highly subjective experience that is determined not only by bottomup perceptual input, but that is strongly conditional on top-down modulation by cognitive factors such as expectations and beliefs (see Atlas & Wager, 2012 for a review). As attention to the body has been proposed to be one of the factors affecting pain perception, as well as mediating the effect of pain anticipation on pain perception (Crombez, Van Damme, & Eccleston, 2005), it is a possibility that the heartbeat tracking task also had an effect on pain perception, although the direction of the potential effect is not certain. While some studies indicate that attention toward pain increases the experience of pain and attention away from pain decreases pain (Miron, Duncan, & Bushnell, 1989; Bantick et al., 2002), there is considerable evidence for the opposite, with results suggesting that increased bodily attention is associated with reduced pain (Leventhal, Brown, Shacham, & Engquist, 1979; Longo et al., 2009). These inconsistencies have been postulated to result from a variety of factors, including differential focus on the affective versus sensory aspects of pain, or the mode of somatic focus (Eccleston, 1995; Seminowicz & Davis, 2007). These theories, however, fail to provide definite evidence for any single mechanism mediating the link between attention to, and perception of bodily signals and the experience of pain, necessitating further empirical investigation. The following chapter describes Experiment 5, in which the relationship between interoceptive accuracy and pain processing is further investigated.

As Experiment 4 found no relationship between changes in heartbeat tracking accuracy and pain sensitivity following social exclusion, explanations

alternative to the numbing effect of social exclusion must be considered in interpreting the results of Experiment 3. As threat captures and holds attention (e.g., Koster, Crombez, Van Damme, Verschuere, & De Houwer, 2004), one could argue that the decrease in heartbeat tracking accuracy following Cyberball exclusion in Experiment 3 might have resulted from a lack of availability of attentional resources necessary to perform the heartbeat counting task, which, instead, were deployed to process the social threat of the exclusion. Consequently, an alternative explanation of the heartbeat tracking accuracy decrease following social exclusion observed in Experiment 3 might be a switch from relying on the predictive control system to relying on the reactive control system of the brain (Tops, Boksem, Luu, & Tucker, 2010; Tops, Boksem, Quirin, IJzerman, & Koole, 2014). Tops and colleagues (2010, 2014) propose that the predictive control system—associated with the posterior medial-dorsal cortical system—processes familiar information and guides behaviour in familiar and highly predictable environments, while the reactive control system—tied to the anterior temporalventrolateral prefrontal cortical system—processes novel, and salient stimuli in unpredictable environments. Tops and colleagues argue that the predictive system, being guided by internal models of self and others, is essential for internally directed cognition and self-reflection, and consequently, being able to access one's own state, whereas the reactive system is guided by the experiential mode which is focused on the here and now, with environmental cues directing ongoing evaluation of action progress. As social exclusion constitutes a highly salient and threatening situation in which individuals must become more vigilant of the surroundings, it likely activates the reactive control system. This is supported by research on the effects of social exclusion on thermoregulation, which shows that socially excluded individuals show decreased skin temperature, most likely due to the reactive system increasing core body temperature, and decreasing skin temperature and blood flow to the extremities (see IJzerman et al., 2012). Consequently, in Experiment 3, social exclusion could have triggered a shift from predictive to reactive control, which could have caused attention to be oriented externally rather than internally, resulting in decreased accuracy in detecting internal bodily signals such as heart beats.

Finally, decreased self-focus and increased other-focus could be used to explain the results of Experiment 3. As social isolation constitutes a threat to the organism, socially rejected individuals are likely to engage in behavioral patterns aimed at reestablishing social bonds following rejection. For example, Lakin, Chartrand and Arkin (2008) observed that after being excluded in a Cyberball game, individuals mimicked a stranger to a larger degree than those who did not experience the social rejection. Further, Hess and Pickett (2010) found that individuals excluded during the Cyberball game showed reduced memory for selfrelated social behaviours, and increased memory for other-related social behaviours, as compared to individuals included in the game. Overall, these results suggest that social exclusion can bring about a decrease in self-focus, and an increase in other-focus. While nonconscious mimicry and other affiliationincreasing behaviours inherently rely on disengaging from the self and reengaging with the other, some researchers have suggested that decreased self-focus in an emotionally painful situation might also serve as a defence strategy in which the individual protects him or herself from aversive self-awareness (e.g., Twenge, Catanese, & Baumeister, 2003), which can bring about distressing thoughts about the self, in light of the socially painful situation (e.g., Heatherton & Baumeister, 1991). However, Hess and Pickett (2010) highlight that by disengaging from the self, the individual can simultaneously avoid the distress brought about by social failure, while freeing attentional resources, which can then be allocated to others and the external world, with the aim to increase affiliation and improve the likelihood of social success in the future. As past research shows that conditions characterized by heightened self-focus are associated with enhanced heartbeat tracking accuracy (Ainley et al., 2012, 2013), it is likely that the decrease in heartbeat tracking accuracy following social exclusion observed in Experiment 3 reflected decreased self-focus and increased other-focus following the exclusion. It should be noted that Experiment 3 did not measure other-focus. While it is likely that social exclusion during the Cyberball game brought about a decrease in self-focus, which in turn resulted in poorer heartbeat tracking accuracy, the exact nature of the mechanism behind this effect posits a topic for future investigation.

Overall, Experiment 3 and 4 investigated the effect of a stressful negative

affective experience of being socially excluded on cardiac interoceptive accuracy, as measured by heartbeat tracking accuracy. Experiment 3 indicated a decrease in heartbeat tracking accuracy from pre- to post-Cyberball in the excluded, but not in the included, individuals. Experiment 4 tested the hypothesis that the exclusionevoked decrease in heartbeat tracking accuracy observed in Experiment 3 was a manifestation of a general pain numbing due to experiencing social pain. Experiment 4 measured heartbeat tracking accuracy and pain sensitivity both before and after the Cyberball game. The results of Experiment 4 indicated no change in heartbeat tracking accuracy or pain sensitivity due to social exclusion. Consequently, alternative explanations of the effect of social exclusion on heartbeat tracking accuracy observed in Experiment 3 were considered, including a shift from predictive to reactive system control as well as decrease in self-focus and increase in other-focus due to social exclusion. Even though the effect of social exclusion on heartbeat tracking accuracy was not replicated in Experiment 4, it must be considered that Experiment 4 did not employ the same design as Experiment 3, introducing a very salient measure of pain anticipation of which could have influenced interoceptive accuracy. Experiment 5, described in the following chapter, directly examined the hypothesis that pain anticipation can affect heartbeat tracking accuracy.

Chapter 5: Stability of Interoceptive Accuracy During Pain Anticipation⁴

5.1 Introduction

Negative affective experiences of public speaking anticipation and social exclusion are social in character; the present study, Experiment 5, investigated the effect of stress and negative affect resultant from heightened physical, rather than social threat, on heartbeat tracking accuracy. Experiment 4 did not find an effect of social exclusion on heartbeat tracking accuracy that was observed in Experiment 3, which could be due to introducing a salient measure of pain assessment in Experiment 4, which could have increased stress and negative affect in individuals, potentially influencing heartbeat tracking accuracy as a consequence. Moreover, in Experiment 4, pain perception was not affected by the social exclusion manipulation, which is contrary to previous research on the topic (e.g., DeWall & Baumeister, 2006; Eisenberger et al., 2003). As pain perception is strongly modulated by top-down cognitive factors such as attention (Villemure & Bushnell, 2002)—including attention to the body (Eccleston, Crombez, Aldrich, & Stannard, 1997)—it is possible that the heartbeat tracking task, which directed attention to interoceptive bodily signals, also affected the perception of painful stimuli after social exclusion. As previous research has not examined the effect of pain anticipation on heartbeat tracking accuracy nor the effect of interoceptive attention on pain perception, Experiment 5 examined whether pain anticipation influences heartbeat tracking accuracy, while also investigating the effect of an interoceptive attention task (engaging in a heartbeat tracking task), as opposed to an exteroceptive attention task (engaging in an auditory tone counting task) and no attentional task, on pain perception.

⁴ Experiment 5 is in revision as Durlik, C., Pincus, T., Cardini, F., & Tsakiris, M. (In preparation). Pain anticipation increases cardiac interoceptive accuracy: an experimental study.

As described in Chapter 4, interoception has been implicated in pain processing. Pain anticipation has been observed to activate the interoceptive centre of the brain, the anterior insula (Chua et al., 1999; Ploghaus et al., 1999). The anterior insula has been found to mediate the effect of cued anticipation on pain perception (Atlas, Bolger, Lindquist, & Wager, 2010) and the likelihood of a threshold pain stimulus being classified as painful can be predicted by increased cross-talk between the left anterior insula and the midcingulate cortex during the anticipation of that stimulus (Wiech et al., 2010). Moreover, activity in the insula has been associated with the pain-evoked increase in sympathetic autonomic nervous system activation (Critchley, Elliott, Mathias, & Dolan, 2000) and has been implicated in the affective component of the experience of pain (Rainville, 2002). Consequently, Pollatos et al. (2012) suggest that the insula "serves as an interface between interoception, interoceptive sensitivity and pain processing" (p. 1684). Nevertheless, while the insula has been implicated in pain anticipation and pain perception, few studies have directly investigated the relationship between interoceptive accuracy and pain processing.

Two published studies (Pollatos et al., 2012; Werner et al., 2009b) and Experiment 4 of the current thesis investigated the relationship between heartbeat tracking accuracy and pain perception, producing varied results. While Pollatos and colleagues found that individuals with higher heartbeat tracking accuracy had lower pain thresholds and lower pain tolerance levels than individuals with lower heartbeat tracking accuracy, the results of the study by Werner et al. and the results of Experiment 4 indicated no significant differences in pain sensitivity between individuals low and high in heartbeat tracking accuracy. As the study by Pollatos et al., the study by Werner et al. and Experiment 4 of the current thesis measured pain sensitivity using different pain modalities (pressure, heat and electrical pain modalities, respectively), which might involve distinct aspects of nociception (Neziri et al., 2011), it might be the case that interoceptive accuracy is selectively related to pain sensitivity in some, but not all, nociceptive modalities. While more research is necessary to delineate the nature of the relationship between trait interoceptive accuracy and pain perception, research investigating state interoceptive accuracy in relation to pain processing is also lacking.

One study to date investigated the way in which state interoceptive accuracy is affected by the stressful negative experience of physical pain. Schulz, Lass-Hennemann et al., (2013) measured changes in heartbeat tracking accuracy and in heartbeat discrimination accuracy in response to a cold pressor task, in which individuals were instructed to leave their hands for 3 minutes in cold water (0-3°C), as compared to a control manipulation, in which individuals left their hands for 3 minutes in comfortably warm water (32-35°C). Schulz, Lass-Hennenmann and colleagues observed that while heartbeat discrimination decreased, heartbeat tracking accuracy increased, in individuals who performed the cold pressor task. Schulz, Lass-Hennenmann et al. suggest that these discrepant results might be accounted for by the competition of cues model (Pennebaker & Lightner, 1980) and that the stressful experience of the cold pressor task might direct attention towards visceral signals, resulting in less attention being deployed on the processing of exteroceptive signals, which is required during the heartbeat discrimination task. As the cold pressor task has been widely used to experimentally induce mild to moderate thermal pain (Ahles, Blanchard, & Leventhal, 1983; Hodes, Howland, Lightfoot, & Cleeland, 1990; Leventhal et al., 1979; Meagher, Arnau, & Rhudy, 2001), the results of Schulz, Lass-Hennenmann et al. suggest that the experience of pain might increase heartbeat tracking accuracy. Nevertheless, because a social evaluative component was also part of the manipulation (presence of a camera and experimenter of opposite sex during the cold pressor task), it cannot be ascertained that the pain manipulation in itself (without the social component) would also increase heartbeat tracking accuracy. Additionally, as the heartbeat tracking measurement was present after the pain-inducing task, the results of the study by Schulz, Lass-Hennenmann et al. do not provide information about the effects of pain anticipation on heartbeat tracking accuracy. As neuroimaging studies have demonstrated a certain degree of dissociation in neural activation associated with anticipation and perception of pain (Ploghaus et al., 1999) and non-painful emotional stimuli (Bermpohl et al., 2006), it remains to be investigated whether the effect of pain perception on interoceptive accuracy observed by Schulz, Lass-Hennenmann et al. extends to pain anticipation.

It is not presently clear whether anticipation of painful stimuli itself affects state interoceptive accuracy. Johnston, Atlas and Wager (2012) observed that anticipation of heat pain improved heat discrimination, suggesting that the prospect of experiencing pain might enhance bodily perception. However, as heat sensations in the study by Johnston et al. were pain-relevant bodily signals, it is not clear whether pain anticipation would also increase the perception of bodily signals which are not directly pain relevant (e.g., heartbeats). It can be hypothesised that pain anticipation would increase interoceptive accuracy due to the negative affective character of the experience. Physically aversive stimuli increase negative affect and evoke strong psychophysiological reactions such as heightened autonomic arousal (see Kyle & McNeil, 2014 for a review), consequently, it is not surprising that the anticipation of pain evokes negative affective reactions such as fear and anxiety, activating interoceptive brain regions, which are also associated with negative affect and salience detection (Chua et al., 1999; Ploghaus et al., 1999).

The present study (Experiment 5) investigated the effect of pain anticipation on interoceptive accuracy, as measured by heartbeat tracking accuracy. Pain anticipation was manipulated using a cued anticipation paradigm, in which participants were visually cued to expect either a low intensity shock (below the pain threshold), a high intensity shock (above the pain threshold) or a shock of an uncertain intensity (either low or high intensity), which were then rated on their intensity and unpleasantness. Both, high intensity shock anticipation condition and uncertain intensity shock anticipation condition were included, as they manipulated fear of shock and anxiety about shock, respectively (Ploghaus, Becerra, Borras, & Borsook, 2003). A certain expectation of an aversive outcome has been associated with fear responding (aimed at dealing with impeding threat) and subsequent hypoalgesia), while uncertainty with regards to an aversive outcome (pertaining to its timing and occurrence) evokes anxiety and results in hyperalgesia (Ploghaus et al., 2003). Most studies investigating cued pain anticipation used uncertain cue conditions, manipulating threat of shock in order to engage attention and increase anxiety in participants; however, recent research indicates that uncertain cue conditions might be associated with neural responses

not necessarily indicative of dealing with pain anticipation and threat of pain (stimulus-targeted preparatory activity), but with coping with the affectively salient and aversive situation of anxiety and uncertainty (Seidel et al., 2015). As both of these affective contexts, fear and anxiety, are of interest in relation to state interoceptive accuracy, the present study (Experiment 5) utilised the cued pain anticipation paradigm employed by Seidel et al. (2015) (also drawing on Sawamoto et al., 2000).

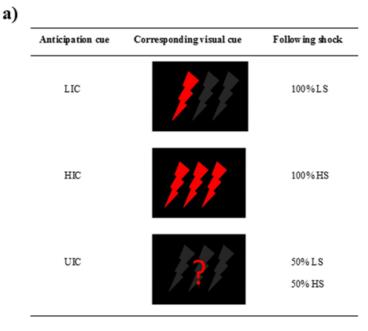
The 3 x 3 factorial design of the present study (Experiment 5) with withinsubjects factors of Anticipation cue (anticipation of a high intensity (painful) electric shock with 100% certainty, anticipation of a low intensity (non-painful) electric shock with 100% certainty and anticipation of an electric shock of an uncertain intensity (50% of the following shocks being painful and 50% of the following shocks being non-painful)) and Task during anticipation (heartbeat tracking task, auditory tone tracking task and no task) allowed for a controlled investigation of the effect of different anticipation conditions on heartbeat tracking accuracy and of the effect of the heartbeat tracking task on pain perception. As individuals performed the heartbeat tracking task in all three anticipation conditions, a direct comparison of the effect of fear induced by the certain pain anticipation condition and anxiety induced by the uncertain anticipation condition on heartbeat tracking accuracy was possible. It was hypothesised that interoceptive accuracy would be increased by the two affectively distressing conditions of pain fear and pain anxiety, as reflected by higher heartbeat tracking accuracy scores during anticipation of high intensity (painful) electric shocks and during anticipation of an electric shocks of uncertain intensity, as compared to anticipation of low intensity (non-painful) electric shocks. As heartbeat tracking accuracy scores as well as insula activity have been associated with the affective (ratings of pain unpleasantness), as opposed to sensory (ratings of pain unpleasantness) dimension of pain perception (Pollatos et al., 2012; Rainville, 2002), it has been considered that potential changes in heartbeat tracking accuracy in response to pain anticipation would be associated with higher pain unpleasantness (rather than intensity) ratings in the present study. Lastly, participants anticipated low, high and uncertain intensity shocks while

performing the heartbeat tracking task (directing attention to interoceptive signals), while performing an auditory tone tracking task (directing attention to exteroceptive signals) and while not being engaged in an explicit attentional task (no task condition), which allowed for an investigation of the effect of interoceptive versus exteroceptive attention on pain perception.

5.2 Methods

5.2.1 Experimental Design

A 3 x 3 within-subjects factorial design was employed, with factors of Anticipation cue (low intensity shock anticipation, high intensity shock anticipation, uncertain intensity shock anticipation) and Task (heartbeat tracking accuracy task, auditory tone tracking task, no task). Participants performed a heartbeat tracking task (see section 5.2.1.1), an auditory tone tracking task (see section 5.2.1.2) and no task while being visually cued (see Figure 5-1a) to anticipate either a low intensity shock (below the pain threshold), a high intensity shock (above the pain threshold) or a shock of an uncertain intensity (either low or high intensity). See section 5.2.1.3 for details regarding shock intensity calibration. A total of 54 shocks were administered (see Table 5-2 for breakdown of trials): 27 high intensity shocks (18 following the high intensity shock cues and 9 following the uncertain shock intensity cues) and 27 low intensity shocks (18 following the low intensity shock cues and 9 following the uncertain intensity cues). The shocks were split into two blocks of 27 trials. Trial order was fully randomised within each block. The two blocks were administered in a counterbalanced order across participants.



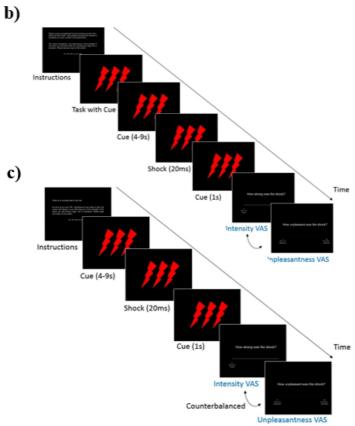


Figure 5-1. Experimental design: a) anticipation cues and their associated shock intensities; b) auditory tone counting trial and heartbeat counting trial procedure; c) No task trial procedure. Notes: LIC: low intensity shock cue, HIC: high intensity shock cue, UIC: uncertain intensity shock cue, LS: low intensity shocks, HS: high intensity shocks.

Table 5-1. Anticipation cue trials within each task condition.

	Task during anticipation			
	Heartbeat tracking	Auditory tone tracking	No task	
Total number of trials	18 trials	18 trials	18 trials	
Trial breakdown	6 LIC trials 6 HIC trials 6 UIC trials (3 followed by LS and 3 followed by	6 LIC trials 6 HIC trials 6 UIC trials (3 followed by LS and 3 followed by	6 LIC trials 6 HIC trials 6 UIC trials (3 followed by LS and 3 followed by	
	HS)	HS)	HS)	

Notes: LIC: Low intensity shock cue, HIC: High intensity shock cue, UIC: uncertain intensity shock cue. LS: low intensity shocks, HS: high intensity shocks.

5.2.1.1 Heartbeat Tracking Task

In line with previous experiments described in the current thesis, HTA was assessed using the Mental Tracking Method (Schandry, 1981). HTA was assessed at baseline, before the main experiment with a block of 25-second, 35-second, and 45-second trials presented in a random order. During pain anticipation, HTA was assessed in 20-second, 25-second, 30-second, 35-second, 40-second and 45-second trials in each of the three anticipation conditions (anticipation of a low intensity shock, anticipation of a high intensity shock, and anticipation of a shock of an uncertain intensity). Six trials were used during the cued pain anticipation task in order to ensure sufficiently high statistical power. Note that the anticipation of uncertain intensity shock trials were followed either by high intensity shocks or by low intensity shocks; having six HTA trials per anticipation condition allowed for low shocks preceded by the uncertain intensity shock anticipation cue and for high shocks preceded by the uncertain intensity shock

anticipation cue to be associated with three HTA trials each, allowing for an investigation of the effect of the HTA task on the perception of these shocks. Participants' true heart rate during the HTA task was monitored using a piezo-electric pulse transducer attached to the participant's right index finger (PowerLab 26T, AD Instruments, UK).

5.2.1.2 Auditory Tone Tracking Task

The auditory tone tracking task served as a control condition for the heartbeat tracking task (Critchley et al., 2004; Pollatos, Schandry et al., 2007; Wiebking et al., 2014; Zaki et al., 2012). During the auditory tone tracking task the participant was instructed to mentally count computer generated audio tones wile anticipating a low intensity shock, a high intensity shock or a shock of an uncertain intensity. The participant was instructed to count the number of audio tones that s/he heard from the moment s/he received an audio computer-generated cue of a recording of the word 'go', signaling the start of the trial, until s/he received a cue of a recording of the word 'stop', signaling the end of the trial and then to verbally report the number of audio tones s/he has counted to the experimenter. Within each anticipation cue condition there were 6 trials of auditory tone tracking lasting 20-s, 25-s, 30-s, 35-s, 40-s, and 45-s, corresponding to the lengths of the heartbeat tracking intervals. The audio tones had a frequency of 333 Hz and ranged from 60 tones per minute to 69 tones per minute with irregular inter-tone intervals, approximating the pace of an average heart rate. No information regarding the length of the individual trials, or feedback regarding participants' performance was given.

5.2.1.3 Electrical Stimulation

As in Experiment 4, electric shocks were delivered through two constant current electrical stimulators (DS7A, Digitimer) via two couples of surface electrodes placed in close proximity on the participants' left inner wrist. The shocks were single constant current rectangular monophasic pulses with duration of 2-ms. Each pair of electrodes was connected to one constant current electrical stimulator. One stimulator delivered low intensity shocks and the other stimulator delivered high intensity shocks. As the two pairs of electrodes were placed in

close proximity, shocks from both stimulators occurred in locations on the wrist that were indiscriminable to the participant. Shock intensities were based on individual pain thresholds obtained during the threshold procedure at the beginning of the experiment, and which was recalibrated between the two experimental blocks (see section 5.2.1.3.1). As in Experiment 4 and based on the procedures of Sawamoto et al. (2000) and Seidel et al. (2015), low intensity shocks were set to an intensity of 70% of the pain threshold intensity and high intensity shocks were set to an intensity of 200% of the pain threshold intensity so that the high intensity shocks were below pain tolerance level and the low intensity shocks were below pain threshold level, but above perceptual threshold level. It should be noted that Sawamoto et al. calibrated painful stimuli at 170-200% of threshold intensity. In Experiment 4, high intensity shocks were calibrated at 170% of the threshold intensity, however, as the present experiment (Experiment 5) explicitly manipulated pain anticipation, high intensity shocks were set to 200% of threshold intensity to ensure that they experienced as painful. As in Seidel et al. (2015), it was ensured that the high shock intensity was below pain tolerance level and at a level that did not cause severe distress to the participant.

5.2.1.3.1 Establishing the Pain Threshold

The same procedure of calibrating the pain threshold that was used in Experiment 4 was used in the present study (Experiment 5). The pain threshold was set through a staircase procedure. Participants received 2-ms shocks on either location on the inner left wrist also in non-fixed time intervals and were asked to verbally report whether the stimulus was painful: 'yes' or 'no'. Once a pain threshold was found, 5 shocks of the pain threshold intensity and 5 shocks of an intensity below the pain threshold intensity were delivered in random order, and participants were asked to verbally report whether each shock was painful: 'yes' or 'no'. In case participant's responses did not indicate that the shocks of the pain threshold intensity were painful and that the shocks of the intensity below pain threshold intensity were not painful, the threshold procedure, as described above, was resumed.

5.2.2 Measures

5.2.2.1 Self-Reported Measures

5.2.2.1.1 Fear of Pain

Fear of pain was measured using the 9 item version of the Fear of Pain Questionnaire (FPQ-9; McNeil & Rainwater, 1998), consisting of three subscales: fear of minor pain, fear of major pain and fear of medical pain, with possible scores ranging from 9 to 45.

5.2.2.1.2 Shock Intensity and Unpleasantness Ratings

Participants were asked to rate shock intensity on a Visual Analogue Scale (VAS) ranging from 0 (not at all strong) to 10 (very strong) and shock unpleasantness also on a VAS scale from 0 (not at all unpleasant) to 10 (very unpleasant).

5.2.2.1.3 Anxiety Ratings

Participants were asked to provide retrospective ratings of anxiety experienced during each anticipation cue condition on a VAS scale ranging from 0 (not at all anxious) to 10 (extremely anxious).

5.2.2.2 Heartbeat Tracking Accuracy Scores

HTA scores obtained during the HTA task were the non-self-report dependent measure.

5.2.3 Procedure

Participants reported demographic information and completed the FPQ-9. The electrodes and the pulse-transducer were then connected by the experimenter and the baseline HTA assessment was completed. Then, the experimenter calibrated the pain threshold and set the low and high shock intensities accordingly. Prior to each experimental trial, information about which task was to be performed while anticipating the upcoming shock (heartbeat tracking task, auditory tone tracking task or no task) was displayed, along with a reminder that a

visual cue indicating which shock strength to anticipate will appear as soon as the trial begins.

The shock was delivered 4-s, 5-s, 6-s, 7-s, 8-s or 9-s (counterbalanced across trials and conditions) from the moment the participant finished the task, or from the beginning of the trial in the no-task condition. As in Seidel et al. (2015) uncertainty about the exact timing of shocks was used across anticipation conditions to ensure engagement of attention during the entire task. One second after shock delivery the participant provided shock intensity and unpleasantness ratings (order counterbalanced across participants). In every trial the visual cue was displayed on the screen from the beginning of the trial until the shock rating questions were displayed. See Figure 5-1b-c for a graphical depiction of the trial structure in the heartbeat tracking task trials, auditory tone tracking task trials and no task trials. After the first experimental block, pain thresholds were recalibrated and shock intensities were adjusted accordingly. After the experiment, participants provided retrospective ratings of anxiety they experienced during the three cued anticipation conditions. Participants were then fully debriefed. The stimuli were controlled via a PC running NI LabVIEW 2011 software, which was also used to record participants' responses.

5.2.4 Data Analysis

5.2.4.1 Fear of Pain Scores

Fear of pain scores were calculated by summing the 9 items on the FPQ-9. The possible range of scores was from 9 to 45, and the sample mean was 26.862 (SD = 4.918). The sample mean and standard deviation are for a sample of 40 participants, as one participant did not complete the questionnaire.

5.2.4.2 Heartbeat Tracking Accuracy Scores

Mean HTA scores were calculated for baseline and for each of the three shock anticipation cue conditions: anticipating a low intensity shock, anticipating a high intensity shock, and anticipating a shock of uncertain intensity. HTA scores were calculated using the following formula:

1/number of trials Σ (1-(| actual heartbeats – reported heartbeats |) / actual heartbeats).

Participants were categorized into two HTA groups, consisting of 20 persons with lower baseline HTA (M = .48, SD = .13) and 20 persons with higher baseline HTA (M = .79, SD = .09), using a median split on the baseline HTA score (Mdn = .67). HTA scores were normally distributed, as indicated by a Shapiro-Wilk test of normality (W = .973, p = .433). See Figure 5-2 for a frequency distribution plot.

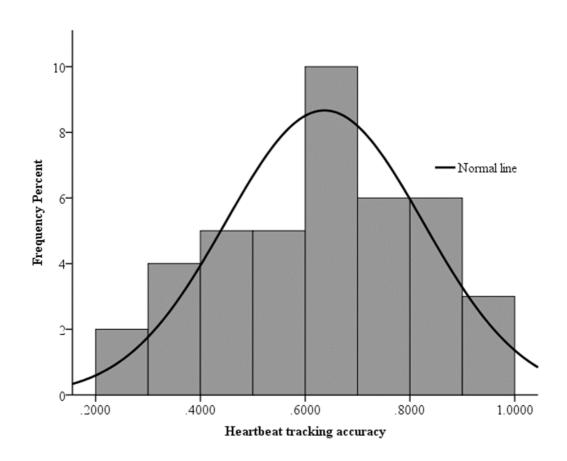


Figure 5-2. Frequency distribution of baseline HTA scores in Experiment 5.

5.2.4.3 Average Heart Rate

Average heart rate was calculated according to the following formula:

1/3 Σ ((actual heartbeats / length of time interval in seconds) * 60 seconds)

5.2.4.4 Shock Intensity and Unpleasantness Ratings

Mean shock intensity and mean shock unpleasantness ratings were calculated for all participants, separately for each of the 4 shock conditions: low intensity shock after anticipating a low intensity shock, high intensity shock after anticipating a high intensity shock, low intensity shock after anticipating a shock of an uncertain intensity and a high intensity shock after anticipating a shock of an uncertain intensity.

5.2.4.5 Data Analysis Overview

Wilcoxon Signed Ranks Tests examined differences in intensity and unpleasantness ratings of low and high intensity shocks and of shock preceded by the different anticipation cues. The effect of anticipation task (heartbeat tracking, auditory tone tracking and no task) on pain perception was tested using Friedman's non-parametric tests on the intensity ratings of high intensity shocks and on unpleasantness ratings of high intensity shocks. The effect of anticipation cue on HTA and HR was assessed using generalized linear mixed-effects models (GLMMs) with fixed factors of Anticipation condition (3 levels: low intensity shock, high intensity shock, unknown intensity shock), Fear of pain (continuous), and the interaction of Anticipation condition and Fear of pain. Participant identification numbers were entered into the model as a random effect because of the repeated measures design of the study, accounting for the interdependence of responses from the same subjects. Correlation analyses were conducted to explore associations between baseline HTA, HTA change, fear of pain and pain perception scores.

5.2.5 Participants

The sample consisted of 41 (38 females; Mean age = 18.65 years, SD = .66 years) first year undergraduate psychology students at Royal Holloway, University of London. Each participant took part in the experiment voluntarily and received course credit in compensation.

5.2.5.1 Data Exclusions

One participant was missing data on the Fear of Pain Questionnaire and was excluded from analyses involving this variable, which then resulted in a sample of 40 (37 females; Mean age = 18.65 years, SD = .66 years).

5.3 Results

5.3.1 Manipulation Check

Wilcoxon Signed Ranks Tests confirmed that painful shocks were rated as significantly more intense (Z = -5.579, p < .001) and more unpleasant (Z = -5.579, p < .001) than non-painful shocks. High intensity shocks preceded by the high intensity shock anticipation cue were rated as more intense and more unpleasant than high intensity shocks preceded by the uncertain shock intensity anticipation cue (Z = -3.939, p < .001, Z = -3.581, p < .001, respectively). Low intensity shocks preceded by the low intensity shock anticipation cue were rated as less intense and less unpleasant than low intensity shocks preceded by the uncertain intensity shock anticipation cue (Z = -4.149, p < .001, Z = -3.743, p < .001). Non-parametric test statistics were calculated due to the data not being normally distributed. Bonferroni corrections for multiple comparisons were used when assessing for significance. Table 5-2 lists the median intensity and unpleasantness ratings per anticipation condition.

Table 5-2. Median intensity and unpleasantness ratings (and ranges) for low and high intensity shocks across anticipation conditions.

Shock intensity	Preceding cue	Intensity VAS	Unpleasantness VAS
Low	UIC	1.89 (4.56)	1.44 (3.33)
	LIC	1.17 (4.83)	1.00 (3.39)
	Total	1.64 (4.64)	1.25 (3.36)
High	UIC	6.89 (5.55)	6.67 (6.33)
	HIC	7.22 (5.66)	6.78 (6.72)
	Total	7.08 (5.61)	6.70 (6.53)

Note: LIC: Low intensity shock cue, HIC: High intensity shock cue, UIC: uncertain intensity shock cue. VAS ratings of low and high intensity shocks are significantly different at $\alpha = .001$ level (1-tailed).

5.3.2 Effect of Anticipation on Pain Perception

The effect of task (heartbeat tracking, auditory tone tracking and no task) on pain perception was tested using Friedman's non-parametric tests on the intensity ratings of high intensity shocks and on unpleasantness ratings of high intensity shocks. Non-parametric analyses were used as shock ratings were not normally distributed. There were no significant differences in high intensity shock intensity ratings (χ^2 (2, N = 41) = 1.252, p = .540) and unpleasantness ratings (χ^2 (2, N = 41) = 2.922, p = .233) based on preceding task. Additionally, there were no significant differences in low intensity shock intensity ratings (χ^2 (2, N = 41) = 6.959, p = .0316; note that p-value was non-significant after Bonferroni correction) and unpleasantness ratings (χ^2 (2, N = 41) =2.392, p = .302) based on preceding task.

5.3.3 Associations Between Baseline Heartbeat Tracking Accuracy, Pain Thresholds and Fear of Pain

The associations between baseline HTA, baseline pain thresholds and fear of pain were explored. The analyses indicated a non-significant trend in the association between baseline HTA and fear of pain. Baseline HTA and baseline pain thresholds were not correlated. Pain thresholds were negatively associated with fear of pain scores. This association remained significant after applying the Bonferroni correction for multiple comparisons (p = .05/3 = .017). See Table 5-3 for correlation coefficients and respective correlation coefficients.

Table 5-3. Associations (along with 95% confidence intervals) between baseline heartbeat tracking accuracy, baseline pain thresholds and fear of pain.

	1.	2.	3.
1. HTA 1	-		
2. Pain threshold 1	084 [381, .299]	-	
3. FOP	.266 [†] [049, .533]	419** [646,124]	-

Note: **: p < .01, †: p < .10. HTA 1: heartbeat tracking accuracy at baseline; Pain threshold 1: pain threshold at baseline; FOP: Fear of pain. Spearman's rho correlation coefficients were computed for correlations involving Pain threshold 1, as this variable was not normally distributed. N = 41 (for calculations including FOP, N = 40).

5.3.4 Effect of Pain Anticipation Cue on Heartbeat Tracking Accuracy

HTA difference scores (HTA during anticipation – HTA at baseline) were entered into a generalized linear mixed-effects model (GLMM) with fixed factors of Anticipation condition (3 levels: low intensity shock, high intensity shock, unknown intensity shock), Fear of pain (continuous), and the interaction of Anticipation condition and Fear of pain. Participant identification number was entered into the model as a random effect because of the repeated measures design of the study, accounting for the interdependence of responses from the same subjects. The analysis indicated that the overall model was significant (F (5, 114)

= 4.141, p = .002). A scatter plot of the observed values against the values predicted by the model indicated good model fit $(R^2 = 0.909)$. The effect Anticipation condition on HTA difference scores (F(2, 114) = 1.773, p = 0.174) and the effect of Fear of pain on HTA difference scores (F(1, 114) = 1.816, p =0.180) did not reach significance. The interaction effect of Anticipation condition and Fear of pain on HTA scores (F(2, 114) = 3.326, p = 0.039) was significant. Subsequent pairwise contrasts performed on HTA difference scores in each Anticipation condition on individuals low, medium and high in Fear of pain (as indicated by mean Fear of pain scores $\pm 1SD$: 26.86 ± 4.88) revealed a significant effect of Anticipation condition on HTA difference scores in individuals high in Fear of pain only (F(2, 114) = 9.203, p < 0.001), with HTA difference scores being the largest in high intensity shock anticipation condition, as compared to HTA difference scores in the unknown intensity shock anticipation condition (t (114) = 4.271, p < 0.001, contrast estimate = 0.35 (SE = 0.008), 95% CI [0.019, (0.051]) and HTA difference scores in low intensity shock condition (t (114) = 2.177, p = 0.032, contrast estimate = 0.027 (SE = 0.012), 95% CI [0.002, 0.051]). There was no significant difference in HTA difference scores between the unknown intensity shock anticipation condition and the low intensity shock anticipation condition (t (114) = -0.742, p = 0.460, contrast estimate = -.008 (SE = 0.011), 95% CI [-0.031, 0.014]). There was no significant effect of the Anticipation condition on HTA difference scores in individuals with mean Fear of pain scores (F(2, 114) = 2.410, p = 0.094) or in individuals with low Fear of pain scores (F(2, 114) = 0.023, p = 0.978), although the effect could be interpreted as trending on significance in the mean Fear of pain group.

In order to ensure that the effect of high intensity shock anticipation cue on HTA was not due to changes in average heart rate (HR), HR difference (HR during anticipation – HR at baseline) were also analysed in a GLMM testing for fixed effects of Anticipation condition, Fear of Pain and the interaction between them, while treating the participant identification number as a random factor. The overall model was significant (F (5, 114) = 4.718, p = 0.001), with a scatter plot of the observed values against the values predicted by the model indicating good model fit (R^2 = 0.985). The main effect of Anticipation condition and interaction

effect of Anticipation condition and Fear of pain were significant (F(2, 114))4.863, p = 0.009 and F(2, 114) = 3.455, p = 0.035, respectively). The effect of Fear of pain was not significant (F(1, 114) = 0.940, p = 0.334). Subsequent pairwise contrasts revealed a significant effect of Anticipation condition on HR difference scores in individuals with low and mean Fear of pain scores (F(2, 114)) = 9.203, p < 0.001, F (2, 114) = 4.097, p = 0.019, respectively) and not in individuals with high Fear of pain scores (F (2, 114) = 0.783 p = 0.460). In individuals low in Fear of pain, HR difference scores were smallest in the unknown intensity shock anticipation condition, as compared to the high intensity shock anticipation condition (t(114) = 4.301, p < 0.001, contrast estimate = 1.380)(SE = 0.321), 95% CI [0.745, 2.016]) and compared to the low intensity shock anticipation condition (t (114) = 3.779, p < 0.001, contrast estimate = 1.372 (SE = 0.363), 95% CI [0.653, 2.090]). HR difference scores were not significantly different between the high intensity shock anticipation condition and the low intensity shock anticipation condition (t (114) = 0.028, p = 0.978, contrast estimate = 0.009 (SE = 0.318), 95% CI [-0.620, 0.638]). In individuals with mean Fear of pain scores, HR difference scores in the unknown intensity shock anticipation condition were significantly lower than in the high intensity shock anticipation condition (t (114) = 2.857, p = 0.005, contrast estimate = 0.764, (SE = 0.267), 95% CI [0.234, 1.293]), but not than HR difference scores in the low intensity shock anticipation condition (t (114) = 1.102, p = 0.296, contrast estimate = 0.296 (SE = 0.268), 95% CI [-0.236, 0.827]). HR difference scores in the low intensity shock anticipation condition and the high intensity shock anticipation condition did not differ significantly (t (114) = -1.506, p = 0.135, contrast estimate = -4.68 (SE = 0.311), 95% CI [-1.084, 0.148]).

Table 5-5. Means (with standard deviations) and medians (with ranges) of heartbeat tracking accuracy scores and heart rate at baseline and during the three cued anticipation conditions.

	НТА		HR	
	Mean (SD)	Median (range)	Mean (SD)	Median (range)
Baseline	.64 (.19)	.67 (.76)	80.17 (14.96)	82.69 (70.63)
Low intensity cue	.70 (.17)	.71 (.65)	79.95 (11.80)	82.38 (45.70)
High intensity cue	.71 (.17)	.78 (.64)	80.25 (11.61)	81.64 (44.14)
Uncertain intensity cue	.69 (.17)	.73 (.60)	79.48 (11.70)	79.48 (44.61)

5.3.5 Associations Between Changes in Heartbeat Tracking Accuracy During Pain Anticipation and Self-Reported Measures

In order to examine whether HTA difference scores due to shock anticipation were associated with the intensity and unpleasantness ratings of shocks in each condition, Spearman's non-parametric correlation coefficients were calculated (all the intensity and unpleasantness ratings were not normally distributed). HTA difference scores during high intensity shock anticipation were not significantly correlated with shock intensity ($r_s = .053$, p = .745, 95% CI [-.262, .358]) or shock unpleasantness ratings ($r_s = -.028$, p = .864, 95% CI [-.336, .286]) of high intensity shocks. HTA difference scores due to low intensity shock anticipation were not significantly correlated with shock intensity ($r_s = -.101$, p = .535, 95% CI [-.399, .217]) or shock unpleasantness ratings ($r_s = -.280$, p = .080, 95% CI [-.544, .034]) of low intensity shocks. Shock intensity ratings and shock unpleasantness ratings of low intensity shocks preceded by the uncertain shock

intensity cue were not significantly associated with HTA difference scores during their anticipation (r_s = .092, p = .571, 95 % CI [-.225, .392]; r_s = -.119, p = .464, 95 % CI [-.415, .199], respectively). Shock intensity ratings and shock unpleasantness ratings of high intensity shocks preceded by the uncertain shock intensity cue were not significantly associated with HTA difference scores during their anticipation (r_s = .041, p = .800, 95 % CI [-.274, .348]; r_s = -.039, p = .811, 95 % CI [-.346, .275], respectively).

Table 5-6 lists the correlation coefficients (along with 95% confidence intervals) between HTA difference scores, and HTA baseline scores, retrospective anxiety scores and fear of pain scores. HTA difference scores in the high shock, low shock and unknown shock anticipation conditions were significantly negatively related to baseline HTA scores indicating that individuals with lower HTA experienced higher changes in HTA throughout the task. HTA difference scores during the task were not significantly associated with retrospective anxiety reports. Fear of pain scores were not significantly related to HTA difference scores in the low and high intensity shock anticipation conditions, but were marginally negatively related to HTA difference scores in the unknown intensity shock anticipation condition. After applying the Bonferroni correction for multiple comparisons (p = .05/9 = .005), only the associations between HTA difference scores and HTA baseline remained significant.

Table 5-6. Associations (along with 95% confidence intervals) between heartbeat tracking accuracy baseline and difference scores across cued anticipation conditions and self-reported measures (retrospective anxiety reports across cued anticipation conditions and fear of pain scores)

	Baseline HTA	Retrospective Anxiety	FOP
1. HTA(D) LIC	475** [685,192]	.021 [292, .33]	133 [426, .186]
2. HTA(D) HIC	492** [696,214]	170 [457, .149]	235 [509, .082]
3. HTA(D) UIC	497** [7,22]	017 [326, .296]	287 [†] [549, .026]

Note: **: p < 0.01, †: p < 0.10. HTA: Heartbeat tracking accuracy; (D): difference scores, LIC: Low intensity shock cue, HIC: High intensity shock cue, UIC: uncertain intensity shock cue; FOP: Fear of pain. Non-parametric Spearman's rho correlation coefficients were calculated for associations involving Retrospective Anxiety ratings associated with LIC and HIC as these variables were non-normally distributed. N = 40.

5.4 Discussion

Experiment 5 investigated changes in heartbeat tracking accuracy (HTA) as a function of cue-manipulated pain anticipation, while also examining potential differences in pain intensity and unpleasantness ratings based on the attentional task (heartbeat tracking task, manipulating interoceptive attention, as compared to an auditory tone tracking task, manipulating exteroceptive attention and to a no task condition) that was performed during anticipation. The results of Experiment 5 indicated that HTA increased the in individuals with high fear of pain, during high intensity (painful) electric shock anticipation condition; In this group, HTA change during the high intensity shock anticipation condition was significantly larger than HTA change during the uncertain shock intensity anticipation condition and than HTA change during the low intensity (non-painful) shock

condition. It should be noted that in the low HTA group, HTA was significantly higher during the pain anticipation task, overall, in comparison to baseline. Larger HTA improvements in lower, as opposed to higher, baseline HTA individuals have been previously observed in research investigating state changes in HTA (e.g., Ainley et al., 2012). Importantly, changes in heart rate did not drive changes in HTA, as average heart rate difference scores did not differ significantly between the anticipation conditions or between anticipation task overall and baseline. The lack of heart rate changes was not taken as indicative of a failed manipulation, because studies on the effects of pain anticipation on heart rate show mixed patterns of responding with some individuals showing increases and others showing decreases in average heart rate due to pain anticipation (Willer, 1975; Fazalbhoy, Birznieks, & Macefield, 2012). Additionally, changes in heart rate due to anticipation of pain can be moderated by various factors—for example, employment of emotion regulation techniques has been found to inhibit heart rate increases during pain anticipation (Braams, Blechert, Boden, & Gross, 2012) which were not measured during the experiment. Of course, it also has to be considered that changes in other cardiac parameters (e.g., stroke volume, blood pressure), which were not measured in the present study, could have accompanied changes in heartbeat tracking accuracy during pain anticipation. As average heart rate obtained from the heartbeat tracking trials of the interoceptive accuracy task are not a sensitive measure of cardiac and autonomic activity, future research should aim to investigate the interaction of autonomic reactivity during pain anticipation and changes in interoceptive accuracy by employing more sensitive measures of physiological reactivity.

HTA change during the high intensity shock anticipation condition was not associated with pain intensity and unpleasantness ratings of the high intensity shocks preceded by high intensity shock anticipation cues. Importantly, high intensity shocks preceded by the high intensity shock anticipation (certain expectancy) cue condition were rated as significantly more intense and significantly more unpleasant than high intensity shocks preceded by the uncertain shock intensity anticipation cue condition. Low intensity shocks preceded by the low intensity shock anticipation (certain expectancy) cue condition were rated as

significantly less intense and significantly less unpleasant than low intensity shocks preceded by the uncertain shock intensity anticipation cue condition. There were no significant differences between ratings of intensity and unpleasantness of shocks preceded by the heartbeat tracking task, as compared to shocks preceded by an auditory tone tracking task and shocks preceded by no task. Additionally, baseline HTA was not associated with pain thresholds or pain intensity and unpleasantness ratings across conditions, which was contrary to the results of the study by Pollatos et al. (2012), but in line with the results of Werner et al. (2009b) and with the results of Experiment 4.

It should be noted, however, that in Experiment 5, baseline HTA was marginally associated with fear of pain scores, which, in turn, were inversely related to pain thresholds. Future research should consider the possibility of fear of pain mediating the relationship between HTA and pain threshold and pain tolerance level via pain-related negative affect exerting a sensitising influence on pain perception. As HTA has been consistently linked with increased emotional reactivity (Pollatos, Herbert et al., 2007) and elevated anxiety (see Domschke et al., 2010 for review), while negative affect has been linked to pain sensitisation (see Janssen, 2002 for review), it is possible that the relationship between HTA and pain perception might differ on an individual level, as a function of negative affect associated with the experience of pain. Overall, more research is needed in order to delineate the exact nature of the relationship between interoceptive accuracy and pain perception. Of course, as mentioned previously, different pain assessment methods in all four studies on the topic—Experiments 4 and 5 of the current thesis, the study by Pollatos et al. and the study by Werner et al-could also account for discrepant results, highlighting the importance of ensuring consistent methodological designs in the investigations on the topic, which can then ease cross-study comparisons.

Importantly, the studies by Werner et al. and by Pollatos et al. focused on interoceptive accuracy and pain sensitivity as trait variables, leaving the role of state cardiac interoceptive accuracy in the experience of pain unexamined. The current study, Experiment 5, is the first study to examine the relationship between pain anticipation and pain perception in relation to state cardiac interoceptive

accuracy. Previous research has found anterior insula activity during pain anticipation (Chua et al., 1999; Ploghaus et al., 1999), and has established the anterior insula as being a critical mediator of the effect of cued anticipation on pain perception (Atlas et al., 2010). These findings, by extension, suggest that interoceptive perception and accuracy might also constitute an important mechanism involved in pain anticipation. Indeed, the results of Experiment 5 indicate that pain anticipation heightens heartbeat tracking accuracy, expanding on previous studies which reported an enhancement in accurate bodily perception (improved heat discrimination) in individuals anticipating pain (Johnston et al., 2012). The findings of Experiment 5 suggest that pain anticipation enhances processing of interoceptive signals, which might constitute an important mechanism through which the body prepares itself to deal with impeding threat. As enhanced heartbeat tracking accuracy during high intensity shock anticipation was associated with higher retrospective reports of anxiety experienced during those trials, it is likely that heightened heartbeat tracking accuracy in this condition was a result of a fear driven attentional bias to bodily sensations, in this case, extending to interoceptive sensations.

Contrary to the hypotheses set out at the beginning of Experiment 5, the uncertain shock intensity anticipation cue condition, which can be interpreted as manipulating pain anxiety, did not bring about an increase in HTA, which was observed only during the high shock anticipation cue condition, which can be interpreted as manipulating pain fear (Ploghaus et al., 2003). The uncertain shock intensity anticipation cue condition was hypothesised to increase HTA as salient, uncertain and anxiety-provoking stimuli have been found to activate the anterior insula (Chang, Yarkoni, Khaw, & Sanfey, 2013; Menon & Uddin, 2010; Sarinopoulos et al., 2010), which is the central brain region processing interoceptive information (Craig, 2009). A direct association between anxiety and interoceptive accuracy has been repeatedly observed (Domschke et al., 2010), whereas anticipatory anxiety evoked by the socially threatening experience of public speaking anticipation has been found to increase HTA (Experiment 1 of the current thesis), suggesting that increased anxiety due to pain anticipation could also increase HTA. Consequently, it might be considered to be surprising that

HTA change during uncertain shock intensity anticipation cue condition was not significantly different from HTA change during low intensity (non-painful) shock anticipation cue condition and was significantly lower than HTA change during high intensity (painful) shock anticipation cue condition. While it is possible that fear, rather than anxiety, associated with pain increases interoceptive accuracy, several other explanations of the observed pattern of results must be considered.

Firstly, it is possible that the high shock anticipation condition did not evoke fear but instead evoked anxiety, whereas the uncertain shock anticipation condition also evoked anxiety, but to a lesser extent than the high shock anticipation condition. Note that increased pain perception has been associated with anxiety rather than fear, which has been observed to bring about reduced pain perception (Rhudy & Meagher, 2000). In Experiment 5 the intensity and unpleasantness ratings of high intensity (painful) shocks were significantly higher if the painful shocks were preceded by the high shock anticipation cues than if the painful shocks were preceded by the uncertain intensity shock anticipation cues. These findings can be contrasted with research indicating that uncertain pain is perceived as more intense and unpleasant than certain pain (Yoshida, Seymour, Klotzenburg, & Dolan, 2013), albeit being in line with findings of studies examining the effects of expectancies on pain, which observed pain perception to be biased in the expected direction (Brown, Seymour, Boyle, El-Deredy, & Jones, 2008; Morton, El-Deredy, Watson, & Jones, 2010; Wiech et al., 2014). Finally, it has been shown that expected emotional events evoke enhanced neural responses in comparison to unexpected emotional events (Lin et al., 2012), which could be further used to explain the enhanced response to the high intensity shock anticipation condition, as compared to the uncertain intensity shock anticipation condition.

Secondly, participants were informed of the number of high and low intensity shocks that were to be delivered during the experiment (because of ethical considerations) and that were associated with each type of cue, it is possible that the threat level associated with each anticipation cue was dependent on the number of high intensity shocks that the cue was associated with. As the uncertain intensity cue was associated with half of the number of high intensity

shocks that the high intensity cue was associated with, the uncertain intensity cue might have acted as a moderate threat signal, whereas the high intensity shock cue might have constituted a high threat signal. Varying levels of threat have been related to differential behavioural and neural responses (Mogg & Bradley, 1998; Straube, Schmidt, Weiss, Mentzel, & Miltner, 2009). Whereas during moderate threat individuals tend to display avoidance behaviour, directing their attention away from the source of threat, which may lead to decreased pain (Mogg & Bradley, 1998), during stronger threat, individuals tend to display preparatory behaviour, where they become more vigilant of expected threatening stimuli, which may lead to increased pain (Gray & McNaughton, 2000; Mogg & Bradley, 1998). Additionally, the interoceptive brain regions, the insular and anterior cingulate cortices, have been observed to show a linear response to anticipatory threat, with activation in these areas increasing from low to moderate to high threat (Drabant et al., 2011). Consequently, it is possible that the high intensity shock anticipation cue condition was subjectively perceived as more threatening and therefore induced higher levels of negative affect than the uncertain intensity shock anticipation cue condition, potentially increasing interoceptive accuracy to a larger extent. A limitation of the current study is that because there were no trial-by-trial measures of anxiety and perceived level of threat, it is not possible to ascertain that participants indeed experienced more negative affect and higher levels of threat during anticipation of the high intensity shocks as compared to anticipating shocks of an uncertain intensity. Future studies should replicate the pain anticipation paradigm of Experiment 5 to assess changes in HTA, while also administering a trial-by-trial assessment of perceived shock expectancy and anxiety that would allow to directly examine whether the level of certainty about the occurrence of a high intensity shock affects HTA.

In summary, the main objective of Experiment 5 was to investigate the effect of a stressful negative affective experience that is not social in character (and which manipulates physical threat) on state interoceptive accuracy, as measured with HTA. Additionally, the study aimed to further examine the relationship between interoceptive accuracy and pain perception, while also testing for the effect of interoceptive attention manipulated by the heartbeat

tracking task on pain perception. As Experiment 1 found that an anxiety evoking manipulation that is social in character (public speaking anticipation) increased HTA, the hypotheses at the beginning of Experiment 5 predicted that an anxiety evoking manipulation that is not social (pain anticipation) would also increase HTA. This prediction was confirmed, as HTA changed to the largest extent during the high shock intensity anticipation condition. Importantly, the results of Experiment 5 provide a potential explanation for Experiment 4 not replicating the decrease in HTA in response to social exclusion that was found in Experiment 3. The results of Experiment 5 suggest that the lack of an effect of social exclusion on heartbeat tracking accuracy in Experiment 4 could have been due to simultaneous and cancelling each other out effects of social exclusion and of pain anticipation on heartbeat tracking accuracy HTA. As in Experiment 4, pain perception was also not affected by social exclusion (contrary to previous findings such as DeWall and Baumeister, 2006; Eisenberger et al., 2003) it was taken into consideration that engaging in the HTA task could have influenced pain perception. As pain perception is subject to top-down modulation by attention (Villemure & Bushnell, 2002)—including attention to the body (Eccleston et al., 1997)—it is possible that the heartbeat tracking task, directing attention to interoceptive bodily signals, affected the perception of painful stimuli after social exclusion. However, the results of Experiment 5 showed that the heartbeat tracking task likely did not affect pain ratings in Experiment 4, as Experiment 5 indicated that the intensity and unpleasantness ratings did not significantly differ based on preceding task during anticipation.

To conclude, Experiment 5 shows that in addition to increasing due to anxiety in a social setting such as public anticipation (as observed in Experiment 1), interoceptive accuracy, as measured by HTA, can increase due to anticipation of a non-social stressor that elicits anxiety via physical threat. Potential changes in HTA might be important in subsequently modulating pain perception. It should be noted that pain is a highly subjective experience that is determined not only by bottom-up perceptual input, but that is also strongly conditional on top-down modulation by cognitive factors such as expectations and beliefs (see Atlas & Wager, 2012 for a review). Attention to the body has been suggested to mediate

the effect of pain anticipation on pain perception (Crombez et al., 2005). However, because an association was not observed between HTA in the high intensity shock anticipation condition and the pain ratings of high intensity shocks, it is not clear whether increased HTA during pain anticipation would have an effect on subsequent pain perception. Future studies should aim to investigate whether changes in interoceptive accuracy during pain anticipation affect subsequent pain perception by employing a trial-by-trial analysis design. It is possible that pain anticipation independently affects state cardiac interoceptive accuracy and pain ratings by means of dissociated mechanisms. Specifically, one of the mechanisms might involve pain anticipation increasing body vigilance, thereby enhancing bodily signal perception and heightening cardiac interoceptive accuracy, while the other mechanism might affect the interpretation of the perceived bodily signals, as painful or not. The relationship between these two could, of course, vary as a function of prior pain expectancies, fear of pain, and learned pain-related behaviours, which vary both between and within healthy and clinical populations (Feuerstein & Beattie, 1995, Pincus, Smeets, Simmonds, & Sullivan, 2010), and while HTA was not associated with pain ratings in the current healthy sample, the association might be observed in clinical pain samples. Future research should employ trial-by-trial analysis of heartbeat tracking accuracy and pain ratings in healthy and clinical samples to carefully investigate this research question. Additionally, as high interoceptive accuracy has been linked to enhanced ability to downregulate negative affect in socially painful situations (Pollatos, Matthias, & Keller, 2015; Werner, Kerschreiter et al., 2013), it is possible that enhanced interoceptive accuracy when anticipating a painful stimulus can help downregulate the anxiety and negative affect associated with the expectation of impending unpleasant and distressing physical stimulus. Future research is needed, however, to ascertain this hypothesis.

Chapter 6: Discussion

6.1 Summary of Background and Aims

Past investigations of interoceptive accuracy in relation to emotional experience have predominantly focused on the way in which inter-individual differences in interoceptive accuracy predict aspects of emotion processing (e.g., Herbert, Pollatos, & Schandry, 2007; Pollatos, Herbert et al., 2007; Pollatos et al., 2005; Pollatos, Traut-Mattausch et al., 2007). As interoceptive accuracy has been considered to be a stable, trait-like variable (Cameron, 2001; Schandry, 1981), state changes in interoceptive accuracy in response to emotional experience have been under examined. The current thesis addressed this gap in the literature, testing the hypothesis that in addition to being a trait variable, interoceptive accuracy also functions as a state variable, which is affected by negative affective and self-focus manipulating contexts. The focus on negative affective experiences in the present thesis was based on the evidence suggesting that interoceptive accuracy might change according to the physiological state (e.g., increased cardiovascular activity (Antony et al., 1995), hunger (Herbert, Herbert et al., 2012), the affective state (e.g., experience of stress (Schulz, Lass-Hennemann et al., 2013; Sturges & Goetsch, 1996)) and the cognitive state (e.g., degree of focus on one's self (Ainley et al., 2012, 2013) of the individual. Consequently, the present thesis examined changes in interoceptive accuracy in response to negative affective experiences manipulating social and physical threat as well as self-focus. State changes in exteroceptive somatosensory perception were also examined alongside interoceptive accuracy in several experiments comprising the present thesis in order to establish whether state changes in interoceptive accuracy generalise to the exteroceptive somatosensory modality. To summarise, the main aims of the series of experiments in the current thesis were to investigate:

- 1) Does interoceptive accuracy change as a state variable in negative affective situations?
- 2) What kind of negative affective situations change state interoceptive accuracy (e.g., situations characterised by social threat or by physical threat)?

3) How general/specific is the effect of negative affective states on state interoceptive accuracy? Does it extend to exteroceptive somatosensory perception accuracy or is it restricted to interoceptive bodily signal processing?

6.2 Summary of Results

Experiment 1 examined the stability of interoceptive accuracy during a stressful negative affective situation that elicited social anxiety via a public speaking anticipation manipulation. Heartbeat tracking accuracy was assessed in participants in the experimental and control conditions two times: at baseline and during anticipation. Participants in the experimental condition, in which they anticipated giving a speech in front of a small audience, displayed a significant increase in heartbeat tracking accuracy from baseline to anticipation. Participants in the control condition, in which they anticipated sharing their thoughts about a reading task, displayed no significant difference in heartbeat tracking accuracy from baseline to anticipation. The effect of public speaking anticipation on heartbeat tracking accuracy was not moderated by baseline heartbeat tracking accuracy, nor by fear of negative evaluation. Interestingly, increases in heartbeat tracking accuracy from pre- to post-manipulation, in the experimental group, were not significantly associated with increases in self-reported anxious mood from pre- to post-manipulation. However, increases in heartbeat tracking accuracy from pre- to post-manipulation in the experimental group were significantly correlated with fear of negative evaluation. Overall, the results of Experiment 1 indicated that interoceptive accuracy can increase in response to a stressful negative affective experience of public speaking anticipation. In line with the cognitive theories of social anxiety (Clark & Wells, 1995), it can be suggested public speaking anticipation increased anxiety (see Jakymin & Harris, 2012 for review) and heartbeat tracking accuracy (as suggested by Ainley et al., 2012) via heightened self-focused attention.

Experiment 2 tested the hypothesis that heartbeat tracking accuracy increases due to heightened social self-focus. In order to investigate whether the potential effect of social self-focus on interoceptive accuracy generalises to the

exteroceptive somatosensory modality, the effect of social self-focus on tactile perception accuracy was examined alongside heartbeat tracking accuracy. All participants completed the heartbeat tracking task and the Somatic Signal Detection Task (SSDT; Lloyd et al., 2008), measuring the detection accuracy of threshold intensity tactile stimuli, during the self-focus condition (video camera turned on and facing the participant) and the non-self-focus condition (video camera turned off and facing away from the participant). The results indicated that heartbeat tracking accuracy did not differ between the self-focus condition and the non-self-focus condition, although the self-focus condition was associated with higher sensitivity in detecting tactile stimuli of threshold intensity, as compared to the non-self-focus condition. Additionally, the results indicated that heartbeat tracking accuracy was not related to sensitivity in detecting tactile stimuli, although it was positively associated with false alarms, independently of self-focus.

Experiment 3 examined state interoceptive accuracy in an emotional context, which was distinct from anticipatory social anxiety (examined in Experiment 1), but which retained the negative affective quality and an explicit social evaluative component (as Experiment 1, but unlike Experiment 2). Heartbeat tracking accuracy was assessed in participants in the experimental and control conditions two times: before and after playing a computerised ball-throwing game, Cyberball (Williams et al., 2000; Williams & Jarvis, 2006). Participants in the experimental condition, in which they were excluded during the Cyberball game, displayed a significant decrease in heartbeat tracking accuracy from pre- to post-Cyberball. Participants in the control condition, in which they were included during the Cyberball game, displayed no significant difference in heartbeat tracking accuracy from pre- to post-Cyberball. The effect of social exclusion on heartbeat tracking accuracy was not moderated by baseline heartbeat tracking accuracy. The decrease in heartbeat tracking accuracy from pre- to post-exclusion was not significantly associated with self-reported mood post-exclusion.

Because interoceptive accuracy has been implicated in pain processing (Pollatos et al., 2012) and social exclusion can affect pain perception—pain sensitising and pain numbing effects have been observed (DeWall & Baumeister,

2006; Eisenberger et al., 2006)—Experiment 4 examined whether the decrease in heartbeat tracking accuracy following social exclusion is accompanied by a change in pain perception. In Experiment 4, participants completed the heartbeat tracking accuracy task and the electrocutaneous pain assessment task both before and after being included (control condition) or excluded (experimental condition) during the Cyberball game. The results indicated no significant effect of social exclusion on heartbeat tracking accuracy or on pain perception. Heartbeat tracking accuracy was not significantly associated with pain thresholds or with pain intensity and unpleasantness ratings. It was hypothesised that Experiment 4 might have failed to replicate the effect of social exclusion on heartbeat tracking accuracy, that was observed in Experiment 3, due to the salient pain measure being present. The pain assessment could have increased participants' anxiety and body vigilance, consequently increasing participants' interoceptive accuracy and cancelling out the effect of social exclusion.

Experiment 5 examined the stability of interoceptive accuracy under the stressful negative affective experience of pain anticipation. The pain anticipation task manipulated negative affect via physical threat, rather than social threat, which was manipulated during public speaking anticipation (in Experiment 1) and social exclusion (in Experiments 3 and 4). In Experiment 5, all participants completed the heartbeat tracking task at baseline and during cued pain anticipation. During cued pain anticipation, participants completed the heartbeat tracking task while being visually cued to anticipate shocks of high intensity (painful), shocks of low intensity (non-painful) and shocks of uncertain intensity (either painful or non-painful). The results indicated that heartbeat tracking accuracy was the highest during anticipation of high intensity (painful) shocks. This effect was not moderated by baseline heartbeat tracking accuracy. Heartbeat tracking accuracy during the high shock anticipation condition was positively associated with retrospective reports of anxiety experienced in these trials. Mean heartbeat tracking accuracy scores were not significantly correlated with mean pain intensity and unpleasantness scores.

6.3 Interpretation

The findings of the experiments comprising the present thesis indicate that interoceptive accuracy is not only a trait, but also a state variable, which fluctuates (increases and decreases) in response to negative affective experiences. Potential mechanisms of emotion-induced changes in interoceptive accuracy might operate on the neural, cognitive (attentional) and physiological level. Probable processes involve alterations to the representations of the interoceptive state of the body in the brain (Craig, 2002), changes to the strength of interoceptive signal (for example, stroke volume) and changes to attentional processes involved in interoceptive perception, such as sustained attention and selective attention to interoceptive signals (Schulz, 2015). Future studies should aim to delineate the mechanisms of changes in interoceptive accuracy due to stressful negative affective experiences and discriminate between the above possibilities. Of course, it has to be considered that neural, cognitive and physiological processes bringing about measurable changes in interoceptive accuracy might not operate exclusively. Instead, any of the above mechanisms might interact and be differentially affected by various types of stress and environmental demands. While the results from the present thesis do not provide evidence regarding which of these processes were affected by the experimental manipulation, the results of the experiments of the current thesis can be interpreted in the context of affective and social self-focus-evoked changes in interoceptive accuracy.

6.3.1 The Effect of Self-Focus on Interoceptive Accuracy

In the present thesis, heartbeat tracking accuracy increased in response to public speaking anticipation as well as pain anticipation and decreased in response to Cyberball exclusion—it should be noted that because Experiment 4 was not a direct replication of Experiment 3 and was likely confounded by the introduction of the pain measure (as indicated by the results of Experiment 5), the effect of social exclusion on interoceptive accuracy is discussed in the context of Experiment 3, rather than Experiment 4. In the present thesis, it was observed that self-focus, manipulated using a video camera (in Experiment 2) did not affect interoceptive accuracy and enhanced only tactile perception accuracy. These

findings can be contrasted with the results of Ainley et al. (2012, 2013), indicating that self-focus manipulated via self-observation in a mirror as well as gazing at photographs of the self and self-referential words can increase heartbeat tracking accuracy in individuals with low baseline heartbeat tracking accuracy. The results of Experiment 2 of the present thesis and the results of Ainley et al. (2012, 2013) might seem contradictory, however, it must be considered that self-focus is not a unitary construct, instead consisting of various facets that differ according to the aspect of the self that is attended to, the valence of the self-focus and the context of the self-focus (Mor & Winquist, 2002). Distinct modes of self-focus direct attention to aspects of the self that are relevant to that specific mode (Carver & Scheier, 1981; Davies, 2005). For example, mirror, self-photograph and selfreferential word gazing manipulations can be interpreted as directing individuals' attention to private aspects of the self, while video-camera manipulations can be interpreted as directing attention to external, observable to others, aspects of the self (Carver & Scheier, 1981; Davies, 2005). Consequently, the results of Experiment 2 and the results of Ainley et al. (2012, 2013) might be indicative of social self-focus enhancing outer (exteroceptive) somatosensory perception and private self-focus enhancing inner (interoceptive) somatosensory perception, respectively. It has to be considered, however, that the manipulations used in Experiment 2 and the studies by Ainley et al. (2012, 2013) were affectively neutral and the effects of private and social self-focus might differ in situations that are of an affective nature.

Negative affect has been associated with heightened self-focus (Mor & Winquist, 2002). Situations that elicit social anxiety (e.g., public speaking anticipation, Experiment 1) can be interpreted as increasing focus on the social aspects of the self (Fenigstein, Scheier, & Buss, 1975; Spurr & Stopa, 2002), whereas situations eliciting anxiety via physical threat (e.g., pain anticipation, Experiment 5) can be interpreted as increasing focus on the private bodily aspects of the self (Ferguson & Ahles, 1998; Miller, Murphy, & Buss, 1981). As Experiments 1 and 5 indicated that public speaking anticipation and pain anticipation, respectively, increased heartbeat tracking accuracy, it can be suggested that negative affective situations that are associated with heightened

self-focus increase interoceptive accuracy, regardless of the mode of self-focus that is evoked. However, an alternative explanation for the results must be considered. While social anxiety has been associated with heightened social self-focus (Fenigstein et al., 1975), it has also been linked to private self-focus, although to a lesser extent (Hope & Heimberg, 1988; Monfries & Kafer, 1994). As in the public speaking anticipation manipulation employed in Experiment 1, participants' heartbeat tracking accuracy was measured following speech preparation and during speech anticipation, rather than during speech delivery, it is possible that participants, at that time, in addition to experiencing social self-focus—involving focus on the self as an object of others' evaluation—also experienced a high level of private self-focus, which involved focus on the self as an agent. Consequently, it is possible that social self-focus did not affect interoceptive accuracy in Experiment 1, which increased during speech anticipation as a result of heightened private self-focus.

Results of Experiment 3 can also be interpreted in the context of self-focus effects on interoceptive accuracy. However, in contrast to public speaking anticipation and pain anticipation, manipulated in Experiments 1 and 5, social exclusion, manipulated in Experiment 3, most likely decreased self-focus and increased other-focus. Even though being socially excluded is a negative affective experience involving undesirable social evaluation, which could be thought to increase self-focus, socially excluded individuals have been observed to show affiliative behaviours that rely on disengaging from the self and reengaging with others, such as increased mimicry of strangers (Lakin et al., 2008), reduced memory for self-related social behaviours and increased memory for other-related social behaviours (Hess & Pickett, 2010) following social exclusion. It has been suggested that decreased self-focus following social exclusion might protect individuals from the distress of social failure (Heatherton & Baumeister, 1991; Twenge et al., 2003), while freeing attentional resources that can be then allocated to the external world, facilitating affiliation and social reconnection (Hess & Pickett, 2010). Consequently, in Experiment 3, interoceptive accuracy might have been reduced following social exclusion via decrease in self-focus and increase in other-focus.

Taken together, the findings from Experiments 1, 2, 3 and 5, of the current thesis suggest that state interoceptive accuracy might increase and decrease in response to situations that affect self-focus. However, it should be considered that the majority of the experiments in the present thesis manipulated negative affect, with the exception of the video camera manipulation, which manipulated social self-focus in an affectively neutral context. Consequently, it is not clear whether positive affective situations would elicit similar changes in interoceptive accuracy. While some studies indicate that high arousal positive affective states (e.g., joy) elicit self-focus (Panayiotou, Brown, & Vrana, 2007), other studies have only found an effect of negative, but not positive affect on self-focus (Wood, Saltzberg, & Goldsamt, 1990) or have observed a self-focus decreasing effect of positive affect (Green, Sedikides, Saltzberg, Wood, & Forzano, 2010; Sedikides, 1992). Potential explanations for the disparate findings on the topic have included varying measures of self-focus (i.e., behavioural versus self-reported) (Silvia & Abele, 2002) as well as interacting effects of mood and situational factors on selffocus (Abele, Silvia, & Zöller-Utz, 2005).

6.3.2 The Effect of Negative Affect on Interoceptive Accuracy

In the present thesis, heartbeat tracking accuracy was found to change due to negative affective experiences that manipulate social threat—i.e., public speaking anxiety (Experiment 1), social exclusion (Experiment 3)—and negative affective experiences that manipulate physical threat—i.e., pain anticipation (Experiment 5). As interoceptive accuracy was found to increase during anticipatory anxiety in a social threat and a physical threat context (Experiments 1 and 5), it can be concluded that the effect of anticipatory anxiety on interoceptive accuracy spans across different types of anticipatory anxiety—characterised both by social and physical threat. The experience of anxiety in response to physical and socio-evaluative threat elevates cortisol levels (see Dickerson & Kemeny, 2004 for a meta-analytic review), which, in turn, can amplify heartbeat evoked potentials (Schulz, Strelzyk et al., 2013), reflecting increased cortical processing of cardiovascular signals and higher cardiac interoceptive accuracy (Pollatos et al., 2005). Even though, evolutionarily, social exclusion constitutes a major threat

to the organism (Brewer, 2004) and experimental manipulations of social exclusion have been found to significantly affect mood and other psychological variables, such as the sense of belonging, control, meaningful existence and selfesteem (see Williams, 2009 for a review), social exclusion does not elicit a classic stress response (Seidel et al., 2013). Heart rate deceleration (Gunther Moor et al., 2010), in addition to acceleration (Iffland et al., 2014) as well as a drop in skin temperature (IJzerman et al., 2010) have been observed in response to experimental social exclusion. Moreover, social exclusion manipulations have not been found to affect cortisol levels (Geniole, Carré, & McCormick, 2011; Zöller, Maroof, Weik, & Deinzer, 2010; Zwolinski, 2012; Seidel et al., 2013), instead decreasing levels of testosterone in both genders and increasing the levels of progesterone in females (Seidel et al., 2013). Lower levels of testosterone and higher levels of progesterone have been linked to reduced power motivation and increased affiliation motivation (Schultheiss, Dargel, & Rohde, 2003; Wirth & Schultheiss, 2006), while the affiliation motive has been found to negatively predict cortisol reactions to psychosocial stress (Wegner, Schuler, & Budde, 2014). Therefore, the lack of a classic stress response to social exclusion might be linked to the increase in the motivation to affiliate following exclusion that has been observed on a behavioural level (Hess & Pickett, 2010; Lakin et al., 2008; Slabbinck, De Houwer, & Van Kenhove, 2012).

Average heart rate was not affected by any of the experimental manipulations employed in the present thesis. Because there is evidence indicating discordance of subjective and objective measures of emotional experience (Mauss et al., 2005; Mauss, Wilhelm, & Gross, 2004) and because significant effects of the experimental manipulations on self-reported and behavioural measures were observed in the current thesis, the manipulations have not been discounted as ineffective. Additionally, average heart rate during completion of the heartbeat tracking accuracy, by itself, is not a comprehensive measure of emotion-related physiological arousal (Mauss & Robinson, 2009). Consequently, future investigations of changes in state interoceptive accuracy in response to negative affective situations could employ measures of physiological reactivity in order to determine whether changes in state interoceptive accuracy

under emotional influences are associated with changes in physiological arousal. Cardiovascular indices of autonomic nervous system activation that should be investigated include blood pressure, total peripheral resistance, cardiac output, pre-ejection period and heart rate variability. A measure of particular interest is heart rate variability, as it reflects the body's ability to shift between states of low and high physiological arousal, which is crucial for emotion regulation in response to stress (Appelhans & Luecken, 2006; Gross, 1998). Consequently, future investigations of the effects of various types of stressors on interoceptive accuracy and physiological arousal should also consider accompanying changes in heart rate variability.

6.3.3 Relationship Between Interoceptive and Exteroceptive Somatosensory Perception

The present thesis explored the association between interoceptive and somatosensory perception. Neural exteroceptive pathways processing interoceptive and exteroceptive signals are highly interconnected (Simmons et al., 2013), yet distinct from one another (e.g., Farb et al., 2013; Hurliman et al., 2005). Interoceptive and exteroceptive somatosensory signals jointly shape body perception and awareness (Adler et al., 2014; Aspell et al., 2013; Suzuki et al., 2013), however, the way in which interoceptive somatosensory signal perception is related to exteroceptive somatosensory signal perception is not well understood. Experiments 2, 4 and 5 examined the relationship between interoceptive accuracy and exteroceptive perception as reflected by heartbeat tracking accuracy and tactile perception of neutral and noxious stimuli, respectively, aiming to distinguish between the following hypotheses: 1) acuity of somatosensory perception spans across interoceptive and exteroceptive modalities (Knapp et al., 1997), rendering a positive correlation between indices of interoceptive and exteroceptive perception accuracy; 2) accuracy of interoceptive and exteroceptive somatosensory perception are inversely related due to a competition of internal and external signals for the attentional resources (Pennebaker & Lighter, 1980).

Experiment 2 found that self-focus affected sensitivity of tactile perception but not interoceptive accuracy, which suggests that exteroceptive and

interoceptive perception might be independently affected by situational factors. Moreover, Experiment 2 failed to find a significant relationship between heartbeat tracking accuracy and measures of sensitivity and hit hate during the threshold tactile stimuli detection task. These results are contrary to the results of Knapp et al. (1997), who observed a positive correlation between the accuracy in detecting vibrotactile stimuli and heartbeat discrimination accuracy. A potential reason for varying results of Experiment 2 and the results of Knapp et al. might be the use of different measures of interoceptive accuracy. Knapp et al. employed the heartbeat discrimination accuracy task (which is more influenced by exteroceptive processing) whereas Experiment 2 of the present thesis used the heartbeat tracking method (which is primarily reliant on interoceptive signal monitoring), which could account for, respectively, larger and smaller correlations between heartbeat perception accuracy and exteroceptive tactile perception observed in the studies. The use of vibrotactile and electrocutneous stimulation to measure tactile processing by Knapp et al. and in Experiment 2, respectively, further complicates cross-study comparisons, as these distinct measurement modalities might tap into distinct aspects of exteroceptive tactile perception.

The results of Experiment 2 did, however, indicate a negative relationship between heartbeat tracking accuracy and false alarm rate during the tactile perception task, independently of self-focus, which might be used as evidence contrary to the hypothesis that somatosensory perception accuracy spans across the interoceptive and exteroceptive modalities, instead partially supporting the competition of internal and external cues hypothesis (Pennebaker & Lighter, 1980). Specifically, it has been suggested that directing attention to interoceptive stimuli might contribute to the occurrence of false alarms by increasing sensory noise, consequently making it more difficult to distinguish between signal and noise (sensations originating outside and inside the body, respectively) when detecting a tactile stimulus (Mirams et al., 2013; Silvia & Gendolla, 2001). While the findings from Experiment 2 indicate that heartbeat tracking accuracy scores were negatively associated with tactile false alarms, the competition of cues hypothesis is not entirely supported by the results, as no significant relationship was found between heartbeat tracking accuracy scores and tactile sensitivity

scores, which provide a more direct measure of being able to distinguish sensory noise from signal than false alarms. Overall, further research is necessary to further examine the relationship between interoceptive accuracy and perception accuracy of threshold tactile stimuli and determine whether there is no significant relationship between interoceptive and exteroceptive somatosensory perception accuracy, whether the relationship between these two modes of body perception is negative, or whether the relationship varies based on specific sub-modalities of interoceptive and exteroceptive somatosensation.

In Experiment 4 and in Experiment 5, heartbeat tracking accuracy was not significantly associated with pain thresholds or with pain intensity and unpleasantness ratings. The lack of a relationship between heartbeat tracking accuracy and pain sensitivity observed in Experiments 4 and 5 is contrary to the results of Pollatos et al. (2012) who observed a significant inverse relationship between heartbeat tracking accuracy and pain thresholds and tolerance to pressure stimuli. However, it should be noted that an association between interoceptive accuracy and pain perception has not always been observed. For example, Werner, Duschek et al., (2009b) failed to observe a significant relationship between cardiac interoceptive accuracy and the perception of heat pain. A potential reason for the disparate results of the present study, of the results of Pollatos et al. and of the results of Werner, Duschek et al. might be the use of varying methods of pain assessment (electrocutaneous pain, pressure pain and heat pain, respectively). Even though it has been suggested that pain thresholds to different types of stimuli (i.e., heat, electric, pressure) measure the same phenomenon of general pain sensitivity (e.g., Neddermeyer et al., 2008), it might be the case that different pain modalities tap into distinct dimensions of nociception (Neziri et al., 2011).

Interestingly, as Experiment 5 observed a positive association between cardiac interoceptive accuracy and fear of pain, which, in turn, was found to negatively correlate with pain thresholds, it might be the case that pain-related affect mediates the relationship between interoceptive accuracy and pain perception. Consequently, future research studies must investigate the association between interoceptive accuracy and the perception of noxious tactile stimuli not

only employing various modalities of pain measurement, but also taking into account potential mediators and moderators of the relationship such as pain related emotions and cognitions.

Overall, the results of the present thesis suggest that bodily perception across interoceptive and exteroceptive sensory modalities is not directly related. These findings are in line with evidence of separate attentional systems processing interoceptive and exteroceptive information in the brain (e.g., Farb et al., 2013; Hurliman et al., 2005) as well as with the internal versus external cue competition model (Pennebaker & Lightner, 1980). Nevertheless, as that combined interoceptive-exteroceptive signals shape body awareness and perception (Adler et al., 2014; Aspell et al., 2013; Suzuki et al., 2013), future research should continue the investigation of the mechanisms through which somatosensory signals are integrated across interoceptive and exteroceptive modalities.

6.4 Limitations

6.4.1 Measurement of Interoceptive Accuracy

The Schandry Mental Tracking Method (1981) is a widely used method of assessing interoceptive accuracy (e.g., Herbert & Pollatos, 2014; Ferri et al., 2013; Furman et al., 2013; Füstös et al., 2013; Koch & Pollatos, 2014; Krautwurst et al., 2014; Michal et al., 2014; Penton et al., 2014; Pollatos, et al., 2008; Pollatos et al. 2012; Schaefer et al., 2014) that involves internal monitoring of heartbeat sensations only and does not conflate interoceptive and exteroceptive processing, as the heartbeat discrimination task (Garfinkel et al., 2015). However, it has been suggested that individuals' heartbeat tracking accuracy might be influenced by their beliefs about heart rate (Ring & Brener, 1996; Brener, Knapp, & Ring, 1995) as well as their expectancies with regard to how various activities (e.g., exercise) ought to affect their heart rate (Ring, Brener, Knapp, & Mailloux, 2015). Consequently, it has been suggested that heartbeat tracking tasks might lack in sensitivity to distinguish between individuals who are more accurate at detecting heartbeat sensations and individuals who merely have accurate beliefs about their heart rate (Brener et al., 1995).

It should be noted, however, that these criticisms are primarily based on studies showing that false heart rate feedback influences heartbeat tracking accuracy (e.g., Berner et al., 1995; Phillips et al., 1999; Ring et al., 2015). Heart rate feedback likely affects heartbeat tracking accuracy simply by priming individuals to count at a specific temporal frequency—if that temporal frequency is slower than their actual heart rate, individuals will show low heartbeat tracking accuracy, if that temporal frequency matches their heart rate, individuals will show increased heartbeat tracking accuracy (as was observed in the above studies). In order to address these issues, it must be ensured that individuals are not provided with feedback about their performance while completing the heartbeat tracking task—as was the case in the experiments comprising the present thesis.

Additionally, it must be considered that most individuals do not have accurate beliefs about their heart rates and tend to underestimate their heart rates during the heartbeat tracking task (Ehlers et al., 1995; Kollenbaum, Dahme, Kirchner, Katenkamp, & Wagner, 1994)—even individuals with relatively high interoceptive accuracy (e.g., Michal et al., 2014). Moreover, heartbeat tracking accuracy has been found to correlate with perceptual sensitivity in the gastric interoceptive modality (Herbert, Muth et al., 2012), suggesting that it is a valid measure of interoceptive accuracy. Finally, it is extremely unlikely that the plethora of research correlating inter-individual variability in heartbeat tracking accuracy with aspects of cognitive-affective processing (e.g., Dunn et al., 2010; Garfinkel, Barrett et al., 2013; Garfinkel, Tiley et al., 2013; Werner, Schweitzer et al., 2013; Werner et al., 2010; Wiens, 2005; Wiens et al., 2000), with increased activation in the insula (Pollatos, Schandry et al., 2007) and with higher amplitudes of heartbeat evoked potentials (Pollatos & Schandry, 2004) constitutes a statistical artifact driven by individuals high in interoceptive accuracy simply having more accurate beliefs about their heart rates.

While the critics of the heartbeat tracking method for assessing cardiac interoceptive accuracy recommend the use of heartbeat discrimination tasks, it should be noted heartbeat discrimination tasks are also characterised by several limitations and performance on these tasks is subject to several potentially

confounding factors. As heartbeat discrimination accuracy tasks require simultaneous processing and comparison of interoceptive and exteroceptive information, heartbeat discrimination accuracy is likely influenced by individuals' cognitive processing fluency—specifically fluency in making simultaneity judgments across modalities (Knapp et al., 1997). Of course, it should be kept in mind that all attempts to operationalise interoceptive accuracy will be inherently subject to task-specific demands, consequently, being affected by factors pertaining to these task-specific demands. It is, nevertheless, possible that interoceptive accuracy, as measured with heartbeat discrimination accuracy, might be differentially affected by situational factors than performance on the heartbeat tracking accuracy tasks. Sturges and Goetsch (1996) observed that mental arithmetic stress increased in heartbeat tracking accuracy in females high in anxiety sensitivity, while Fairclough and Goodwin (2007) found that mental arithmetic stress decreased heartbeat discrimination accuracy in females. Additionally, Schulz, Lass-Hennemann et al. (2013) observed that physical stress, induced using the cold stressor task increased heartbeat tracking accuracy, but decreased heartbeat discrimination accuracy.

Taken together, these findings suggest that the way in which stressful negative affective experiences affect interoceptive accuracy might depend on the measurement method. The discrepancy in the effects of stress on heartbeat tracking and discrimination accuracy can be potentially due to stress enhancing the perception of interoceptive sensations (measured by the heartbeat tracking task), but impairing the ability to simultaneously process and integrate interoceptive and exteroceptive signals (required during the heartbeat discrimination task). Future research could investigate whether the way in which interoceptive accuracy is affected by public speaking anticipation; social self-focus, social exclusion and pain anticipation is dependent on the method of interoceptive accuracy assessment. Importantly, state changes in interoceptive accuracy in response to emotional and self-focus situations should be investigated using a multi-method approach utilising both behavioural and neuroimaging methods of assessing interoception. Measuring of changes in heartbeat tracking accuracy, heartbeat discrimination accuracy, insula activity and the amplitude of

heartbeat evoked potentials in response to experimental manipulations of affect and self-focus can help circumvent the limitations associated with individual methods of assessing interception, while at the same time providing a more detailed account of the way in which interoception fluctuates in various socioaffective contexts.

6.4.2 Generalisability of Results to Other Interoceptive Modalities

Interoceptive modalities include all sensations that originate within the body, such as cardiac, respiratory, genital, urinary, gastric, intestinal sensations. Because in the present thesis only cardiac signal perception was examined, it cannot be assumed that the results generalise to interoceptive modalities other than the cardiac modality. However, considering a class of afferent fibres has been found to monitor the condition of all internal organs of the body, converging in the insula (Craig, 2002, 2009), which, in turn, is activated by a range of visceral sensations (see Craig, 2009 for a review), it is likely that accuracy in perceiving interoceptive signals covaries across interoceptive modalities. Whitehead and Drescher (1980) found that heartbeat discrimination accuracy was significantly associated with the ability to accurately detect gastrointestinal signals (stomach contractions), while Herbert, Muth et al. (2012) observed that individuals with higher heartbeat tracking accuracy ingested lesser volumes of water during the Water Load Test, despite similar subjective levels of fullness or nausea—likely due to stronger perception of the interoceptive cues signalling fullness. Overall, it can be concluded that cardiac and gastrointestinal perception accuracy correspond to one another within individuals, which is in line with the evidence that the anterior insula supports the perception of cardiac signals (Critchley et al., 2004; Pollatos, Schandry et al., 2007) as well as the perception of gastrointestinal signals arising in the rectum, stomach, and oesophagus (Aziz et al., 2000; Moisset et al., 2010; Craig, 2009).

On the contrary, Steptoe & Noll (1997) found a lack of correspondence between perception of heartbeats, breathing, and sweating in response to emotional experience. Additionally, the physiological responses of different visceral systems (during emotional experience, for example) have been found to

be only modestly associated with one another (Mauss et al., 2005). Consequently, it is possible that perception of signals in different interoceptive modalities is differentially affected by emotion-eliciting contexts, such as ones manipulated in the present thesis (i.e., situations eliciting negative affect through social and physical threat). For example, meditators have been found to have increased respiratory perception accuracy, as indicated by superior ability to detect and discriminate resistive respiratory loads, in comparison to non-meditators, despite not having superior cardiac perception accuracy (Daubenmier, Sze, Kerr, Kemeny, & Mehling, 2013), consequently suggesting that meditation training might selectively increase respiratory interoceptive accuracy, rather than interoceptive accuracy in all modalities. Nevertheless, before future research can ascertain the cross-correlation of interoceptive accuracy across modalities both at baseline, and in response to situational factors, standardised objective cross-modal interoceptive accuracy tests that are both valid and reliable must be developed.

6.4.4 Moderating Variables

In the present thesis, several factors potentially affecting the experimental effects on state interoceptive accuracy were considered, including sex, baseline heartbeat tracking accuracy as well as inter-individual difference variables, which could affect the effectiveness of the manipulation, such as fear of negative evaluation and fear of pain. No effects of sex or baseline interoceptive accuracy were observed throughout the experiments. While past research indicates that sex, BMI and age might influence interoceptive accuracy (Cameron, 2001), in the present thesis no sex differences were found in heartbeat tracking accuracy scores, while BMI and age effects were not investigated. It has to be considered that the samples investigated in the present studies could have been not large enough to provide sufficient statistical power to detect sex differences and perhaps all female samples (due to the low availability of male participants) could have been recruited instead. The effects of BMI and age on interoceptive accuracy were not investigated, as the experimental samples in the present thesis were rather small and comprised of young and healthy adults, not yielding themselves to investigations of BMI and age effects, which would require larger samples with a

varied distribution on these variables. Additionally, it should be noted that not all past research has observed sex or BMI differences in interoceptive accuracy (e.g., Khalsa, Rudrauf, & Tranel, 2009).

The studies reported in the current thesis investigated young adults; consequently, the results obtained may not be generalisable to individuals of all ages. This is a considerable limitation, as it has been suggested that interoceptive accuracy might decline with age (Allen, Vassallo, & Khattab, 2009; Khalsa, Rudrauf, & Tranel, 2009), as part of a general age-related decline in processing of bodily signals (Brodoehl, Klingner, Stieglitz, & Witte, 2013; Shaffer & Harrison, 2007). Of course, it should be considered that older individuals' performance on tasks assessing bodily signal processing might be impaired due to general declines in cognitive processing affecting working memory (see Salthouse, 1990 for a review) and processing speed (Bashore, Ridderinkhof, & van der Molen, 1997). This might be especially true for tasks assessing heartbeat discrimination accuracy as these require individuals to simultaneously process both interoceptive and exteroceptive signals, and simultaneously compare them—a complex task that might be more difficult for older, than younger individuals, due to potential differences in interoceptive and exteroceptive signal integration between younger and older individuals. Even though age-related changes in heartbeat tracking accuracy have not been directly examined, it is possible that heartbeat tracking accuracy is also lower in older individuals than younger individuals. Future research should assess age-related changes in heartbeat tracking accuracy, as well as other interoceptive modalities, also investigating how perception of interoceptive somatosensory signals is associated with the perception of exteroceptive somatosensory signals in older adults—both at baseline, and in response to emotion-eliciting manipulations.

6.5 Future Research Directions

Overall, further research is necessary to examine the mechanisms through which negative affective experiences impact state interoceptive accuracy. It is likely that state changes in interoceptive accuracy in response to negative affective experiences and self-focus are associated with increased neural activity in brain

regions associated with interoception, such as the insula, as well as with higher amplitudes of heartbeat evoked potentials in these socio-affective contexts. This is based on the research observing that anticipation of physically and emotionally aversive stimuli increases insula activity (Chua et al., 1999; Ploghaus et al., 1999; Simmons et al., 2004; Simmons et al., 2011; Simmons et al., 2006) as well as evidence from the experiments described in the present thesis, which show that anticipation of physically and emotionally aversive events (i.e., pain anticipation and public speaking anticipation) increases interoceptive accuracy. However, in order to ascertain the neural mechanisms of state changes in interoceptive accuracy, research studies investigating interoceptive accuracy and brain activity in socio-affective contexts simultaneously are needed. Furthermore, more research is necessary to determine whether state changes in interoceptive accuracy in response to affective contexts are driven by attentional mechanisms (e.g., changes in self-focus) or by physiological arousal (e.g., changes in cardiac activity) associated with affective states. This research question can be approached by investigating changes in state interoceptive accuracy in response to affective situations that vary in arousal, valence and mode of self-focus elicited, while employing multiple measures of physiological reactivity.

Future investigations should additionally examine state changes in multiple modalities and facets of interoception and their relationship with various modes of exteroceptive somatosensory perception, while taking into account a range of potential moderating variables, such as age, clinical status and culture. Both depressed and anxious individuals are likely to respond to experimental manipulations of negative affect and self-focus differently to healthy subjects. Individuals impacted by clinical depression are characterized by reduced emotional reactivity (self-reported emotional experience as well as physiological reactivity) to positive and negative stimuli (see Bylsma, Morris, & Rottenberg, 2008 for a meta-analytic review). Anxious individuals, on the other hand, are generally characterized by amplified emotional reactivity to negative affective stimuli (e.g., Goldin, Manber, Hakimi, Canli, & Gross, 2009; Macatee & Cougle, 2013). Consequently, future research should investigate the way in which negative affective and self-focus manipulations employed in the present thesis affect state

interoceptive accuracy in clinical samples of depressed and anxious individuals.

Future research could further consider potential cultural differences in interoceptive accuracy, in emotional experience, and in the effect of emotional experience on state interoceptive accuracy. Ma-Kellams (2014) proposes that there might be differences between individuals born and raised in Western societies (e.g., North America) and individuals born and raised in non-Western societies (e.g., East Asia) in their levels of interoceptive accuracy, as well as the subjective facets of interoception, such as interoceptive sensibility, measuring individuals' self-reported tendency to be interoceptively cognisant (Garfinkel et al., 2015). Importantly, it is possibile that the modulation of interoceptive accuracy by contextual factors might be culture dependent. Even though Maister and Tsakiris (2014) did not observe differences in baseline heartbeat tracking accuracy in East Asian individuals and Western individuals, they did find that East Asian individuals did not improve in heartbeat tracking accuracy as a result of a self-focus manipulation, as opposed to Western individuals (with lower baseline heartbeat tracking accuracy) who displayed an increase in heartbeat tracking accuracy due to heightened self-focus, as manipulated with a selfphotograph displayed during the heartbeat tracking task. Consequently, future research should explore the possibility that interoceptive accuracy (perhaps also interoceptive awareness and interoceptive sensibility) is modulated by situational factors, such as negative affect and self-focus, in a culturally-dependent manner.

6.6 Conclusion

Interoceptive accuracy has been observed to have high test-retest reliability (Mussgay et al., 1999), suggesting that it is a trait variable. However, taken together, the results of the current thesis indicate that interoceptive accuracy functions not only as a trait, but also as a state variable that fluctuates in response to environmental demands. Interoceptive accuracy has been observed to increase in response to negative affective situations that are traditionally associated with the classic stress response and increase self-focus (evoked by both psychosocial and physical threat—public speaking anticipation and pain anticipation, respectively). Interoceptive accuracy, however, has been observed to decrease in

response to a negative affective situation that is not traditionally associated with the classic stress response and decreases self-focus (social exclusion). The results of the present thesis suggest that changes in interoceptive accuracy span across contexts that are both social (i.e., public speaking anticipation) and non-social (i.e., pain anticipation), however, more research is necessary to determine whether changes in state interoceptive accuracy are restricted to negative affective situations, or whether they also characterise positive affective situations. The results of the present thesis indicated that changes in state interoceptive accuracy are not limited to individuals with low baseline interoceptive accuracy and can occur in individuals both low and high in baseline interoceptive accuracy. It has to be considered that the observed changes in interoceptive accuracy in the experiments comprising this thesis were characterised by small effect sizes, representing changes in interoceptive accuracy that were of a small degree. For example, interoceptive accuracy of individuals with low baseline can increase as a result of a manipulation, but, most likely, it will not increase to an extent large enough that would warrant re-classification of the individual as high in interoceptive accuracy. Additionally, while the duration of the effects was not investigated in the present thesis, changes in interoceptive accuracy are likely to be of a very brief duration that is time-locked to the exposure to the emotioninducing stimulus or environment (e.g., pain stimulus, public speaking anticipation) and that does not last beyond that point. Future research should investigate the duration of changes in interoceptive accuracy. Exteroceptive somatosensory perception involving neutral and noxious tactile stimuli has largely been found to be unrelated to interoceptive accuracy, with the exception of false reports of threshold tactile stimuli being inversely related to interoceptive accuracy. Overall, the results of the present thesis suggest that changes in interoceptive accuracy do not generalise to the exteroceptive somatosensory modality.

6.6.1 Implications and Applications

The findings of the experiments comprising the present thesis further the current understanding of the way in which cardiac interoceptive perception functions as a state variable that is subject to modulation by social and affective

contexts. The experimental findings encompassed by the chapters are novel in that they provide evidence for the existence of a bi-directional relationship between interoception and emotion, in which in addition to interoceptive accuracy influencing emotional experience in a trait-like manner, emotional experience also influences interoceptive accuracy as a state-variable. Importantly, the studies furthered the understanding of the way in which cardiac interoceptive perception accuracy is related to other modes of body perception, such as noxious and neutral tactile perception.

While it is possible that changes in interoceptive accuracy in stressful negative affective experiences are non-functional consequences of the application of the stressor, it is likely that that changes to the perception of bodily signals are of benefit to the organism. The potential effect of altered interoceptive accuracy on cognitive and affective processes is highlighted by copious evidence implicating interoception in emotional experience (Wiens, 2005). Even though the results of the experiments of the current thesis indicated that changes in interoceptive accuracy were not associated with changes in mood, it is likely that mood measures in the present studies lacked sensitivity. Consequently, the results of the thesis should not be interpreted as contrary to the James-Lange (1884, 1887) peripheralist model of emotion and supportive of the Cannon (1929) view that emotion does not require afferent bodily feedback. Moreover, recall that interoceptive accuracy has been found to influence cognitive processes such as memory (e.g., Garfinkel, Barrett et al., 2013; Werner et al., 2010) and decisionmaking (e.g., Dunn et al., 2010; Werner, Schweitzer et al., 2013). Additionally, altered interoceptive processing has been implicated in psychopathology, including anxiety (see Domschke et al., 2010 for a comprehensive review) and depression (Dunn et al., 2007), which have been associated with impairments in memory (e.g., Burt, Zembar, & Niederehe, 1995; Kizilbash, Vanderploeg, & Curtiss, 2002) as well as impairments in social and financial decision-making (e.g., Miu, Heilman, & Houser, 2008; Wang et al., 2014). Consequently, the findings of the present thesis can function as a platform for future research on the role of interoception in influencing cognitive information processing in healthy and clinical samples, which can aim to determine whether state changes in interoceptive accuracy in affective and self-focus inducing contexts influence subsequent cognitive-affective processing.

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Appendix

7.1 A List of Pros and Cons of Animal Use in Research That Was Provided to Participants in the Control Group in Experiment 1

PROS of Animal Use	CONS of Animal Use
in Medical Research	in Medical Research
The benefits of using animal in research outweigh the harm done to animals.	It causes suffering to animals
The use of animals in research is prevalent because they share at least 200 common illnesses and diseases with humans.	Level of suffering and the number of animals involved are both so high that the benefits to humanity don't provide moral justification.
It allows for research design that could not be used on humans.	If an experiment violates the rights of an animal, then it is morally wrong, because it is wrong to violate rights.
Using animals in research affords the scientist to monitor reactions to stimuli and other variables in complex organs and tissue, while allowing the scientist to minimize environmental variables.	The possible benefits to humanity of performing the experiment are completely irrelevant to the morality of the case, because rights should never be violated.
Animals are used in scientific research to further science. They are	The benefits to human beings are not proven
used most often in: I. Disease Treatment II. Prevention III. Treatment of Injuries	The harm that will be done by the experiment is known beforehand, but the benefit is unknown.
IV. Basic Medical TestingV. Medical Diagnosis	The harm that will be done to the animals is certain to happen if the
Animal studies are conducted to help decide whether a particular drug should be tested on people, and to eliminate potential ineffective or dangerous from being used with human beings. If a drug passes the animal test it's then tested on a small human group before large scale	experiment is carried out. The harm done to human beings by not doing the experiment is unknown because no-one knows how likely the experiment is to succeed or what benefits it might produce if it did succeed.
clinical trials.	Experimental drugs and

treatments that have been found

- Animals in research have made possible many scientific breakthroughs that humans benefit from each day.
 - I. Vaccinations
 - II. Anesthesia
 - III. Antibiotics
 - IV. Numerous medical treatments for various diseases
- Research on animals can be used to obtain knowledge that will help animals—e.g. breeding programs for endangered species, vaccines for cats and dogs etc.
- 85 % of the animals used in research are rodents rats and mice that have been bred for laboratory use
- Most laboratory tests on animals are simple single type tests - change in diet, drawing a simple blood sample, administering a drug.
- Suffering is minimised in all experiments. Animals are given anesthetics if a procedure is going to be invasive in any way.
- Dogs, cats and non-human primates account for only 3 out of 1000 subjects in experimentation.
- Humans are still the largest group that is used for research and experimentation and beats out all other lab animals when it comes to testing.
- Computer models can be of use when learning about a process or disease, but data for these models comes from animal studies. Also, computer

- effective on animal models will not necessarily work in people.
- Animals and humans do not get the same diseases. As a result, animal research focuses on artificially inducing symptoms of human cancer and attempting to treat those symptoms.
- Scientists use animals in biological and medical research more as a matter of tradition, not because animal research has proved particularly successful or better than other modes of experimentation.
- There is growing awareness of the limitations of animal research and its inability to make reliable predictions about human health.
- The biomedical research community and its affiliated trade associations routinely attempt to convince the general public, media, and government representatives that the current controversy over the use of animals is a life-and-death contest pitting defenders of human health and scientific advancement against hordes of anti-science, anti-human, emotional, irrational activists. Such a deliberate, simplistic dichotomy is not only false, but ignores the very real and welldocumented ethical and scientific problems associated with the use of animal experiments that characterize modern biomedical research, testing, and its associated industries.
- Any benefits to human beings

- models point to gaps for further study in living things.
- In vitro experiments usually use tissues or cells taken from animals or humans, but scientists are not able to replicate the whole complexity of a living organism in test tube or a plastic dish. Such research provides a knowledge base for further study using animals.
- that animal testing does provide could be produced in other ways.
- Alternatives to animal research already exist.
- The biomedical community
 would instead be better served by
 promoting increased funding and
 research efforts for the
 development of non-animal
 models that overcome the
 pressing ethical and scientific
 limitations of an increasingly
 archaic system of animal
 experimentation.

Sources from which the above points were taken are as follows:

- http://www.bbc.co.uk/ethics/animals/using/experiments 1.shtml
- http://science.education.nih.gov/animalresearchfs06.pdf
- http://www.experiment-resources.com/animals-in-research.html
- http://whitecoatwelfare.org/aat-text.shtml
- http://www.aavs.org/site/c.bkLTKfOSLhK6E/b.6456997/k.3D74/Problems_with_Animal_Re search.htm