University of Brighton

NEW INSIGHTS INTO THE UNDERSTANDING OF EXERCISE TOLERANCE AND REGULATION: A PLACE FOR CARDIAC INTEROCEPTION.

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ABSTRACT

Perception of physiological states, termed interoception, is proposed to influence the regulation of exercise intensity including decisions associated with pacing and task ending. Importantly, individuals are known to differ in their accuracy and awareness of interoceptive signals at rest. However, the potential influence of these differences on exercise regulation and tolerance remains poorly understood. Moreover, individual differences in sensitivity to interoceptive signals may be partially influenced by a person’s physiological characteristics such as resting heart rate, which may be modified following prolonged exercise engagement. This thesis aimed to examine the influence of interoception on exercise regulation and tolerance.

Study 1 examined the influence of aerobic fitness parameters on cardiac interoception. Greater accuracy in heartbeat perception corresponded with significantly greater aerobic fitness. Partial correlations supported this finding, indicating significant positive relationships between markers of aerobic fitness (power output (PO) and oxygen consumption at ventilatory thresholds and peak) with heartbeat perception accuracy and awareness when controlling for age, gender, and body composition, but not resting heart rate. Extending on these findings, Study 2 examined the influence of a 4-week exercise intervention on aerobic fitness and interoception. The exercise intervention did not significantly influence changes in either aerobic fitness or interoceptive abilities. These null effects indicated that repeated exposure to augmented interoceptive feedback alone was not sufficient to alter a person’s interoceptive abilities. In Study 3, the influence of interoception on time-to-task failure (TTF) in a constant-load exercise task (80% PO_{peak}) was examined. Interoceptive accuracy did not significantly influence TTF. Furthermore, physiological responses and ratings of perceived exertion (RPE) were not significantly different between good and poor heartbeat perceivers, suggesting that interoceptive accuracy did not affect exercise tolerance. Finally, Study 4 examined the regulation of exercise work rates at perceived *light* (RPE10 on the Borg 6-20 scale) and *hard-to-very hard* (RPE16) efforts between good and poor heartbeat perceivers. Good perceivers exhibited greater changes in PO between conditions compared with poor perceivers with differing pacing strategies evident between groups over the first 5-minutes of both conditions. Additionally, good perceivers experienced lower physiological strain (i.e., heart rate and respiratory exchange ratio) in RPE10 but not

RPE16, suggesting that interoception may influence sensitivity to allostatic demand at low intensities.

In conclusion, these findings suggest that interoception is influenced by adaptations associated with aerobic fitness but is not modifiable following short-term exercise interventions. Moreover, differences in interoceptive accuracy may influence the regulation of self-paced exercise but do not affect exercise tolerance under constant load.

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LIST OF ABBREVIATIONS

$\%PO_{peak}$	Percentage of the peak power output
$\%PO_{VT1}$	Percentage of the power output at the first ventilatory threshold
$\%PO_{VT2}$	Percentage of the power output at the second ventilatory threshold
$\%Trial_{mean}$	Percentage of average power output for the trial
$[La^-]_c$	Blood lactate concentration
$[La^-]_{c\ end}$	End blood lactate concentration
Δ	Change
a.u.	Arbitrary unit
ACC	Anterior cingulate cortex
ANCOVA	Analysis of covariance
ANOVA	Analysis of variance
ATP	Adenosine triphosphate
AUC	Area under the curve
BRUMS	Brunel University mood scale
CGM	Central governor model
CI	Confidence intervals
cm	Centimetre
CO_2	Carbon dioxide
CON	Control group
DLPFC	Dorsolateral prefrontal cortex
ES	Effect size
EX	Exercise intervention group
fast-RT	Fast ramp graded exercise test
f_c	Heart rate
$f_{c\ end}$	End heart rate
$f_{c\ peak}$	Peak heart rate
$f_{c\ rest}$	Resting heart rate
g	Hedge's g effect size

GOOD	Good heartbeat perceivers
GXT	Graded exercise task
h	Hours
H^+	Hydrogen ions
HBT	Heartbeat tracking task
HDB	Heartbeat discrimination task
Hz	Hertz
IC	Insula cortex
IGT	Iowa gambling task
IPAQ	International physical activity questionnaire
kg	Kilogram
$L \cdot min^{-1}$	Litres per minute
LPFC	Lateral prefrontal cortex
$METs \cdot wk^{-1}$	Metabolic equivalents per week
$mL \cdot kg^{-1} \cdot min^{-1}$	Millilitres per kilogram per minute
$mL \cdot min^{-1}$	Millilitres per minute
$mmol \cdot L^{-1}$	Millimoles per litre
mm	Millimetre
ms	Milliseconds
MS-RT	Multi-stage incremental ramp test
n or N	Number of samples/ participants
NTS	Nucleus tractus solarius
O_2	Oxygen
PAG	Periaqueductal grey
PB	Parabrachial nucleus
PCO_2	Partial pressure of carbon dioxide
PE	Prediction error
PFC	Prefrontal cortex
PO	Power output
PO_{abs}	Absolute power output
POMS	Profile of mood states
POOR	Poor heartbeat perceivers

PO_{peak}	Peak power output
POST-BEST	Best performance for training group post-training intervention
POST-WORST	Worst performance for training group post-training intervention
PRE	Pre-training
PWC150	Power output at a heart rate of 150 b·min^{-1}
r	Pearson's correlation coefficient **or** non-parametric effect size estimate
r·min^{-1}	Revolutions per minute
RER	Respiratory exchange ratio
ROC	Receiver operator characteristic
RPE	Rating of perceived exertion
r_s	Spearman's rank correlation coefficient
s	Second (unit of time)
s.u. or SU	Standardised unit
SI	Primary somatosensory cortex
SII	Secondary somatosensory cortex
SMH	Somatic marker hypothesis
T_{lim} or TTF	Time-to-task failure
$\dot{V}CO_2$	Rate of carbon dioxide production
$\dot{V}_E$	Minute ventilation
$\dot{V}_E \cdot \dot{V}CO_2^{-1}$	Ventilatory equivalent for carbon dioxide
$\dot{V}_E \cdot \dot{V}O_2^{-1}$	Ventilatory equivalent for oxygen
VMPFC	Ventromedial prefrontal cortex
VM_{PO}	Posterior ventromedial nucleus
$\dot{V}O_2$	Rate of oxygen consumption
$\dot{V}O_{2\,max}$	Maximal rate of oxygen consumption
$\dot{V}O_{2\,peak}$	Peak rate of oxygen consumption
V_T	Tidal volume
VT_1	First ventilatory threshold
VT_2	Second ventilatory threshold

W	Watts
$W \cdot kg^{-1}$	Watts per kilogram of body mass
yrs	Years of age
η_p^2	Partial eta squared

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DECLARATION

I declare that the research contained in this thesis, unless otherwise formally indicated within the text, is the original work of the author. The thesis has not been previously submitted to this or any other university for a degree and does not incorporate any material already submitted for a degree.

Signed: [redacted]

Dated: 06/01/2021

CHAPTER 1. INTRODUCTION

Interoception can be broadly defined as the process of sensing, interpreting, and integrating information related to the physiological condition of the body (Khalsa, 2018). According to Sherrington's (1954) original classification, interoception can be considered as distinct from other aspects of sensory perception, such as our experience of stimuli emerging from outside of our body (exteroception) and also the perception of our body's position in space (proprioception). Information carried along interoceptive neural pathways plays a fundamental role in maintaining homeostasis. Interoceptive afferent signalling is linked to lower-level allostatic control processes (such as the regulation of cardiovascular, respiratory, and sudomotor functions) that are largely governed pre-consciously by peripheral, brainstem, and subcortical structures (Craig, 1996). However, interoception also encompasses our conscious perception of physiological states, including pain, temperature, abdominal sensations that correspond to hunger or nausea, bladder or bowel fullness, itchiness, muscle *milieu*, visceral sensations, and others (Craig, 2002). Conscious perception of these 'feelings' possesses affective and motivational functions to guide behaviour towards actions that satisfy the ongoing drive to minimise deviations from homeostatic bounds (Critchley & Harrison, 2013). Consequently, these ascending interoceptive pathways may be considered to form the afferent branch of a larger "emotional/motor system" that functions within the limbic system, contributing to the generation of emotional experience (Craig, 2002; Critchley & Harrison, 2013).

Interoception can be assessed using a variety of methods. However, perhaps the most common approach to assessing interoception is the use of perceptual tasks that investigate a person's sensitivity to visceral sensations emerging from their body, notably tests of heartbeat perception (Rainer Schandry, 1981; Whitehead, Drescher, Heiman, & Blackwell, 1977). These tasks have allowed the quantification of people's conscious sensitivity to interoceptive stimuli. It has been demonstrated that people vary considerably in their capacity to access interoceptive sensations, and these individual differences are considered relevant to the experience of emotions (Khalsa et al., 2018), decision-making (Werner, Duschek, & Schandry, 2009), and behaviour (Critchley & Garfinkel, 2018). Proposal of a formalised taxonomy that defines cardiac interoception as a multi-dimensional construct comprised of interoceptive accuracy (an objective measure of a person's interoceptive sensitivity), interoceptive sensibility (a person's subjective or self-evaluative perspective of their interoceptive ability), and interoceptive awareness (a metacognitive construct evaluating the correspondence between objective interoceptive accuracy and subjective report) have been described (Garfinkel, Seth, Barrett, Suzuki, & Critchley, 2015). Interestingly there is some evidence that engaging in exercise may result in acute transient improvements in interoceptive accuracy (e.g., Jones & Hollandsworth, 1981). However, there are currently inconsistent findings regarding the long-term influence of physical activity behaviour and changes in aerobic fitness on interoception (Georgiou et al., 2015; Machado et al., 2019; Perakakis, Luque-Casado, Ciria, Ivanov, & Sanabria, 2017), with poor definition of the possible mechanisms involved. Further, there has been no consideration of the effect of a person's aerobic fitness and physical activity behaviour on measures of interoceptive sensibility and interoceptive awareness. Accordingly, the first aim of this thesis was to investigate the potential role of aerobic fitness adaptations on these three different dimensions of cardiac interoception.

Exercise is a complex, dynamic behaviour that poses numerous acute pressures to the overriding requirement for sustained homeostasis. Management of these allostatic demands is achieved through nested systems involving, for example, lower-level systems such as autonomic reflexes within higher-order systems such as behavioural regulation which are likely to be influenced by bottom-up information signalling along interoceptive afferent pathways and are therefore exercise intensity-dependent. The past 25 years have seen an increasing acknowledgement of the importance of this higher-order psychophysiological process, with the development of several prominent theoretical frameworks for a deeper understanding of behavioural regulation during physical exercise (Hureau, Romer, & Amann, 2018; St Clair Gibson, Swart, & Tucker, 2017; Venhorst, Micklewright, & Noakes, 2018d). Broadly speaking, these frameworks describe an extracellular control system that integrates interoceptive feedback alongside endogenous and exogenous reference signals within the brain to mediate ongoing exercise intensity in a manner designed to mitigate potential dyshomeostasis. As part of this process, the emergence of subjective perceptions of exertion and fatigue with their associated effects on affective and motivational drive are considered to be an important factor influencing exercise performance (Greenhouse-Tucknott, Wrightson, Raynsford, Harrison, & Dekerle, 2020). Indeed, studies have shown that manipulation of the transduction (Pollak et al., 2014; Schlader, Simmons, Stannard, & Mündel, 2011), transmission (Amann, Sidhu, Weavil, Mangum, & Venturelli, 2015; Blain et al., 2016), and processing (Okano et al., 2015) of interoceptive signals may influence subjective ratings of perceived exertion and its relationship to muscular work during exercise. These effects reflect other reported observations that increased attention to interoceptive sensations (internal focus) results in reduced exercise intensity during self-paced exercise at a person's 'preferred' exercise work rate (Fillingim & Fine, 1986; Pennebaker & Lightner, 1980).

Despite the proposed importance of interoception in the regulation of exercise intensity, including decisions associated with pacing and task ending, relatively little consideration has been given to the influence of individual differences in interoceptive sensitivity on this process. Of the few available studies, the association between cardiac interoception and exercise regulation is largely equivocal. Consequently, the second aim of this thesis was to provide new and original insights into the potential role of cardiac interoception on the regulation of exercise intensity and exercise tolerance.

To summarise, the purpose of the present thesis was to examine (1) the influence of aerobic fitness on cardiac interoception, and (2) the influence of cardiac interoception on the regulation of exercise intensity. These two research questions were examined across four separate experimental studies (Chapters 4-7). A brief overview of the structure and content of the present thesis is provided below:

Chapter 2 provides a review of the literature pertaining to interoception and the factors influencing exercise tolerance and exercise regulation.

Chapter 3 presents the common methods used throughout the experimental chapters of this thesis.

Chapter 4 examines the potential relationship between measures of cardiac interoception, aerobic fitness, and physical activity.

Chapter 5, extending on the findings of Chapter 4, investigates the potential influence of a short-term exercise training intervention on markers of aerobic fitness and cardiac interoception.

Chapter 6 examines the possible influence of cardiac interoception on exercise tolerance in a constant load cycling task.

Chapter 7 investigates the potential role of cardiac interoception on the regulation of exercise intensity at fixed ratings of perceived exertion.

Chapter 8 discusses the results from the experimental chapters, including principal findings, progression of the research area, limitations and assumptions, and future directions.

Chapter 9 provides a conclusion to the present thesis.

CHAPTER 2. LITERATURE REVIEW

2.1. Interoception

Interoception describes a broad range of sensory and perceptual mechanisms related to the processing of stimuli emerging from within the body (Vaitl, 1996). This form of visceral perception encompasses many of the major physiological systems related to cardiovascular, pulmonary, gastrointestinal, hormonal, and metabolic processes (Cameron, 2009). Information related to these processes is largely sensed across various afferent receptors and interpreted centrally in the brain (Craig, 2003).

Interoception is distinct from other forms of sensory perception such as those related to the external environment (exteroception) and in some accounts, also distinct from proprioception (sense of motion and position in space) (Craig, 2002; Vaitl, 1996). In contrast to exteroceptive and proprioceptive senses, interoception is predominantly a precognitive sensory system which, in many instances is vague and difficult to interpret, but capable of reaching conscious awareness (Ceunen, Vlaeyen, & Diest, 2016; Harshaw, 2015). Indeed, Vaitl (1996) suggests that awareness of the plurality of interoceptive information only becomes consciously available under situations where considerable variations from normative stasis occur.

A further distinction of interoception is its apparent resistance to experimental manipulation (Fairclough & Goodwin, 2007; Khalsa et al., 2008). Consequently, interoception may represent a trait variable. However, as discussed in section 2.6.2, interoception is possibly influenced by exercise. There is some evidence of a positive relationship between aerobic fitness and performance in tests of cardiac perception (Jones & Hollandsworth, 1981). Additionally, several studies have reported transient improvements in cardiac perception both during and immediately succeeding physical activity (Jones & Hollandsworth, 1981; Montgomery, Jones, & Hollandsworth, 1984). However, at present, this evidence is not strongly supported within a larger evidence base and is confounded by contrasting findings (Montgomery et al., 1984).

An important aspect of interoception is its role in the regulation and maintenance of homeostasis (Craig, 2003; Strigo & Craig, 2016). Afferent feedback provides information related to the physiological condition of the different structures within the body. Within exercise contexts, examples of this relate to the availability of substrates involved in cellular respiration or changes in body temperature related to metabolic heat production.

This information influences subsequent allostatic responses required to sustain cellular and systemic function. Allostasis occurs at both physiological and behavioural levels (Barrett, Quigley, & Hamilton, 2016; Kleckner, Zhang, Touroutoglou, & Chanes, 2017). Related to the examples given above, physiological changes may relate to cardiovascular responses, an increase in gluconeogenesis, or in the case of metabolic heat production an increase in blood flow to surface capillaries to aid the dissipation of heat. Whereas behavioural aspects of allostasis relate to changes in exercise work rate, consumption of nutrients to increase the availability of necessary substrates, or withdrawal from the exercise task.

In the following sections, various facets of interoception will be discussed. Firstly, exploring the neural basis of its sensation and perception, including the current understanding of the structures within the brain involved with the processing and interpretation of the information related to the milieu intérieur. Subsequently, the role of interoception on behaviour and emotion will be explored. A review of several predominant theories in this area is presented. Over the final sections, the role of interoception and afferent feedback during exercise will be presented, exploring the role of interoception on exercise pacing and its influence on the perceptual and emotional experience during physical activity.

2.2. Neurobiological Constructs Supporting Interoception

Interoception involves several neuroanatomical structures that convey visceral sensations from the periphery to mid and forebrain structures. Early anatomical evidence of these sensory processes was first highlighted in the work of Pavlov (1927) and Sherrington (1954). Advancements in techniques and technologies have aided an almost complete mapping of interoceptive pathways from visceral receptors to the major cortical and subcortical structures that process these signals. Understanding of these processes is at the centre of several predominant contemporary accounts of the role of somatic signalling (interoception) on emotion (Dunn et al., 2010; Seth, 2013; Strigo & Craig, 2016; Wiens, 2005), perception (Dahme, Richter, & Mass, 1996; Kadota et al., 2010), behaviour (Murphy, Brewer, Catmur, & Bird, 2016), and the sense of self (Craig, 2014; Seth, 2013). The purpose of the following section is to describe the neurobiological structures involved within the interoceptive network.

2.2.1. Ascending Afferent Pathways: From Receptor to Brain

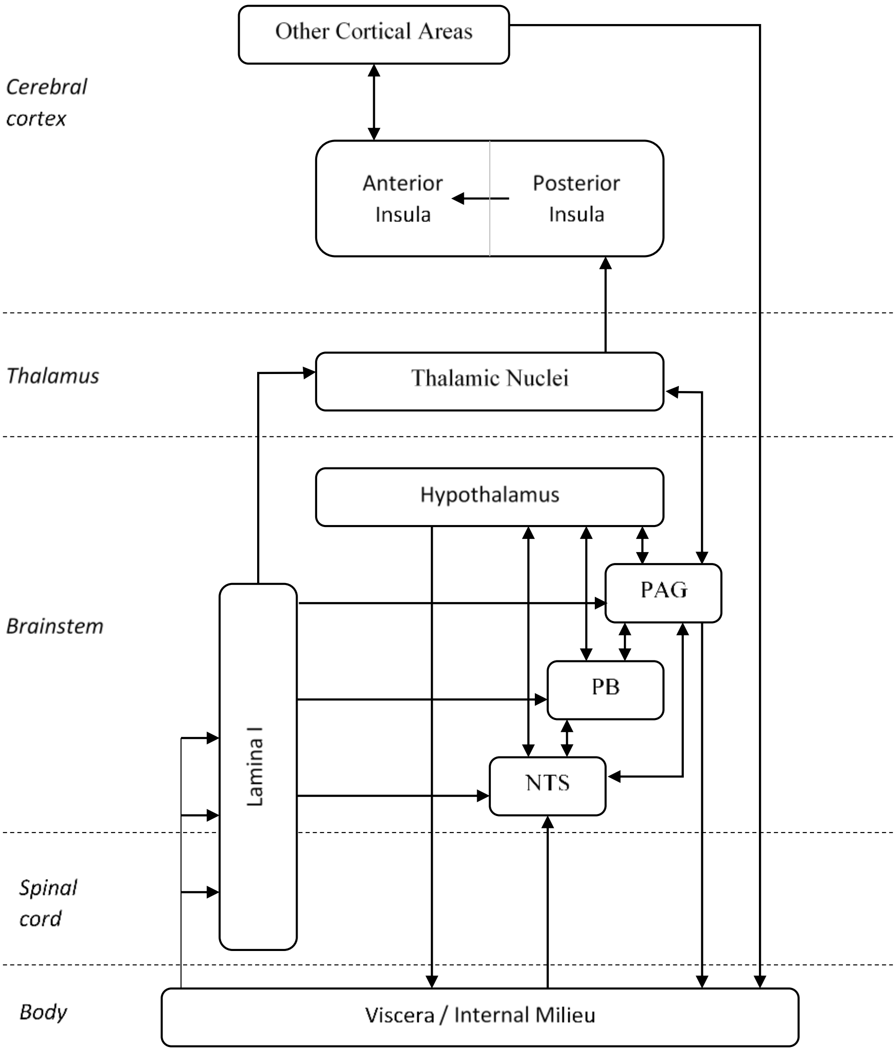


Figure 2.1. Interoceptive pathways. Nucleus tractus solitarius (NTS), parabrachial nucleus (PB) and periaqueductal grey (PAG). Arrows indicate direction of information signalling. Adapted from Craig (2014).

Interoception is supported by several classes of sensory neurons (Craig, 2002; Sherrington, 1954). These different sensory neurons have specific receptor fields which enable selective discrimination of mechanical, chemical, thermal, noxious, and other stimuli (Andrew & Craig, 2001; Craig, 2014; Mitchell, Kaufman, & Iwamoto, 1983; Nakamura & Morrison, 2008). Their information conveys all homeostatic relevant signals from the body. Stimulation of these receptors excites the small-diameter axons of their sensory neurons which enter the spinal column via two predominant pathways. In the spinothalamic pathway, lamina I neurons, located in the most superficial portion of the dorsal horn of the spinal grey matter, receive input from the small-diameter sensory neurons which innervate the body (Craig, 2014). Sensory input to lamina I neurons projects contralaterally across to the lateral spinothalamic tract, located in the middle of the spinal white matter, and ascends to intermediate targets within the spinal column before projecting to several targets in brainstem, mid- and forebrain structures.

Evidence for the role of these lamina I neurons as the principal constituent pathway for conveying interoceptive afferent signals is predominantly drawn from studies of animal models. For instance, through examination of neuronal activation in the rodent spinal cord, Doyle and Hunt (1999) demonstrated that expression (i.e., activity) of neurokinin-1 sensitive lamina I neurons was positively associated with the intensity of noxious cutaneous cooling (10°C and 4°C), this effect was not reported for other afferent signalling pathways (laminae III/IV). Comparable findings have also been reported for populations of neurons in lamina I responding to innocuous cutaneous warming, with a positive linear stimulus-response relationship that plateaus at the threshold for noxious (painful) thermal stimulus (Andrew & Craig, 2001a). The specificity of these receptor fields is supported by observations made by Ran, Zhang, and Craig (1998) who described the presence of three discrete populations of morphologically distinct neuronal bodies that are selectively responsive to either nociceptive stimulation or innocuous thermal stimulation, as well as a group of neurons characterised by polymodal receptor fields (responsive to heat, pinch, and cold stimulation) projecting from the superficial dorsal horn in 41 feline subjects. Extending beyond thermal and pain sensation, Wilson and colleagues (2002) reported that a small population of lamina I neurons (projecting to the brainstem) was selectively activated by evoked isometric contraction, with activation of these neurons occurring ~15-s after the onset of the contraction with excitatory activity maintained for >60-s following cessation of the contraction. The delay in the onset of this activation and its subsequent maintenance during recovery suggested that information carried along this class of lamina I neuron was involved in signalling changes in the metabolic status of the active muscle tissue. Taken together, the findings from these studies support the notion that lamina I afferent neurons provide selective discrimination of specific sensory inputs related to the physiological condition of the body and are distinct from other spinal laminae pathways.

Ascending spinothalamic lamina I projections converge with a separate pathway of ascending small-diameter sensory fibres that innervate tissues such as the tongue, the pharynx, the heart, and gastrointestinal system (medullothalamic pathway), at the solitary nucleus (NTS) which is located within the medulla oblongata (Craig, 1996; Holstege, 1988; McAllen, Neil, & Loewy, 1982). The medulla is involved in autonomic functions concerned with the regulation of ventilatory, cardiovascular, vasomotor activity (Benarroch, 1993). Projection sites from these ascending afferent pathways within the medulla support the efficient regulation of these autonomic processes. For instance, Menétrey and Basbaum (1987) have reported that lamina I neurons from both spinal and trigeminal pathways project to the NTS, using retrograde labelling techniques, with corresponding regions of the medulla shown to be involved in cardiovascular responses to both skeletal muscle activity (Ally, Nauli, & Maher, 2002; Phattanarudee, Towiwat, Maher, & Ally, 2013) and increased dietary salt intake (Adams, Bardgett, & Stocker, 2009). Further, Polgár and colleagues (2010) identified lamina I projections from cervical and lumbar segments to both periaqueductal grey (PAG) and parabrachial (PB) regions of the brainstem. Like the medulla, these structures support the regulation of allostatic reflexes. The activity of the PAG is shown to be involved in the processing of nociceptive inputs and may also influence respiratory rhythm (i.e., respiratory frequency; Kaur et al., 2013) and cardiovascular responses (*for review see* Davern, 2014). Comparatively, nuclei in the PB are reportedly involved in projecting signals related to physiological stress following hypertonic saline infusions (Larsen & Mikkelsen, 1995) as well as thermal nociceptive stimulus (Pan, Castro-Lopes, & Coimbra, 1999) to areas of the hypothalamus (particularly the periventricular nucleus). Importantly, lamina I projections to these brainstem sites (NTS, PB, PAG) also provide intermediate relay points within a larger afferent interoceptive pathway, which signal spinofugally to thalamic nuclei.

Much of the terminal projections from these ascending pathways of lamina I neurons are observed in the thalamus, which is evidenced in anatomic studies using immunohistochemical staining techniques that have been applied to identify the presence of lamina 1 neurons in these regions (Blomqvist, Zhang, & Craig, 2000). Importantly, activation of these thalamic regions is associated with the processing of interoceptive stimuli in higher cortical regions. In accordance with the observation of lamina I signalling of thermal stimuli described previously, micro-stimulation of the posterior ventromedial nucleus (VM_{PO}) has been shown to result in the perception of cold sensation in humans, with a positive relationship reported between stimulation intensity and subjective rating of cold (Davis et al., 1999). Similarly, altered perception of pain and temperature has been described in persons presenting with thalamic lesions in the ventral posterior complex (Montes et al., 2005). With respect to changes in cardiac function, Kimmerly and colleagues (2005) have shown that the activation mediodorsal nucleus of the thalamus was inversely associated with increasing heart rate. The authors further observed changes in the activity of several cortical regions including the insula, anterior cingulate, and amygdala suggesting that this region of the thalamus may be part of a larger cortical network regulating autonomic cardiovascular function. Accordingly, these thalamic regions are proposed to represent a preliminary relay centre for projecting interoceptive afferent information to several other major cortical sites including the dorsal posterior insula and anterior cingulate cortex (Carstens, Leah, Lechner, & Zimmermann, 1990). Activation of these higher cortical sites is directly correlated with various aspects of subjective physical and emotional experience (Harrison, Gray, Gianaros, & Critchley, 2010; Lamm & Singer, 2010; Medford & Critchley, 2010; Meyer, Strittmatter, Fischer, Georg, & Schmitz, 2004).

2.2.2. Role of the Insula Cortex

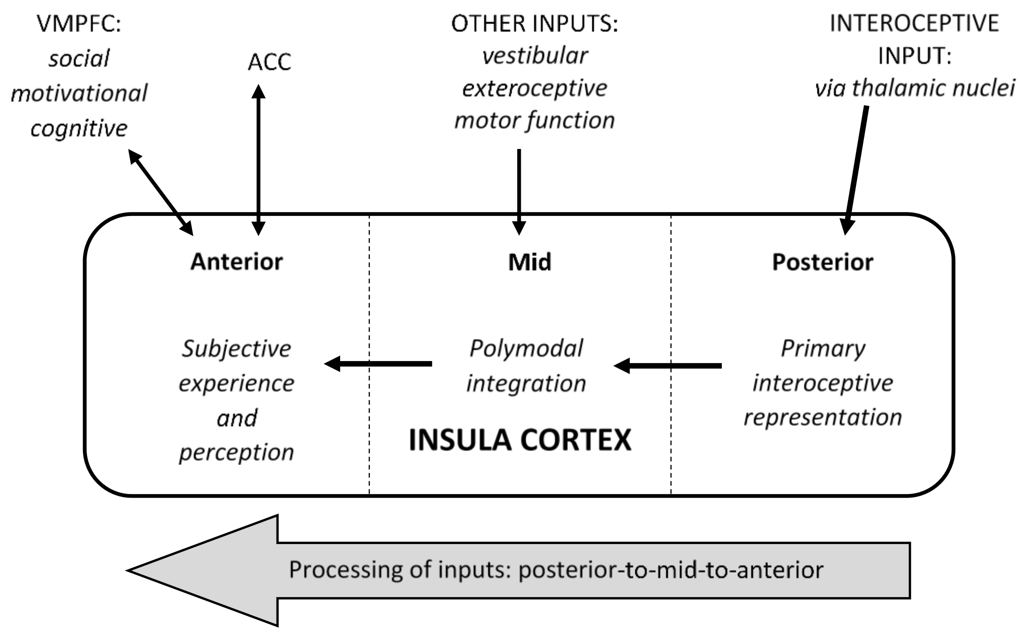


Figure 2.2. Posterior-to-anterior processing of interoceptive afferent inputs within the insula cortex. Ventromedial prefrontal cortex (VMPFC), anterior cingulate cortex (ACC).

The insula cortex is considered to be the primary cortical region representing interoceptive afferent inputs (Benarroch, 1993; Craig, 2003; Ebisch et al., 2011; Garfinkel, Seth, Barrett, Suzuki, & Critchley, 2015; Jones et al., 2015; Meyer, Strittmatter, Fischer, Georg, & Schmitz, 2004). The insular cortex is located in the deep fold of the lateral sulcus separating the temporal lobe from the parietal and frontal lobes (Uddin, Nomi, Hébert-Seropian, Ghaziri, & Boucher, 2017). Anatomically, the insular cortex can be roughly divided into three portions according to their cytoarchitectural differences: a posterior granular portion (posterior insula), a middle dysgranular portion (mid insula), and an anterior agranular portion (anterior insula) (Mesulam & Mufson, 1985; Nieuwenhuys, 2012). Differences in the anatomical structure of these three sections are thought to reflect different roles in the processing and representation of interoceptive afferent feedback (Evrard, 2019).

A relatively early paper by Jones and Burton (1976) provides a detailed description of the changes in the cytoarchitecture of the insula and the concentration of thalamic terminal projections to the insular cortex in primates. The authors reported that the majority of the terminal projections of these ascending thalamic neurons are observed within the dorsal posterior insula. As a result of this high concentration of thalamic inputs to the posterior insula, it is proposed that this region of the insula cortex represents the primary integration site for interoceptive inputs emanating from the body (Craig, 2014).

Functional models of the insula cortex indicate a forward flow of interoceptive information from the dorsal posterior insula to the mid-insula and finally to the anterior insula (Cerliani et al., 2012; Cloutman, Binney, Drakesmith, Parker, & Lambon Ralph, 2012; Ghaziri et al., 2017). Importantly, within this feedforward processing, the mid-insula functions to integrate interoceptive information with inputs from other sensory sources. For instance, the dorsal region of the mid-insula has been shown to receive inputs from somatosensory cortices (Burton, Fabri, & Alloway, 1995; Cipolloni & Pandya, 1999), motor and supplementary motor cortices (Gerbella, Borra, Rozzi, & Luppino, 2014), is responsive to inputs related to innocuous non-affective tactile stimulation (Davidovic, Starck, & Olausson, 2019) as well as mechanoreceptive and baroreceptive stimulation (Zhang, Dougherty, & Oppenheimer, 1999). These findings support the notion that the dorsal mid-insula acts as a principle region for representing intrapersonal identification of body ownership that contributes to our sense of agency (*for review see* Karnath & Baier, 2010).

Ventrally, the mid-insula has been shown to receive inputs from limbic structures of the brain. For instance, Stefanacci and Amaral demonstrated that the ventral mid-insula shares connections with several regions of the amygdala using both anterograde tracing (Stefanacci & Amaral, 2002), retrograde tracing (Stefanacci & Amaral, 2000). The amygdala is reportedly involved in social interaction (Bickart, Wright, Dautoff, Dickerson, & Barrett, 2011), processing of external threat (Feinstein et al., 2013; Terburg et al., 2012) in addition to more generalised emotional processing including implicit emotional learning and memory, emotional modulation of memory, emotional influences on attention and perception, emotion and social behaviour, emotion inhibition and regulation, and addiction (*for review see* Phelps & LeDoux, 2005). Additionally, the ventral mid-insula also receives inputs from the ventromedial striatum (Chikama, McFarland, Amaral, & Haber, 1997) and pre-supplementary motor area (Luppino, Matelli, Camarda, & Rizzolatti, 1993). Interaction between these cortical regions is thought to be involved in modulating social behaviours (Caruana, Jezzini, Sbriscia-Fioretti, Rizzolatti, & Gallese, 2011). Finally, the ventral mid-insula appears to be selectively activated by conspecific vocal auditory stimuli (Remedios, Logothetis, & Kayser, 2009) and facial recognition (Ku, Tolias, Logothetis, & Goense, 2011). Consideration of the combined nature of these inputs to the ventral mid-insula suggests that this region is involved in integrating interoceptive, emotional-motivational, and extra-personal experience, which can be broadly defined as representing interpersonal experience as opposed to the intrapersonal identification of the “self” that is putatively derived in the dorsal mid-insula (Evrard, 2019).

Information from the mid-insula is further represented onto the anterior insula, where emotional and hedonic appraisal of this spectrum of information becomes available to subjective conscious experience (Craig, 2009; Critchley, Wiens, Rotshtein, Öhman, & Dolan, 2004; Lamm & Singer, 2010). Related to the appraisal of physical sensations from the body, von Leupoldt and colleagues (2008) demonstrated that activation of the right anterior insula and right amygdala were significantly associated with subjective ratings of unpleasantness in conditions of severe inspiratory resistive load. These findings are supported by Schon et al. (2008) who reported that individuals with ischemic lesions of the right insula, extending to the anterior region, were associated with reduced perception of both dyspnoea and pain (noxious cold), measured according to subjective ratings of both intensity and unpleasantness, compared with healthy controls. In accordance with the perception of noxious cold described above, evidence across a range of studies demonstrate that activation of anterior insula cortex is associate with the subjective evaluation of thermal stimuli (Craig, Chen, Bandy, & Reiman, 2000; Nagashima, Tokizawa, & Marui, 2018; Olausson et al., 2005). For instance, Craig et al. (2000) reported that whilst graded cooling resulted in activation of contralateral sites within the dorsal margin of the posterior and mid insula, subjective ratings of the perceived intensity of cooling were most strongly correlated with activation in the ipsilateral anterior insular and orbitofrontal cortices. Extending these findings to examine subjective perceptions of warmth, Olausson and colleagues (2005) reported significant activation of the right anterior insula when weighted to visual analogue scale responses of perceived thermal intensity, with the ipsilateral anterior cingulate cortex responsive to changes to innocuous cutaneous thermal stimulation. Accordingly, the findings across these studies indicate that the anterior insula is involved in the subjective appraisal of a range of physical sensations emerging from the body.

Conscious perception of cardiac events also appears to emerge in the anterior insula. To assess the basis of cardiac awareness, Critchley and colleagues (2004) examined regional brain activity in response to both a heartbeat discrimination task (*see* Section 2.4 for further description of task) and an exteroceptive task evaluating differences in auditory tones. Data from their fMRI analyses indicated that the anterior insular cortex was selectively activated in the heartbeat perception task but not the exteroceptive task. Additionally, a significant positive correlation was observed for activation of the right anterior insula and relative performance in the heartbeat discrimination task (r = .62). Consonant with this fMRI data, the authors further reported that grey matter volume in the right anterior insula was significantly correlated with both the relative performance in the heartbeat discrimination task (r = .39) and also the participant's subjective appraisal of their own interoceptive sensibility (r = .35) according to the Porge's Body Perception Questionnaire. Finally, examining the potential role of the anterior insula in emotional experience, the authors reported that subjective ratings of anxiety were significantly correlated with both performance in the heartbeat discrimination task (r = .64) and activity of the right anterior insula during the heartbeat discrimination task (r = .65). Interpretation of these findings supports theoretical assertions that awareness of visceral sensations provides a fundamental substrate for the experience of subjective feeling states and emotion.

The anterior insula is widely connected with other cortical brain structures. In particular, the anterior insula cortex and anterior cingulate cortex (ACC) are proposed to work in conjunction as part of the wider limbic system (Gu, Hof, Friston, & Fan, 2013). Within this system, the anterior insula is described as being the limbic-sensory cortex, because of the aforementioned role in processing afferent sensory inputs, and the ACC as being the limbic-motor cortex, because of its role in emotional control, error processing, economic valuations, and evaluation of motor functions (Craig, 2002). Consequently, the anterior insular cortex appears to be responsible for the input component of interoception, whereas the ACC is responsible for the output component (Medford & Critchley, 2010). These two structures share bidirectional connections with structures within the prefrontal cortex as well as lower-order structures such as the amygdala, striatum, and thalamus. These connections serve to moderate decision-making and behaviour, emotion, valuation of reward and cost (Critchley & Garfinkel, 2018).

In conclusion, the literature presented above provides support for the presence of a distinct neural pathway that supports the detection, transmission, and processing of interoceptive stimuli. Input of interoceptive changes to brainstem structures such as the NTS, PAG, and PB support the maintenance of homeostasis through autonomic reflexes. Importantly, ascending interoceptive inputs appear to converge in the insula cortex, where a feedforward process of these inputs to the anterior insula cortex results in the emergence of these signals into conscious awareness. Additionally, the insula cortex is richly connected with other cortical regions. Finally, as demonstrated by Critchley and colleagues (2004), functional and structural differences in the anterior insula are positively associated with performance in a heartbeat detection task, which correspondingly is also associated with differences in subjective emotional experience. These findings suggest that (1) that heartbeat perception tasks may provide a valid technique for assessing interindividual differences in interoceptive characteristics, and (2) that emotions and subjective feeling states may be embodied in the perception of bodily states. The following sections will explore these two topics in greater detail; firstly, examining the use of heartbeat detection tasks as a measure of interoception and secondly, evaluating the putative role of interoception on emotion.

2.3. Measurement of Cardiac Interoception

Individuals are known to vary significantly in their ability to accurately perceive interoceptive signals. Examination of these differences has been elucidated largely through tests of visceral perception related to the function of three major physiological systems: heart (cardiac interoception), lungs (respiratory interoception), and digestive system (gastrointestinal interoception) (Vaitl, 1996). Importantly, the application of these techniques under controlled conditions demonstrates good test-retest reliability (r = .58; Mussgay, Klinkenberg, & Rüddel, 1999), suggesting that a person's interoceptive characteristics are likely to represent a relatively stable trait characteristic (Cameron, 2001). While differences in the ability to accurately perceive interoceptive signals are not fully appreciated (Verdejo-Garcia, Clark, & Dunn, 2012) these effects likely relate to the relative strength of interoceptive signals arising in the body (see Section 2.3.5 for further discussion). Furthermore, as discussed subsequently (Section 2.4), a substantial body of available evidence supports the association between differences in interoceptive ability and the experience of subjective feeling states, emotion, as well as clinical disorders such as anxiety and depression (Domschke, Stevens, Pfleiderer, & Gerlach, 2010; Eggart, Lange, Binser, Queri, & Müller-Oerlinghausen, 2019). For the purpose of this thesis, the following section will concentrate specifically on the use of heartbeat detection tasks as a technique for assessing interoception.

2.3.1. Methods of Assessing Heartbeat Perception

Cardiac perception tests are among the most widely utilised psychometric tool for assessing interoception. The basis of this popularity is largely pragmatic. Heartbeats provide distinct physiological events that can be easily measured without the use of invasive procedures (e.g., using an electrocardiogram or pulse oximeter). Some of the earliest reported uses of heartbeat perception as a measure of interoception date back to the late seventies early eighties (Sandman, Walker, & Berka, 1982; Rainer Schandry, 1981; Whitehead et al., 1977) and have since been widely validated against behavioural and neurophysiological measures (Critchley, Wiens, Rotshtein, Öhman, et al., 2004; Dunn, Galton, et al., 2010; Pollatos, Kirsch, & Schandry, 2005a; Vaitl, 1996).

Cardiac interoception can be defined as the process of sensing, storing, and representing information about the state of the cardiovascular system. In accordance with other interoceptive modalities (e.g., Hölzl, Erasmus, & Möltner, 1996), cardiac interoception can be deconstructed into five different aspects: attention (observing internal bodily sensations), detection threshold (presence or absence of conscious report), symptom magnitude (intensity of symptoms), accuracy (correct or precise monitoring), discrimination (localised sensation to specific sensory inputs, differentiated from other sensations), or self-report (subjective judgements of one’s own experiences). Each of these facets can be investigated, depending on the tool being utilised. With this in mind, Khalsa and Lapidus (2016) provide an appraisal of the capacity of the five most common approaches in examining cardiac interoception, shown below (Table 2.1). The five approaches described by the authors included: (1) heartbeat tracking (counting) tasks (Rainer Schandry, 1981), heartbeat discrimination tasks (Whitehead et al., 1977), heartbeat tapping or phase adjustment tasks (Ludwick-Rosenthal & Neufeld, 1985; Palmer, Ainley, & Tsakiris, 2016; Plans et al., 2020), heartbeat perturbation through either pharmacological manipulation (Khalsa, Rudrauf, Sandesara, Olshansky, & Tranel, 2009) and physical exertion (Jones & Hollandsworth, 1981; Pollatos, Herbert, Kaufmann, Auer, & Schandry, 2007), and subjective self-report measures of attention to interoceptive processes (e.g., Body Perception Questionnaire, Porges, 1993).

Table 2.1. Identification of different psychophysiological constructs (attention, detection, discrimination, intensity, accuracy, and self-report) related to cardiac interoception that are captured using the five most common approaches for assessing heartbeat perception (heartbeat attention, heartbeat counting, heartbeat tapping, heartbeat detection, and heartbeat perturbation tasks). See text for details. Adapted from Khalsa and Lapidus (2016).

	Heartbeat Attention	Heartbeat Counting	Heartbeat Tapping	Heartbeat Detection	Heartbeat Perturbation
Attention	✓	✓	✓	✓	✓
Detection			✓	✓	✓
Discrimination				✓	✓
Intensity					✓
Accuracy		✓	✓	✓	✓
Self-report	✓	✓	✓	✓	✓

Despite the scope for the application of these different cardiac interoceptive tools, the literature around cardiac perception is largely divided between studies that either use tasks of heartbeat tracking or heartbeat discrimination. Heartbeat tracking methods, also referred to as the ‘mental tracking task’ or ‘heartbeat counting task’, assess the ability of an individual to accurately count, and subsequently report, the number of heartbeats occurring over an undisclosed time period. The most widely used protocol for heartbeat tracking is the mental tracking method developed by Rainer Schandry (Schandry, 1981). Briefly, this method requires subjects to be connected to some form of a pulse recording device, typically either pulse oximeter or electrocardiogram. Subjects are asked to count their heartbeats over several intervals without palpitating for their own pulse. Performance in these tasks is determined by the accuracy of the reported number of heartbeats (those perceived by the participant) and the actual number of heartbeats recorded by the device. Averaging across all trials provides a single metric for interoceptive accuracy. Application of heartbeat tracking methods in the literature often varies in both the number of trials employed and the duration of the individual trials used with each study, suggesting a lack of agreement on standardised protocol for these tasks.

Zamariola and colleagues (2018) examining accuracy scores between three commonly utilised time durations and reported that accuracy was significantly lower for the 45-s interval compared with both for 25-s and 35-s (*p's* $< .01$) intervals, these later intervals were not significantly different from each other ($p = .48$). However, retrospective analysis of this temporal postulate by Ainley and colleagues (2020) found conflicting findings to those of Zamariola *et al*. (2018) reporting no significant differences in accuracy scores between task intervals of 25-s, 35-s, and 45-s (*p's* $> .19$). Differences in these findings appeared to result largely from the variance in resting heart rate values between the different time interval conditions reported by Zamariola *et al.* (2018) brought about either through measurement error or experimental procedures that did not ensure stable resting-state conditions among their cohort. Nevertheless, time intervals reported in the literature for heartbeat tracking tasks are typically short in duration (20-100 seconds) and the influence of prolonged durations (> 2-min) on heartbeat perception accuracy remains unclear but is likely to be diminished as a consequence of factors such as boredom and limited attentional focus.

For heartbeat discrimination tasks, subjects are presented with a series of either audible tones or flashes of light that are presented either 'simultaneous' (in-sync) or 'non-simultaneous' (out-of-sync) with the subject's heartbeats. The original development of this task by Whitehead and colleagues (1977) utilised delays of 128-ms after the R-wave (peak ventricular depolarization) for the in-sync condition and 384-ms delay after the R-wave for the out-of-sync condition. The authors argued that the rationale for these temporal delays reflected, for the in-sync condition, the time taken from the occurrence of the R-wave to the presentation of the blood pressure pulse in the neck or wrist (occurring between 100 and 150-ms after the R-wave). Conversely, the rationale for the time delay for the out-of-sync condition was not explicitly provided but may have been too temporally proximal to the synchronous condition as the authors reported a grand median *d*' of 0.33 (0.05 –1.56), indicating that most participants struggled to discriminate between stimuli presented at these two intervals. Notably, only ~25% of participants achieved the *d*' criterion for classification as 'good' heartbeat perceivers (accuracy score $\geq .75$). Subsequent evidence has confirmed that these time delays may not be optimal for capturing in-sync and -out-of-sync perceptual judgements (Brener, Liu, & Ring, 1993; Wiens & Palmer, 2001; Yates, Jones, Marie, & Hogben, 1985). For instance, Yates and colleagues (1985) examined synchronicity judgements, among healthy young males, between the occurrence of the R-wave and a visual stimulus across time delays of 0-ms, 100-ms, 200-ms, 300-ms, 400-ms, and 500-ms. The authors reported a quadratic (inverted U) trend in synchronicity judgements with the 200-ms, 300-ms, and 400-ms conditions being perceived as in-sync in more than 50% of trials, whereas less than 50% of trials for 0-ms, 100-ms, and 500-ms were deemed synchronous. Extending on these findings, Wiens and Palmer (2001) reported similar quadratic trends in reports of heartbeat synchronicity judgements. However, in contrast to Yates *et al.* (1985), the data indicated that synchronicity judgements for 0-ms, 100-ms, and 200-ms delays were found to be above the threshold for chance, whereas delays of 300 to 500-ms delays were below the threshold for chance. Importantly, the data indicated that the highest synchronicity judgements were reported at 200-ms delay and the lowest synchronicity judgements at 500-ms delay. Further, differentiating between 'good' and 'poor' heartbeat perceivers, the authors demonstrated that the differences in synchronicity judgements between conditions were driven predominantly by the responses from 'good' perceivers with responses for 'poor' perceivers found to be largely equivocal between the different delay intervals.

Comparison of these two cardiac perception tasks indicates a moderate positive correlation (r_s = .59, p < .01) in performance (heartbeat perception accuracy) in non-clinical cohorts with the strongest correspondence observed in very good and very poor heartbeat perceivers (Table 2.2; Knoll & Hodapp, 1992). However, significant correlations are not always observed, particularly in small samples (Phillips, Jones, Rieger, & Snell, 1999; Schulz, Lass-Hennemann, Sütterlin, Schächinger, & Vögele, 2013). Further, a recent meta-analysis of the relationship for heartbeat perception accuracy between these two tasks indicated a pooled correlation coefficient of 0.21 (95%CI [0.13, 0.29]) determined through random effects modelling of data obtained from 23 separate studies with a combined sample size of n = 1444 (Hickman, Seyedsalehi, Cook, Bird, & Murphy, 2020). This relatively weak positive correlation suggests that whilst these tasks may examine the same fundamental construct, distinctions, and limitations with the way in which each method assesses heartbeat perception suggests they may examine subtly different aspects of cardiac interoception.

Table 2.2. Bivariate distribution of participants categorised according to performance in both the heartbeat tracking task (HBT) and heartbeat discrimination task (HBD). Adapted from Knoll and Hodapp (1992).

		HBT			
		Very Poor	Poor	Good	Very Good
HBD	Very Good	1	1	4	10
	Good	3	4	5	3
	Poor	4	3	5	3
	Very Poor	8	7	1	0

Both of these methods for assessing cardiac interoception have their limitations, for which they are criticised. For instance, despite its widespread use, performance in the heartbeat tracking task is potentially biased by subject's perceptions of their resting heart rate and temporal estimations of the interval durations. Data reported by Desmedt *et al.* (2020) indicated that heartbeat tracking accuracy was moderately and positively correlated with both time estimation (r = .41) and knowledge of resting heart rate (r = .45). However, weaker non-significant correlations have also been reported previously (r_s = .20, p = .06; Knoll & Hodapp, 1992). Examining the effect of feedback training using both contingent and non-contingent feedback of heartbeats, Ring and colleagues (2015) reported improvements in heartbeat tracking accuracy in both intervention groups compared with a control group receiving no feedback training. Importantly, the improvements between the two intervention groups were comparable and coincided with similar reported changes in beliefs related to resting heart rates. Given these effects, the authors argued that improvements in heartbeat tracking accuracy were related to changes in participant beliefs regarding their resting heart rate, allowing for more accurate temporal estimation, rather than explicit improvements in the detection of 'actual' heartbeats. Taken together, these findings indicate that some individuals may be able to demonstrate good accuracy in the heartbeat tracking task without necessarily being able to perceive their heartbeat. Discrimination protocols are considered more robust in this regard as the presentation of the external stimuli are typically provided at the same frequency as the subject's heartbeat, irrespective of whether the condition is 'simultaneous' or 'non-simultaneous'.

One of the major criticisms of heartbeat discrimination tests is that they require participants to correlate an exteroceptive stimulus with an interoceptive signal. Performance under these contexts may not, therefore, be measuring interoceptive sensitivity alone, but the ability to attend to both internal and external stimuli simultaneously. Consonantly, discrimination tasks are disadvantaged in the context that most individuals score below chance, thereby reducing sensitivity to individual differences (Eshkevari, Rieger, Musiat, & Treasure, 2014). This has implications on the sample size required to reliably detect statistically significant effects. For instance, Kleckner, Woodworm, Simmons, Feldman Barret, and Quigley (2016) demonstrated, for a true effect size of 0.3, then using 20, 50, or 100 trials would yield an observed effect size that is on average 65%, 80%, or 90% of the true value respectively in an 'infinite sample'. Moreover, the authors further reported (using the same assumed true effect) smaller samples exhibited greater variability (larger confidence intervals) in the relationship between observed effect size and true effect size. For example, testing 25, 50, or 200 participants using 60 trials would yield an observed effect size that is 60–93%, 69–91%, or 77–87% of its true value. These sample and trial number requirement generally exceed those typically reported in the literature, suggesting an underpowering of the data. Nevertheless, despite these confounds these two methods of cardiac perception have supported much of the knowledge generated around interoception since their inception.

2.3.2. Different Dimensions of Heartbeat Perception

Historically, the use of different heartbeat perception protocols in addition to the use of various terms, such as 'interoceptive accuracy', 'interoceptive awareness', 'interoceptive sensitivity', and others, has confounded meta-analytical interpretation of research findings. More recently, attempts have been made to unify these constructs and generate a more parsimonious account of cardiac interoception (Garfinkel & Critchley, 2013; Garfinkel et al., 2015).

The model proposed by Garfinkel and colleagues (2013, 2015) consists of three broad themes: interoceptive accuracy, interoceptive sensibility, and interoceptive awareness. Interoceptive accuracy is used to define the process of accurately detecting and tracking internal bodily sensations. This is an objective empirical measure of behavioural performance and distinct from subjective measures. Interoceptive accuracy can be determined performance in either discrimination or tracking-based tasks and provides the categorisation of individuals as either 'good' or 'poor' perceivers. Categorisation can be made based on whether performance is above or below chance, heuristic demarcation thresholds, or by dividing the sample per a median split of the scores. For the heartbeat tracking task, Schandry and colleagues (Montoya, Schandry, & Müller, 1993; Weitkunat & Schandry, 1990) have typically demarcated their samples based on an accuracy score of 85% (or error scores of 15% depending on the equation being used); however, examples of median split criterion have also been reported by the same research group (Schandry et al., 1986). The use of this threshold appears largely heuristic but is thought to be suitably stringent to limit false categorisation of individuals whose task performance is underpinned by temporal estimation or chance. For heartbeat discrimination tasks, application of signal detection measures of sensitivity (d'), quadratic trend analysis (χ) or median split have been commonly used to discriminate between good and poor perceivers (Garfinkel et al., 2015; Whitehead et al., 1977; Wiens & Palmer, 2001)

Interoceptive sensibility represents a subjective or self-evaluative perspective interoceptive ability (Terasawa, Shibata, Moriguchi, & Umeda, 2013). This is defined by the beliefs of the person in their capacity to perceive visceral function regardless of empirical behavioural performance. Interoceptive sensibility can be assessed using questionnaire-based approaches (Porges, 1993), providing a generalised measure of sensibility, or through continuous rating-based scales of confidence during tests interoceptive ability, which provide an axis-specific measure of interoceptive sensibility (Garfinkel et al., 2015).

The final theme presented within the model is interoceptive awareness. In this context, interoceptive awareness refers to the degree of correspondence between objective interoceptive accuracy and subjective report (i.e., interoceptive sensibility measured using a confidence rating scale). In this definition, interoceptive awareness represents a metacognitive construct. Interoceptive awareness during the heartbeat discrimination task can be determined using receiver operating characteristic (ROC) curve analysis (Pintea, Sebastian Moldovan, 2009) of the extent to which confidence predicts accuracy. In the heartbeat tracking tasks, interoceptive awareness is quantified using a within-participant Pearson's correlation coefficient between confidence and accuracy providing an alternative index of interoceptive awareness to the ROC curve analysis approach.

Support for this model is still relatively in its infancy; however, there is already emerging evidence to substantiate the main tenets. For instance, Garfinkel and colleagues (2015) examined the basis of this model using both the heartbeat tracking and heartbeat discrimination tasks to assess cardiac interoception. Using a stepwise forward linear regression analysis, the authors reported that both axis-specific sensibility and awareness predicted interoceptive accuracy, and these associations were lowered when interoceptive awareness was entered as the dependent variable instead. This finding supports 1) the conceptual partial independence of the three interoceptive dimensions, and 2) the primacy of interoceptive accuracy as the core (central) construct underpinning both interoceptive sensibility and awareness. Further analysis revealed that measures of accuracy (r = .32) and sensibility (r = .71) obtained from the two separate heartbeat perception tasks were significantly correlated, thereby corroborating the concurrent validity of these constructs across different measures of cardiac interoception. However, the two awareness measures were not correlated (r = -.10). Finally, comparing between good and poor heartbeat perceivers demonstrated correlations between accuracy and sensibility (both tracking and discrimination tasks) and also between accuracy and awareness (tracking task only) were observed for the good perceiver group but not the poor perceiver group. This suggests that correspondence between the accuracy (core construct) and high order dimensions (sensibility and awareness) only emerges in individuals that exceed a basic threshold for detection of cardiac stimuli.

A recent systematic review by Hickman and colleagues (2020) examined the concurrent validity of accuracy, sensibility, and awareness measures obtained between tracking and discrimination tasks. As reported previously, the analysis of 22 studies demonstrated a small positive random effects model correlation of 0.21 (95%CI [0.13, 0.29]). By comparison, sensibility demonstrated a moderate random effects model correlation of 0.60 (95%CI [0.48, 0.70]; 7 studies) whereas awareness demonstrated a negligible random effects model correlation 0.09 (95%CI [-0.02, 0.20]; 6 studies). Importantly, follow-up examination of the available data revealed that these findings were not subject to publication bias.

Further examination of this three-dimensional model of interoception has shown that correspondence between cardiac and respiratory axes occurs for awareness (r = .36) but not accuracy or sensibility (Garfinkel et al., 2016). Additions to this model have also been proposed. For instance, the addition of trait measures of interoceptive sensibility (e.g., Body Perception Questionnaire) that may be used to provide a gauge of trait interoceptive prediction error (tIPE), calculated as the discrepancy between z-scored accuracy and sensibility, for both tracking and discrimination scores, have been applied in clinical cohorts such as autism spectrum disorder and Tourette's (Garfinkel et al., 2016; Rae et al., 2020; Rae, Larsson, Garfinkel, & Critchley, 2019). Additionally, Forkmann *et al.* (2016) report that cardiac function (e.g., heart rate) may provide a core construct underpinning interoceptive dimensions of accuracy, sensibility, and awareness. However, their findings were only significant for interoceptive dimensions pertaining to the tracking task.

2.3.3. Inter-Individual Differences in Cardiac Interoception

Individuals have been found to differ considerably in their ability to accurately perceive interoceptive signals (e.g., heartbeats). Various physiological and demographic factors have been shown to influence this inter-individual difference in heartbeat perception. In particular, cardiovascular factors have been shown to influence heartbeat perception accuracy. For instance, inverse relationships are reported between accuracy and resting heart rate for both tracking and discrimination tasks (Forkmann et al., 2016; Knapp-Kline & Kline, 2005). Lower resting heart rates are associated with greater stroke volume, increased measures of myocardial contractile force, and greater momentum of ejected blood mass, which have all been shown to be moderately and positively correlated with heartbeat perception accuracy (Schandry, Bestler, & Montoya, 1993). By contrast, Ring and colleagues (1994) demonstrated that postural manipulation of heart rate, stroke volume, and changes to the momentum of ejected blood did not influence either heartbeat perception accuracy or the observed temporal delay between the presentation of the R-wave and a person's subsequent perception of their heartbeats. Importantly, the authors identified that postural manipulations did not alter the contractility of the heart. Based on these observations, Ring *et al.* (1994) suggested that contractility was the key construct underpinning heartbeat perception accuracy, not stroke volume or heart rate. Furthermore, higher blood pressure is also associated with greater performance in tests of heartbeat perception (O'Brien, Reid, & Jones, 1998). These findings raise the possibility that performance in heartbeat perception tasks may encompass sensory perceptions generated from the transmission of cutaneous mechanosensitive fibres as well as sensory inputs emerging along interoceptive pathways from the heart.

In accordance with the findings above, the superior performance observed among males compared with females (e.g., Harver, Katkin, & Bloch, 1993) appears to be largely driven by differences in body composition (Jones, Jones, Rouse, Scott, & Caldwell, 1987). An inverse relationship is also reported for body mass index and cardiac interoceptive accuracy (Cameron, 2001), however, this finding is not consistent across all studies (Dunn, Stefanovitch, et al., 2010). Finally, age has been reported to influence interoceptive accuracy in certain contexts. In adults, interoceptive accuracy has been shown to decline with age (Khalsa, Rudrauf, & Tranel, 2009). However, children and adolescents appear to demonstrate interoceptive accuracy scores that comparable to those reported healthy adult cohorts (Georgiou et al., 2015).

The presence of inter-individual differences in cardiac interoception has allowed researchers to compare differences between ‘good’ and ‘poor’ heartbeat perceivers. Determination of group membership is often made according to either heuristic or statistical (e.g., median score) demarcation of the data. Application of this approach has shown that good and poor perceivers differ in reported emotional intensity (e.g., Dunn, Galton, et al., 2010; Ludwick-Rosenthal & Neufeld, 1985), decision-making (Werner, Jung, Duschek, & Schandry, 2009), body ownership (Suzuki, Garfinkel, Critchley, & Seth, 2013), and cardiac-autonomic responses to aversive or emotional stimuli (Herbert, Pollatos, Flor, Enck, & Schandry, 2010; Pollatos, Herbert, et al., 2007) and more. However, despite the value of this methodology for expounding the influence of interoception, it should be noted that the creation of a ‘good’ vs ‘poor’ dichotomy is not without its potential limitations. In particular, dichotomising individuals according to selected demarcation thresholds creates scenarios whereby individuals with similar scores may be classified differently from one another (Figure 2.3). This scenario has important implications on the ability to detect significant effects (statistical power) as the subsequent groups may not be sufficiently different from one another. To overcome this limitation, the application of more discriminate approaches may be warranted.

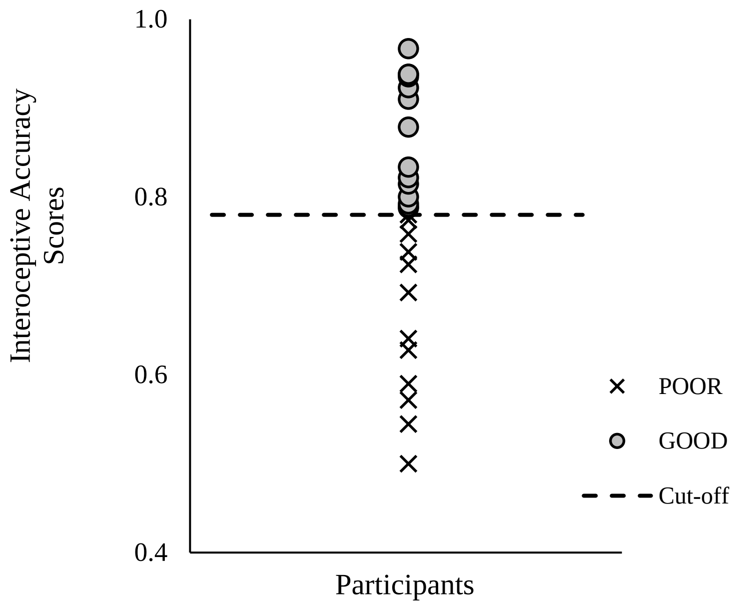


Figure 2.3. Example of the dichotomisation of individuals as good (GOOD; n =14) or poor (POOR; n = 14) heartbeat perceivers according to a demarcation threshold (Cut-off; based on the group median score) highlights issues related to this approach. Specifically, it shows that a number of individuals close to the demarcation threshold are classified differently from one another despite comparable accuracy scores.

2.3.4. Manipulating Cardiac Interoception

Interoceptive accuracy is sometimes considered to be a trait characteristic, owing to its reported resistance to experimental manipulation (Cameron, 2001). However, this perspective does not account for the transient vicissitudes in cardiac interoceptive accuracy shown in other studies. For instance, Jones and colleagues (1981) demonstrated that heart rate discrimination accuracy improved significantly, compared to baseline, in sedentary and moderately-fit individuals following an acute bout of submaximal cycling exercise, which increased heart rate to 75% of the person's predicted maximum heart rate. However, these improvements were only evident for the initial ~10-minutes post-exercise, suggesting that improvements in accuracy were linked to increases in physiological arousal. This effect was confirmed in a subsequent study by the same research group further demonstrated that heart rate discrimination accuracy was significantly improved both during treadmill exercise and also in the immediate recovery period following exercise termination (Montgomery et al., 1984). Extending these findings, Antony *et al.* (1995) demonstrated that these effects were also evident in participants with either panic disorder or social phobia following aerobic exercise at 80% of the estimated heart rate reserve. Specifically, significant improvements in interoceptive accuracy (heartbeat tracking task) were reported over the first 5-minutes following exercise termination compared with baseline. Interestingly, Schultz and colleagues (2013) report that measures of heartbeat perception accuracy obtained from the tracking and discrimination tasks may be differentially modulated by acute physiological stress. Specifically, the authors found that the cold pressor task resulted in increased tracking accuracy but decreased discrimination accuracy. The difference in these findings is likely to reflect a competition of attentional resources, with the cold pressor task inducing an additional demand for directing attention to self. This will affect the tracking task (attention of self) differently from the discrimination task (interoceptive-exteroceptive integration) according to attentional demands, hence the directional effects on heartbeat perception accuracy reported above. In a separate measure of cardiac interoception, pharmacological manipulation of cardiac arousal using isoproterenol has also been robustly shown to improve cardiac perception accuracy in a dose-dependent manner and may be used as an alternative approach to examining individual differences in cardiac interoception (Khalsa, Rudrauf, Hassanpour, Davidson, & Tranel, 2020; Khalsa, Rudrauf, Sandesara, et al., 2009).

Cardiac interoceptive accuracy may also be modulated under contexts of increased attention to self. Accordingly, Ainley *et al*. (2012) reported that mirror self-observation resulted in significant improvements in heartbeat tracking accuracy among low interoceptive accuracy participants. However, this effect was not observed for ‘high’ interoceptive accuracy individuals, suggesting that malleability of interoceptive accuracy may be dependent on a person’s baseline interoceptive characteristics. This effect was broadly consistent with the findings of Maister and Tsakiris (2014) who reported that interoceptive accuracy was increased during photographic self-observation among individuals of low baseline interoceptive accuracy but not high interoceptive accuracy. In a subsequent study, Ainley and colleagues (2013) found that heighten attention to bodily of the self (photograph of their own face) and narrative aspects of the self (self-relevant words) both resulted in significant improvements in heartbeat tracking accuracy from baseline. No differences were reported between the two conditions, suggesting that this was a generalised effect of self-attention and not specific to a given manipulation. Finally, it has been found that anticipation of public speaking, and associated fear of negative evaluation, resulted in significant increases in heartbeat tracking accuracy (Durlik, Brown, & Tsakiris, 2014). Importantly, no changes in physiological arousal (i.e., heart rate) were observed, consequently the authors proposed that heightened self-attention may have been the primary factor facilitating the observed improvement in interoceptive accuracy. Taken together, these findings indicate that both increased physical arousal and increased attention to self may contribute to a transient augmentation in cardiac interoceptive accuracy, suggesting that interoceptive accuracy is characterised by both trait and state attributes.

2.3.5. The Emergence of Heartbeat Perception

The presence of a sensory apparatus, capable of detecting and signalling changes to the heart, is fundamental to the notion of heartbeat perception. The heart is innervated by two separate sensory pathways, which project to either the medulla (vagus nerve) or spinal cord (sympathetic). Both pathways predominantly convey mechano-sensitive information with the distal nerve fibre bodies signalling changes related to specific receptor fields (i.e., stimuli). For instance, the vagus nerve receives inputs from two types of myelinated nerve fibres that innervate the atrial chambers and respond to changes in atrial systolic pressure (type A fibres) and slow-adapting stretch receptors that are responsive to alterations in atrial wall tension (type B fibres). The vagus nerve also receives inputs from myelinated fibres innervating the lower chambers of the heart (ventricles), that are responsive to increases in intraventricular pressure during contraction. Populations of unmyelinated nerve fibres also emerge from the vagus nerve, innervating all chambers of the heart. These unmyelinated fibres are responsive to a range of mechanical stimuli (e.g., atrial filling and contraction, ventricular end-diastolic pressure) with their principal function to provide inhibitory influence on cardiovascular reflexes.

Sympathetic afferent nerves from the heart enter the spinal cord at the upper thoracic vertebrae (T1, T2, T3) and project information via spinal lamina I, in the manner previously described (Section 2.2). Similar to the vagus nerve, branches of the sympathetic nerve can be divided according to the chambers of the heart being innervated (atrium or ventricles) and consist of both myelinated and unmyelinated fibres. Interestingly, this pathway seems to be involved in the signalling of both mechanoceptive and nociceptive stimuli, the latter related to the perception of anginal pain (Foreman, 1999). The mechanisms underpinning cardiac nociception are not entirely clear but suggest the presence of polymodal receptors that are sensitive to both extreme mechanical stress and chemical stress (Camici & Pagani, 2006). However, the magnitude of patient-reported pain perception often does not correspond to the magnitude of disease or insult inflicted on the heart, with considerable myocardial ischemia sometimes occurring with the complete absence of conscious perception (Rosen, 1996). This blunted sensitivity raises a key question about mechanisms involved in bringing cardiac perceptions to conscious awareness and is particularly pertinent to the use of heartbeat perception tasks as a measure of interoception.

Despite the widespread application of heartbeat perception tasks in the literature, relatively scant attention has been given to describing the mechanisms involved in bringing the perception of hearts to conscious awareness. With this in mind, Ainley, Apps, Fotopoulou, and Tsakiris (2016) proposed a model of heartbeat perception, which is founded on emerging concepts of how the brain functions. Their model draws on concepts of ‘free energy’ and is operationalised according to Bayesian statistical analogues of predictive processing (Friston & Kiebel, 2009; Parr, Rees, & Friston, 2018). Fundamental to these models is the notion that humans, like all living organisms, are only able to subsist within a relatively narrow range of ‘desirable’ states, which reflect the maintenance of homeostasis. Consequently, the principal drive of homeostasis can be considered in terms of an ongoing need to minimise deviations from these desirable states and are described as a minimisation of free energy (an information theory measure that bounds the degree of ‘surprise’ experienced within a generative model) (Friston, 2010). One of the major challenges to free energy minimisation is the limitation that all living organisms experience a lack of veridical access to the ‘true’ state of their environment. To overcome this limitation and reduce potential long-term surprise, it is argued that the brain continuously attempts to generate accurate internal models that predict the hidden state of the environment by comparing prior predictions of expected sensory information (priors) with incoming sensory information (Friston & Kiebel, 2009). This concept applies equally to the brain’s models of both the external (exteroception) and internal (proprioception and interoception) world.

Our brain’s internal generative models are constantly optimised by comparing prior predictions (i.e., beliefs about the hidden state of the world) with emerging sensory information. It is proposed that these comparisons occur within a hierarchical series of recurrent loops where ascending sensory inputs are compared against descending priors at various levels. Prediction errors (PE) arise in conditions where incoming sensory information is not fully accounted for within the brain’s prior probabilistic predictions. Within this hierarchical framework, only PE emerging at lower levels of the hierarchy are passed on to higher levels of hierarchy. Resolution of PE is thought to occur in three different ways: 1) by updating internal models to bring beliefs in line with sensory inputs,

2) by influencing ascending sensory signals through action to bring sensory inputs in line with sensory expectations (active inference), and (3) updating the precision afforded to ascending PE (Seth, 2015). Percepts are formed when PE is minimised across all levels of the hierarchy, through a process described as perceptual inference (Ainley, Apps, Fotopoulou, & Tsakiris, 2016).

The perception of heartbeats can be readily explained within these predictive coding concepts. Firstly, it is acknowledged that healthy individuals do not readily perceive their heartbeats under normative conditions. This suggests that PE between expected and actual sensory inputs from the heart is often minimal and can be fully resolved at lower levels of the hierarchy, thereby occurring below the level of conscious perceptual inference. However, conscious perception of cardiac function may transpire in contexts where unexpected or substantial changes in cardiodynamics occur, which cannot be resolved at lower levels of the hierarchy and might instead necessitate an array of behavioural responses to attenuate potential aggregations to free energy.

To illustrate this point, consider the following scenarios. Firstly, the experience of palpitations, cardiac arrhythmias, or other clinical forms of tachycardia, the symptoms of which are strongly perceived by the person concerned (Thavendiranathan, Bagai, Khoo, Dorian, & Choudhry, 2009). In these contexts, cardiac PE can be considered to emerge from the evaluation of precise mechanosensory information from the heart (related to abnormal heart rhythm and/or unexplained increases in heart rate) that are not accounted for within the brain's prior modelling of the hearts "normative" function. Importantly, these PE cannot be immediately resolved through lower-order autonomic control processes or by sampling additional sensory information and are consequently raised to the uppermost levels of the hierarchy. Subsequent minimisation of these PE across all levels of the hierarchy is therefore achieved through perceptual inference, resulting in the manifestation of an overt categorical perception of cardiac dysfunction.

Secondly, we can consider the effect of exercise on the formation of percepts related to cardiovascular strain. Unlike the cardiac dysfunctions described above, exercise-induced changes to cardiac function maybe partly accounted for by 1) the initial formation of appropriate priors that consider the potential physiological changes resulting from physical activity, and 2) active inferential sampling of other physiological systems (e.g., skeletal muscle and lung function) that substantiate these changes in cardiac function as "appropriate" in the context of the ongoing behaviour. Consequently, exercise-induced cardiac PE may be resolved or amalgamated with other interoceptive PE to form more generalised perceptions (e.g., RPE, subjective fatigue), which likely reflect more multi-system appraisal of the challenge of free-energy minimisation over immediate or future temporal scales (Greenhouse-Tucknott, Butterworth, Wrightson, Smeeton, et al., 2021; Noakes, 2012). Nevertheless, it could be expected that the process of directing attention towards cardiac function during exercise (*the role of attention on the formation of PE is described in the subsequent paragraph*) or a sudden cessation of exercise behaviour (leading to amended prior expectations of future cardiac functional characteristics and diminished somatosensory and proprioceptive explanations for current cardiac PE) may facilitate more precise categorical perception of cardiac function, thereby facilitating transient improvements in cardioceptive accuracy compared with rest, as previously reported (Jones & Hollandsworth, 1981).

Finally, we can consider how the perception (or misperception) of sudden changes to cardiac function may arise anxiety disorders (e.g., perceived heart palpitations in panic attacks; Margraf, Ehlers, & Roth, 1987). A recent computational study, based on active inference and predictive processing, argued that these events may emerge in four different contexts (Maisto, Barca, Van den Bergh, & Pezzulo, 2021). Firstly, the presence of incorrect prior beliefs (which are overly precise) may dominate sensory information and prevent corrective updates to the generative model – leading to illusions or disorders of body schema (Edwards, Adams, Brown, Pareés, & Friston, 2012). Secondly, and comparable to the first context, is the presence of uninformative sensory signals that fail to prompt appropriate updates to the generative model. Thirdly, the authors argue that imprecise mapping of transition states, related to imprecise knowledge of the previous context (e.g., the cause and resolution of previous panic attacks) that may lead to a condition of hypervigilance where sensory information along certain channels are incorrectly prioritised over others, Finally, the authors propose that a miscalibration of the parameters of the generative models, through over-exposure of aversive learning events, may lead to 'safety' focussed active inferential behaviours (e.g., avoiding challenging situations), which reduces the agents perceived long-term capacity to manage free-energy in future contexts. This reduction in perceived capacity to copy with aversive contexts may be associated with greater cardiac reactivity (Peira, Fredrikson, & Pourtois, 2014), with greater cardiac reactivity likely facilitating the formation of cardiac PE.

For heartbeat perception tasks, Ainley and colleagues (2016) argue that the transient ability of some individuals to accurately perceive their heartbeats occurs because the characteristics of ascending sensory inputs are not fully explained by the brain's prior beliefs. Importantly, it is proposed that the top-down process of directing attention towards heartbeats may function to increase the precision afforded to the incoming cardiac sensory signals, which results in the formation of more precise PE that cannot be fully resolved at lower levels of the hierarchy. Evidence for this effect can be gleaned from the measurement of heartbeat evoked potentials (HEP) and their relationship with cardiac interoceptive accuracy. HEP are believed to reflect a neural correlate of the sensory processing of cardiac activity (MacKinnon, Gevirtz, McCraty, & Brown, 2013). Attention towards heartbeats has been shown to increase the magnitude of this electrophysiological signal (Petzschner et al., 2019). Further, more accurate heartbeat perceivers have been shown to demonstrate strong HEP signals compared with poor heartbeat perceivers (Herbert, Pollatos, & Schandry, 2007; Pollatos & Schandry, 2004). Taken together, this process of directing attention appears to enable the signals that emerge from the heart to form percepts, which are capable of reaching conscious awareness. This may also explain the differences in the accuracy of cardiac perception reported between individuals.

Several other factors within this predictive coding model may also account for individual differences in heartbeat perception accuracy. Firstly, cardiodynamic factors such as lower resting heart rates, increased stroke volume, and greater blood ejection momentum may be represented as stronger (i.e., more precise) sensory signals emerging from the heart (Ring et al., 1994; Schandry et al., 1993). Indirectly, higher blood pressure and lower body compositions may also facilitate cardiac perception along a similar process by providing precise auxiliary sensory information that contributes to the precision of subsequent cardiac PE. Secondly, the precision of the brain's prior expectations is also worth consideration. More precise priors will be innately more sensitive to small deviations in sensory inputs from the expected predictions than priors that are less precise. Greater precision of priors, therefore, substantiates more precise PE whenever small deviations in cardiac sensory data occurs. This results more readily in updates to internal models at higher levels of the hierarchy from where conscious heartbeat perception emerges, which subsequently form new prior predictions for future sensory inputs.

2.4. Role of Interoception in Emotion

2.4.1. The Role of Visceral Signalling in Emotional Processing

Emotions can be described as the subjective conscious experience generated by psychophysiological processes which are induced in a myriad of organs and brain circuits and expressed in both physiological and behavioural adaptations (Damasio & Carvalho, 2013; Wiens, 2005). Many theories of emotion have postulated a close relationship between physiological changes and emotional experience, arguing that emotions are generated at least in part from perceptions of bodily feelings. The earliest accounts of this paradigm were independently presented by William James (James, 1884) and Carl Lange and incorporated into the so-called James-Lange theory of emotion. The main idea proposed by James-Lange is that all emotions are generated in the brain from bodily responses to perceptions of the environment. This idea has been interpreted as suggesting that specific patterns of autonomic activation proceed concomitant emotional experience and that the absence of these physiological responses prohibits their emergence. An example of this is the emotion of fear, which the theory suggests emerges from physiological reactions such as increased heart rate, sweating, and pupil dilation when a threat is perceived by exteroceptive sensory organs.

However, James-Lange theory does not account for emotional experiences which are generated cognitively and occurring despite the absence of specific physiological cues, for which it is criticised (Bard, 1928; Cannon, 1927; Harrison et al., 2010). Indeed, noted physiologist Walter Cannon argued that changes in the viscera could not account for the range of human emotions given that similar physiological changes can result in markedly different emotional experiences (Cannon, 1927). Moreover, Cannon contended that perceptual sensitivity to somatic signalling was too insensitive and changes too slowly to adequately support complex emotional experiences. Several studies have supported this argument, both in animal models and in humans. For instance, Bard (1928) and Sherrington (1954) reported that expressive behavioural responses in animals remained intact following surgical transection of the spinal cord and sympathetic division of the autonomic nervous system. This finding is in keeping with reports in humans with spinal cord damage and neurodegenerative conditions affecting visceral sensation, whereby subjective evaluation of emotional response was not substantially diminished (Lowe & Carroll, 1985). Moreover, experimental manipulations of autonomic arousal using adrenalin have not been shown to adequately elicit strong or specific emotional responses despite marked changes in sympathetic activation (Marañon, 1924, cited in Cannon, 1927). Taken together these findings support Cannon's view that emotions are not anchored to physiological responses in the body. Indeed, Cannon and Bard theorised that emotion emerges from thalamic processing which proceeds physiological change (Dror, 2014). Nevertheless, despite this body of evidence, contemporary perspectives on emotion still posit a role of visceral sensation (Dalgleish, 2004). However, their frameworks provide a more nuanced explanation of the interaction between the body and the brain.

2.4.2. Contemporary Perspectives on the Embodiment of Emotion

The ideas developed by Schachter and Singer (1962) and Damasio (1995) pervade many of the frameworks by which emotion continues to be interpreted and examined. Both models broadly suggest that visceral sensation aids the efficient interpretation of emotional experience alongside cognitive factors, which are influenced by contextual perceptions. This stance is particularly evident in Damasio's rationalisation for his somatic marker hypothesis (SMH) in which he states "the core of an emotion is a collection of changes in body state and brain state" and is compatible with the ideas formulated by Schachter and Singer (Damasio, 1995, p.20; Schachter & Singer, 1962). SMH was initially conceptualised from observations in neurological patients with focal damage in the frontal lobe. Patients were described to have impairment in personal and social decision-making following damage to the ventromedial portion of the prefrontal cortex (VMPFC). This impairment emerged despite otherwise largely preserved intellectual function. However, the changes were accompanied by a compromised ability to express or experience emotions in contexts where those emotional experiences would be presumed to be present (Damasio, Everitt, & Bishop, 1996).

The anatomical framework for SMH postulates that emotions are generated via two predominant pathways. In the first pathway, emotions are evoked by changes in the body that are projected to the brain, which Damasio refers to as the "body loop". This idea is in keeping with Jamesian concepts of embodiment. In the second pathway, cognitive representations of emotions can be activated in the brain without being directly elicited by a sensory stimulus – called the "as-if body loop". Per Damasio, this pathway is conditioned through learned associations between previously experienced stimuli and physiological responses. "As-if" associations aid the speedier generation of emotions to occur, bypassing the temporally inefficient process of eliciting and interpreting somatic vicissitudes. This also accommodates for criticisms of James-Lange by allowing for an alternate mechanism by which emotions can be experienced not directly reliant on physiological changes. However, it is not experimentally clear how the brain decides between these two pathways. Regardless of the mechanism of pathway activation, emotions are generated predominantly within limbic system structures including the amygdala, anterior cingulate cortex, hypothalamus, brain stem, and basal forebrain. These structures both interpret and elicit body state responses following perception of a given stimulus. This process generates a dispositional representation which is expressed as primary emotions. Reciprocal activation between VMPFC and limbic structures, supported by input from somatosensory cortices (particularly within the right hemisphere), aids representation of more complex emotional appraisal related to systematic associations between stimuli, on the one hand, and primary emotions and subsequent feelings, on the other.

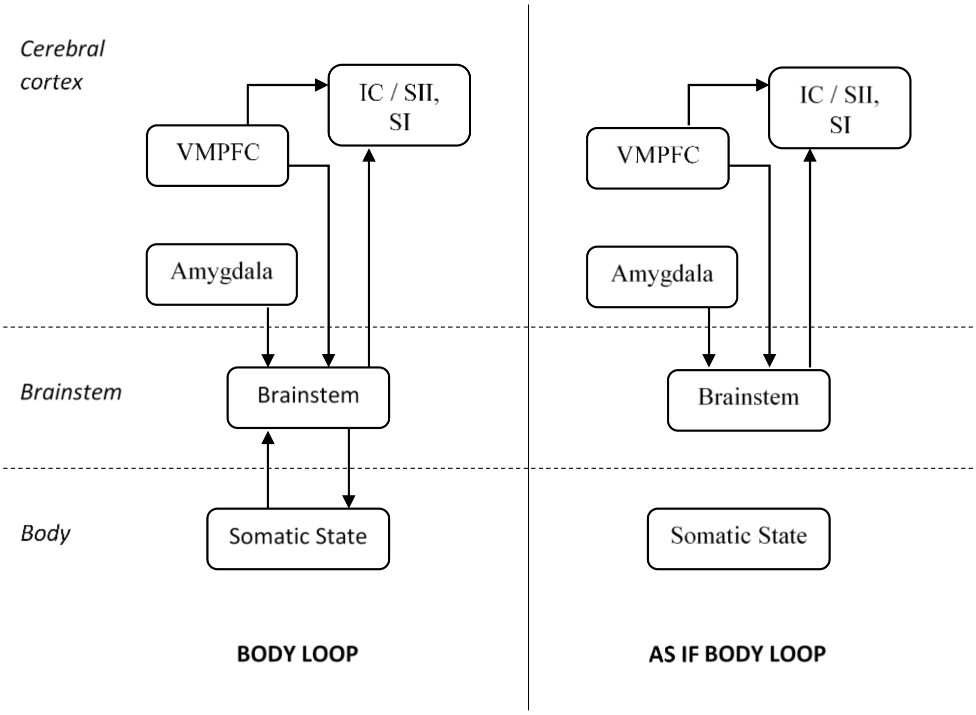


Figure 2.4. Differing neural pathways underlying the 'body loop' and 'as if body loop' proposed in somatic marker hypothesis. Ventromedial prefrontal cortex (VMPFC), insula cortex (IC) and primary somatosensory cortex (SI), secondary somatosensory cortex (SII). Adapted from Bechara and Damasio (2005).

Empirical evidence substantiating SMH was developed through a series of studies based around an experimental gambling task assessing implicit decision-making (Iowa Gambling Task, IGT; (Bechara, Damasio, Damasio, & Anderson, 1994; Bechara & Damasio, 2005). Results from these studies supported the role of the prefrontal cortex in decision-making by demonstrating an inhibition in performance and learning in the IGT in VMPFC lesion patients compared to healthy controls and patients with non-frontal lobe damage (Bechara et al., 1994). Additionally, findings reported in a subsequent study (Bechara, Tranel, Damasio, & Damasio, 1996) showed differentiated somatic state responses (skin conductance response) over the course of the IGT between controls and

VMPFC lesion patients in advance of deciding which deck of cards to select from. This result was interpreted by the authors as providing support for the role of somatic states in biasing decision-making. Moreover, Bechara and colleagues (Bechara, Damasio, Damasio, & Lee, 1999) further demonstrated differential roles for amygdala and VMPFC in lesion patient groups. Their findings demonstrated that both groups exhibited impaired performance during the gambling task with reduced skin conductance responses. Additionally, the amygdala lesion group displayed diminished conductance responses to both reward and punishment to the IGT and a subsequent conditioning task, which was not observed in the VMPFC group or healthy controls. The authors interpreted these findings in support of SMH, suggesting that the amygdala is involved in generating emotions and somatic state responses whereas VMPFC is predominantly involved in the integration and appraisal of somatic states.

2.5. The Regulation of Physiological Resources during Exercise

Exercise represents a complex and dynamic behaviour that poses acute pressures to the overriding requirement for sustained homeostasis. Various parameters are involved in meeting the physiological demands presented during exercise, which can be distinguished into allostatic processes involving either physiological or behavioural responses (Egan & Zierath, 2012; St Clair Gibson et al., 2017). In the following sections, both sets of responses are covered in relation to endurance exercise. This section will first cover the physiological determinants of endurance exercise performance before reviewing the behavioural functions that constrain performance within homeostatic-set boundaries.

2.5.1. Physiological Determinants of Endurance Exercise Performance

Exercise triggers an increase in metabolic demand by the working tissues (i.e., skeletal muscle). Meeting this demand is realised through a cascade of physiological processes; occurring at every level from the biochemical reactions involved in the resynthesis of high energy phosphate molecules, which underlie all cellular processes, to the systems supporting these metabolic processes including cardiovascular, pulmonary, endocrine, and thermoregulatory (Egan & Zierath, 2012; Zierath & Wallberg-Henriksson, 2015). These processes are coordinated through autonomic reflexes, which respond to changing allostatic demands. Sustained exercise participation (i.e., exercise tolerance) is only possible by the extent to which these processes can meet ongoing metabolic requirements (Hawley, Maughan, & Hargreaves, 2015).

Several physiological metrics are used to describe the faculty of these various physiological systems to sustain ongoing physical activity. Within the context of prolonged endurance exercise, the capacity to sustain exercise is predominantly determined by the capacity of the individual to meet the oxygen demands required for continued cellular respiration (Robergs, Ghiasvand, & Parker, 2004). Within the literature, the upper limit for oxygen consumption is often referred to as either the maximal aerobic capacity ($\dot{V}O_{2\ max}$) or peak aerobic capacity ($\dot{V}O_{2\ peak}$). Although these terms are often used interchangeably, there are key differences in these terms that reflect potential distinctions in the criteria used to determine a person's aerobic capacity. The established definition for $\dot{V}O_{2\ max}$ is the 'maximum volume of oxygen consumed by the body each minute during large muscle group exercise at sea level', which requires the observation of a plateau in $\dot{V}O_2$ (< 150 mL·min^{-1} or < 2 mL·kg^{-1}·min^{-1}) despite an increase in exercise work rate (Winter, Jones, Davison, Bromley, & Mercer, 2007). A number of auxiliary criteria may also be applied to establish a maximal effort: a respiratory exchange ratio (RER) ≥ 1.15 or above, a maximum heart rate ($f_{c\ peak}$) within ± 10 b·min^{-1} of age-predicted maximum (220 – age), or blood lactate concentration > 8 mmol·L^{-1}. These criteria are often applied as many participants do not achieve this plateau during graded exercise testing (Midgley & Carroll, 2009). By contrast $\dot{V}O_{2\ peak}$ simply refers to the highest observed value for $\dot{V}O_2$ obtained during a test.

Maximal oxygen consumption is one of the strongest physiological discriminators of potential endurance exercise performance (Joyner & Coyle, 2008). In heterogeneous fitness samples, individuals with higher aerobic capacities typically demonstrate an ability to sustain higher work rates for a given duration than those with comparably lower aerobic capacities. $\dot{V}O_{2\ peak}$ is therefore a key determinant of endurance exercise performance. $\dot{V}O_{2\ peak}$ is largely governed by the capacity of the ventilatory and cardiovascular systems to deliver oxygenated blood to the muscle; and the ability of those tissues to utilise that oxygen (Bassett & Howley, 2000; Walsh, 2000). However, transporting and using oxygen for energy metabolism is a relatively slow process and often requires the support of other biochemical reactions to ensure continual cellular respiration particularly under situations of precipitously changing metabolic demand (Noakes, 2000; Weston et al., 1997).

Most endurance events are undertaken at intensities below $\dot{V}O_{2\ max}$. Indeed, work rates at around $\dot{V}O_{2\ max}$ can only be sustained for a few minutes before reaching a point of uncompensable fatigue and exercise termination (Jones, Vanhatalo, Burnley, Morton, & Poole, 2010; Jones, Wilkerson, Dimenna, Fulford, & Poole, 2008). Therefore, the ability to sustain a high fraction of $\dot{V}O_{2\ max}$ without undue fatigue, described as an athlete's functional capacity, has been proposed as a more implicit determinant of success in most prolonged endurance events (Bassett, & Howley, 2000). It is suggested that functional capacity is determined, at least in part, by the body's ability to attenuate the accumulation of certain fatiguing metabolites, particularly the accretion of hydrogen ions (Robergs et al., 2004). Processing and removal of hydrogen ions from the cell is achieved through both oxidative and non-oxidative pathways. The relative contribution of non-oxidative processes is thought to increase in a positive curvilinear response to changes in exercise work rate (Costill, 1970). Blood lactate concentrations are often used as an indirect measure to reflect these non-oxidative processes involved in transporting hydrogen ions away from the mitochondria (Hill, Long, & Lupton, 1924; Wasserman, Whipp, Koyal, & Beaver, 1973). Lactate thresholds and their corresponding ventilatory thresholds have been used to discriminate performance capability in many different endurance events (Faude, Kindermann, & Meyer, 2009). These physiological measures have been used to identify the presence of transition periods (thresholds) from so-called aerobic intensity exercise to anaerobic intensity exercise (Wasserman et al., 1973). Modelling of the $[La^-]_c$ and ventilatory responses during exercise, researchers have described the presence of either a dual-phase single breakaway model or three-phase double breakaway model (Faude et al., 2009).

A causal relationship between lactate and ventilatory responses has previously been described. Wasserman and colleagues (1973) demonstrated that the disproportionate increase in $\dot{V}_E$ during progressive intensity exercise was associated with the accretion of H^+ and the partial pressure of CO_2 (PCO_2) in arterial blood. Further, Jones and Ehrsam (1982) demonstrated stoichiometric increases in $\dot{V}_E$ occurring in conjunction with increases in H^+ and $[La^-]_c$. However, other researchers have argued that this relationship may be coincidental rather than causal. For instance, Cecca and colleagues (1986) found that ventilatory responses were not significantly altered during progressive intensity exercise under experimentally elevated acidosis. Similarly, Neary et al. (1985) examined lactate and ventilatory thresholds under normal conditions, and under glycogen depleted and/or previously exercise. The authors reported the ventilatory thresholds remained unchanged despite significant alteration in lactate responses in glycogen depletion and fatigued states. Additionally, in people with McArdle's syndrome (a genetic condition resulting in a lack of muscle phosphorylase) ventilatory thresholds have been found despite an absence of $[La^-]_c$ or H^+ in the blood. Nevertheless, both lactate thresholds and ventilatory thresholds have been widely used to describe the functional capacity to perform work and are considered to be an important determinant of endurance exercise performance (Loat & Rhodes, 1993).

Another important determinant of endurance exercise performance is the ability of an individual to convert the chemical energy generated by cellular respiration into mechanical work, termed efficiency or economy (Joyner & Coyle, 2008). Efficiency describes the proportion of work done relative to the energy expended and is generally expressed as a percentage (Gaesser & Brooks, 1975). Efficiency can be evaluated in terms of gross (no correction), net (change in mechanical work and energy expenditure corrected resting metabolic rate), and delta (change in mechanical work and energy expenditure between two different steady-state intensities) (Matomäki, Linnamo, & Kyröläinen, 2019). Whereas, economy is used to describe the oxygen cost associated with a given work rate (e.g., $\dot{V}O_2$ whilst running at 16 $km \cdot h^{-1}$ or PO at $\dot{V}O_{2\,max}$; (Joyner & Coyle, 2008; Winter et al., 2006). Numerous factors are thought to influence efficiency/ economy including muscle fibre composition (Coyle, Sidossis, Horowitz, & Beltz, 1992; Mogensen, Bagger, Pedersen, Fernström, & Sahlin, 2006) training status (Esteve-Lanao, Lucia, deKoning, & Foster, 2008), as well as environmental factors such as temperature (Hettinga et al., 2007) and also mechanical factors such as cycling cadence (Pierre, Nicolas, & Frédérique, 2006).

Other physiological control mechanisms are involved in maintaining homeostasis during exercise, including those related to thermoregulation, humeral factors, and the mobilisation of substrates to metabolically active tissues. These functions as well as others demonstrate the complex coordinated response that occurs every time we engage in physical activity. These responses occur because of behavioural decisions to initiate and maintain bouts of increased physical activity. Therefore, engagement in exercise produces two predominant competing drives: 1) the drive to maintain homeostasis, and 2) the motivation to engage in physical activity. The interaction between these drives raises broader questions about how exercise is regulated. In the following section, this topic will begin to be addressed, discussing the behavioural processes involved in regulating exercise workloads within homeostatic bounds; balanced against goal-directed motivational drives to achieve desired performance outcomes.

2.5.2. Exercise Pacing

Completion of a given exercise task and maximisation of athletic performance requires athletes to distribute their energetic expenditure in an optimal manner. Pacing describes the observed behavioural regulation of these physiological resources during an exercise task (Mauger, 2014). Pacing is often an implicit behavioural response based on ongoing contextual knowledge of the exercise demands, but may also be influenced by predetermined strategic decisions (Mauger, Jones, & Williams, 2010; Renfree, West, Corbett, Rhoden, & St Clair Gibson, 2012; Roelands, De Koning, Foster, Hettinga, & Meeusen, 2013). One of the major complexities of exercise pacing is the factors involved in its emergence. Athletes are required to make continuous operational decisions around their given work rates based on current knowledge and teleoanticipatory expectations of physiological (e.g., substrate availability, thermal tolerance, neuromuscular fatigue, cardiovascular capacity) and environmental factors (e.g., duration of the task, ambient conditions, topography, the actions of other athletes) (Mauger, 2014; Roelands, De Koning, Foster, Hettinga, & Meeusen, 2013). Tucker (2009) argues that effective pacing relies on the accurate appraisal of these factors and the existence of a perceptual template with which to compare against.

2.5.3. The Role of Perceptual Responses in Exercise Pacing

The perception of the physiological condition of the body is a key construct supporting optimal behavioural regulation of energy expenditure during bouts of exercise (Tucker, 2009). As such the perception of bodily sensations such as fatigue, exertion, effort, temperature, and pain as well as the associated affective consequences of these perceptions are likely to influence athletes' decisions to speed up, slow down, or even stop exercising all together. The generation of these perceptions is still somewhat contested among different researchers (e.g., Marcora, 2008), however, their widespread use in the study of exercise pacing and engagement has provided substantial understanding around behavioural regulation of physiological resources during exercise.

Rating of perceived exertion (RPE) is arguably the most widely utilised psychometric tool for assessing perceptions of physiological strain during exercise (Russell, 1997; Watt & Grove, 2002). The RPE scale was first developed by Gunnar Borg (Borg, 1982). During his seminal study, Borg demonstrated a strong coupling between heart rate and perceived exercise intensity during a graded exercise task. This led to the development of his well-known '6 to 20' nomogram for perceived exertion. The utility of RPE has since been demonstrated across a range of exercise contexts. For instance, RPE has been shown to be sensitive to changes in physiological strain- as denoted by increases in cardiac and ventilatory output, and blood lactate; in constant load (Garcin, Vautier, Vandewalle, Wolff, & Monod, 1998), self-paced time trial (Mauger, Jones, & Williams, 2010; Tucker, 2009), incremental exercise (Mauger & Sculthorpe, 2012), repeated bout exercise tasks (Castle et al., 2006; Skein, Duffield, Edge, Short, & Mündel, 2011). Furthermore, manipulation of substrate availability (Burke et al., 2017), environmental conditions of temperature (Potteiger & Weber, 1994) and oxygen availability (Noakes et al., 2001), the use of pharmacological interventions such as stimulants (Doherty & Smith, 2005) and analgesics (Amann, Sidhu, Weavil, Mangum, & Venturelli, 2015; Mauger et al., 2014), and training adaptations have been shown to alter the relationship be RPE and exercise work rates using repeated measures designed studies. The findings demonstrate the robustness of RPE as tool for psychometric assessment of whole-body perceptions of physiological strain, supporting its widespread application in the research literature around exercise.

2.5.4. Afferent Feedback Models of Exercise Regulation

Afferent feedback is purported to contribute to the central processing component that underlies the regulation of exercise performance (Tucker, 2009). In one of the earliest proposed frameworks on the topic, Ulmer (1996) described a closed-loop model of extracellular regulation. The model proposes that efferent motor signals exert influence on both spatial-temporal aspects of motion and metabolic demands of active tissues. Extending on principles of feedback loops in motor control, Ulmer argued the presence of a similar feedback control mechanism involved in regulating energy expenditure. Feedback from working muscles and other tissues around the body are integrated along with information related to endogenous and exogenous reference signals and predictive calculations of future exercise demands (teleoanticipation) to set the rate of muscular metabolism in line with anticipated endpoints. This process occurs in what Ulmer describes as a ‘regulation centre’ situated inside the brain. In a further extension of motor control principles, the model suggests a ‘metabolic aspect’ of motor learning which includes the optimal adjustment of energy expenditure during exercise.

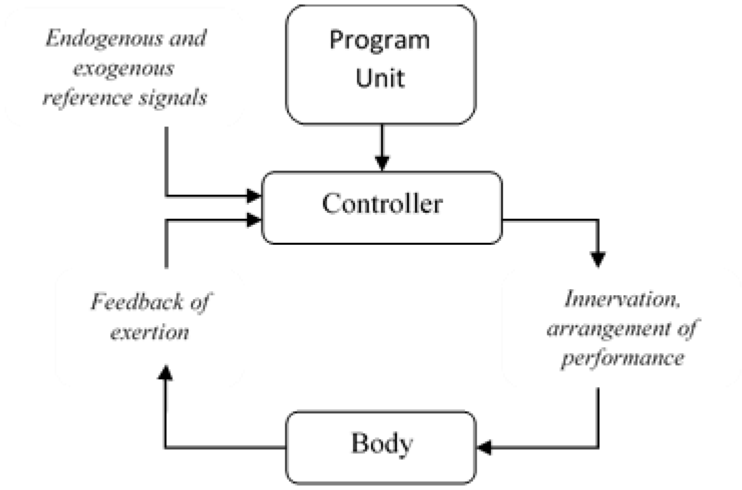


Figure 2.5. Ulmer's model of extracellular regulation. Adapted from Ulmer (1996).

The ideas presented in Ulmer’s framework provide the basis for numerous subsequent models (Amann et al., 2011; Noakes et al., 2001; Roelands et al., 2013; St Clair Gibson et al., 2017; Tucker, 2009). Perhaps the most prominent of these models is the ‘central governor model’ (CGM) proposed by Noakes (2000). In its original conception, the CGM argued the presence of a subconscious neural ‘governor’ (analogous to Ulmer’s ‘regulation centre’) that acts to limit exercise performance in order to avoid a catastrophic failure to physiological systems, principally the onset of myocardial ischemia (Figure 2.6). Within this model, exercise intensity (i.e., efferent neural drive to the exercising muscles) is continuously regulated in accordance with emerging afferent sensory cues that are compared with predicted homeostatic templates (Tucker, 2009). The CGM also accounts for conscious perceptions such as fatigue and exertion that arise during exercise. For instance, the model suggests that fatigue represents the product of the error differences between predicted exercise-induced changes in physiological state and the actual disturbances of physiological state. The role of these conscious perceptions appears to act as a homeostatic-relevant emotional construct, which functions to bias exercise behaviour, with the overriding purpose of preventing over-exertion and preserving the integrity of the soma.

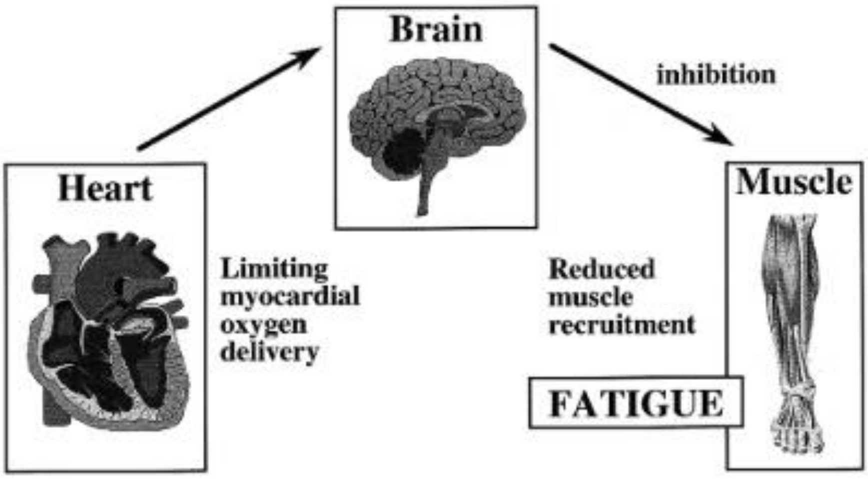


Figure 2.6. The central governor model of exercise regulation involved in limiting myocardial ischemia (Noakes, 2000).

The ‘integrative governor’ represents one recent extension of the CGM (St Clair Gibson et al., 2017). Rather than arguing for the dichotomic position between centrally and peripherally acting agents as the principle regulatory determinant of exercise tolerance, the authors instead suggest that regulation of exercise performance represents an ongoing competition between the demands of central (psychological motivational) and peripheral (physiological protection requirements) drives. The resolution of these antagonistic drives is continuously mediated through an application of the relative weighting (i.e., importance) of these two drives. Accordingly, this process reflects a complex decision-making process based on the comparison between system states, which results in observable oscillations occurring across all systems of the body (physiological and behavioural).

The Three-Dimensional Dynamical Systems Framework by Venhorst and colleagues (Venhorst, Micklewright, & Noakes, 2018a, 2018b, 2018c, 2018d) provides a further, nuanced, development of the psychophysiological concepts pertaining to the regulation of exercise behaviour. Drawing on non-linear dynamical systems theory, this three-dimensional framework proposes a model of exercise regulation that extends beyond gestalt perceptions of fatigue and exertion to consider the interaction between sensory, affective, and cognitive processes in regulating physiological systems and influencing performance fatigability. Examining the tenets of this model, Venhorst *et al.* (Venhorst et al., 2018c) demonstrated that athletes ‘falling behind’ in a simulated head-to-head competition experience significant deteriorations in core affect, leading to the development of an action crisis (a measure of intra-psychic conflict between further goal pursuit and goal disengagement), that subsequently contributes to an increase in cortisol response, that finally results in an observable decrement to overall performance. Modelling of this data in a subsequent study revealed that changes in affective valence significantly mediated the observed relationship between ‘falling behind’ and the experience of action crisis, accounting for ~35% of the variance shared between these two factors (Venhorst et al., 2018a).

Finally, afferent feedback model, and its subsequent ‘sensory tolerance limit’ variation, proposed by Amann and colleagues (Amann et al., 2011; Hureau et al., 2016), suggests that central motor drive to the working muscles is regulated in accordance with either: feedback principally from metabosensitive group III/IV (afferent feedback model) signally changes in the working muscles (e.g., leg muscles during exercise), or a more global feedback loop that incorporate sensory inputs arising from both the working muscles as well as sensory inputs from muscles indirectly in the exercise (e.g., respiratory muscles during cycling) and also corollary discharge associated with central motor command. Both iterations of this model suggest that these feedback loops regulate exercise in accordance with a hypothetical critical limit for the tolerance of afferent sensory input. In support of this, Amann *et al*. (2007) have shown that manipulation of arterial O_2 concentrations results in significant improvements in exhaustive exercise performance but does not alter the level of peripheral fatigue attained at the end of the exercise bout. Further, greater levels of peripheral fatigue reported for smaller muscle group exercise (e.g., single limb versus double limb) can be accounted for within the sensory tolerance limit, as fatigue of smaller groups of motor units results in smaller metabolic perturbation as well as a decreased contribution from cardiovascular and ventilatory systems, thereby decreasing the global afferent sensory input.

2.5.5. The Role of Perception in Regulating Exercise Intensity

A major strength of these psychophysiological models is their capacity to explain common features of self-paced exercise, which are not readily compatible with purely physiological explanations of fatigue (Renfree et al., 2012). Particularly, the observation that athletes are able to volitionally increase their work rates toward the end of an exercise bout (so-called ‘end spurt’) at a point when physiological perturbations are presumably at their greatest (Figure 2.7). This observable scenario cannot be readily explained by purely physiological models, where the summation of physiological resources steadily declines over the course of an exercise bout with the aggregate of fatiguing processes being greatest at the end. Tucker (2009) argues that the observation of an end spurt is indicative of a physiological reserve that is preserved until near the end of the exercise. Key to this process is the perceptual mechanisms that govern pacing.

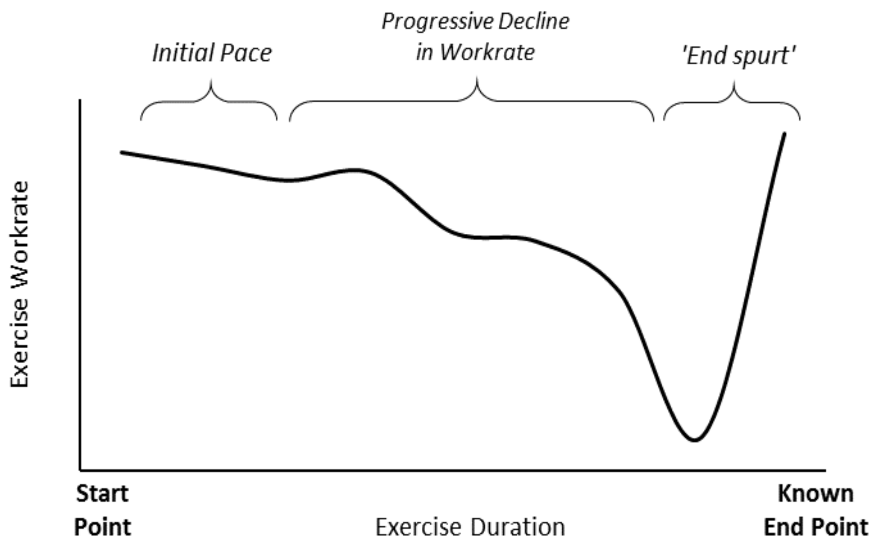


Figure 2.7. Hypothetical pacing profile during prolonged self-paced exercise.

RPE is proposed to be one of the primary perceptual cues used in regulating work rate (Tucker, 2009). Under self-paced time-trial based protocols, RPE has been shown to increase steadily throughout the course of an exercise bout, reaching peak values towards the end (Renfree et al., 2012; Swart, Lindsay, Lambert, Brown, & Noakes, 2012). Under time-trial based exercise protocols, the absolute rate at which RPE increases is largely dependent on the duration of the exercise task (Eston, Stansfield, Westoby, & Parfitt, 2012). However, when RPE is normalised to relative exercise duration (i.e., percentage completion) the rate of change in reported scores becomes comparable regardless of the absolute exercise period. This observation supports the notion of a pre-set exercise strategy/template for performance. The basis of this template appears to be derived from teleoanticipatory expectations of exercise duration. For instance, Rejeski and Ribisl (1980) evaluated the role of expected exercise duration on the perception of effort. The authors reported that RPE was lower, even though physiological variables (e.g., heart rate) were comparable when they were told they would be cycling for 30 minutes as opposed to 20 minutes, but when the exercise was terminated after only 20 minutes. Similarly, the effects of distance feedback have been examined across several studies (Albertus et al., 2005; Nikolopoulos, Arkinstall, & Hawley, 2001). The plurality of findings in these studies support the idea that RPE increases according to expected exercise duration, that this expectation is predominantly established at the outset of the exercise task, and furthermore that RPE can be dissociated from physiological variables when feedback is inaccurate. This latter finding, that RPE is dissociable from physiological changes, would appear to contradict the role of afferent feedback in the emergence of perceived exertion; however, this is not necessarily the case. Manipulations of the exogenous availability of oxygen have been shown to influence pacing strategy, with increases in external work rates observed under conditions of hyperoxia and decreases in external work rates observed in hypoxia (Noakes et al., 2001). Despite the differences in external work rates, RPE remained similar between normoxia and the manipulated environments, which reflected the comparable physiological responses. Similar findings have also been reported under high ambient temperatures where work rates are reduced in order to mediate the rise in physiological strain (Tucker, Marle, Lambert, & Noakes, 2006).

From an alternate perspective, manipulation of perceived exertion has also been shown to influence exercise pacing and performance. Amann et al. (2009) showed that blocking afferent feedback of group III and IV neural fibres using an intrathecal lumbar epidural application of fentanyl (an opioid analgesic), produced a disengagement between RPE and work rate, and encouraged the adoption of higher power outputs at the outset of exercise. Furthermore, the authors reported that the substantially higher outputs at the outset of exercise in the fentanyl condition exacerbated peripheral fatigue during the latter portions of the exercise task and was associated with impaired performance (slower finish times) in the exercise task. Interpretation of these findings could suggest that afferent feedback acts as a regulatory mechanism for the optimal management of physiological resources during exercise. Similarly, results from pharmacology-based studies demonstrate that manipulating neurotransmitters serotonin and dopamine is capable of influencing exercise performance by altering the central processing component of perceived exertion (see for review Roelands et al., 2013). Broadly speaking, it appears that dopaminergic drugs appear to exert an ergogenic effect, enhancing exercise performance, whereas serotonergic and noradrenergic inhibit exercise performance. Similarly, the use of exogenously applied bolus of metabolites (protons, lactate, and ATP) to the abductor pollicis brevis muscle of the hand produced sensations of muscular fatigue (low concentrations) and pain (high concentrations) (Pollak et al., 2014). This effect was observed only when the combination of the metabolites was used, but not in the conditions where the individual metabolites were injected in isolation, suggesting a synergistic signalling role of these chemicals.

Whilst many of these homeostatic regulatory models describe exercise-related modulatory control of muscular effort and provide an explanation of the underlying mechanisms involved; they do not account for the reasons why an individual engages in exercise. Indeed, if sustainment of homeostasis is the predominant drive of these mechanisms then engagement in exercise would be counter-intuitive, given that exercise itself presents several challenges to the maintenance of homeostasis (St Clair Gibson et al., 2017). Additionally, and specific to the original CGM, the observation that manipulation of motivational incentives influences exercise behaviour and performance raises further issues within the idea of an overriding homeostatic regulator existing independently of conscious influence (Inzlicht & Marcora, 2016). Finally, Walsh (2000) argues that in a variable systems design the lower work capacity of skeletal muscle compared with the heart means that volitional exhaustion will always occur below the exercise tolerance limit of the myocardium. Consequently, the necessity for a 'central governor' which acts to preserve the condition of the heart appears to be unnecessary.

2.5.6. Corollary Discharge, Perception of Effort, and Impact on Pacing

Other researchers have argued against closed-loop afferent feedback models, suggesting that they are "unnecessarily complex" (Marcora, 2008). Alternative models such as Marcora's psychobiological model proposes that exercise pacing represents a form of volitional task engagement/disengagement (Marcora, 2008; Marcora & Staiano, 2010; Pageaux, 2014). Based on Brehm and Self's (1989) theory of motivational intensity, the psychobiological model postulates that task disengagement (i.e.,, exhaustion) occurs either when 1) the effort required to sustain a given workload is equal to the maximum level of effort the subject is willing to exert to succeed in the exercise task or, 2) the subject believes that they have exerted a true maximal effort and continuation of exercise is unfeasible. In this instance, RPE represents effort-related decision-making processes that compare current demands of exercise against the maximum degree of effort an individual is willing to exert. Consequently, factors altering either effort perception or potential motivation are believed to influence the conscious decisions to modulate the expenditure of effort, thereby influencing exercise pacing and performance (Marcora et al., 2008). This proposition of effort perception is conceptually more keeping with the aforementioned observations that exercise performance can be influenced by the introduction of even modest motivational incentives and is less reliant of homeostatic considerations.

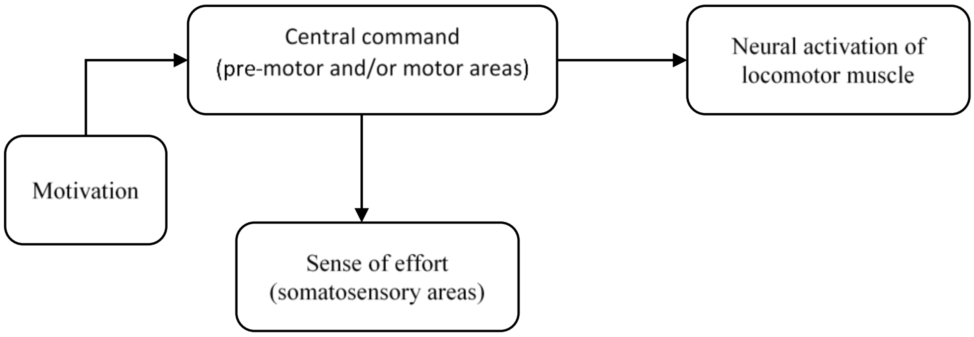


Figure 2.8. Psychobiological model of exercise pacing. Adapted from Marcora (2008)

Empirical support for this psychobiological model of exercise regulation is often cited from experiments involving tasks aimed at altering cognitive activity, resulting in an enhanced perception of effort and impaired performance of both prolonged (Brownsberger, Edwards, Crowther, & Cottrell, 2013; Pageaux, Lepers, Dietz, & Marcora, 2014) and intermittent (Smith, Marcora, & Coutts, 2015) exercise. For example, Marcora et al. (Marcora, Staiano, & Manning, 2009) demonstrated that the use of a cognitive task aimed at inducing ‘mental fatigue’ resulted in an increased perception of exertion and reduced tolerance (defined in relation to the time-to-task failure) in a constant-load cycle task at 80% of peak power output. This effect occurred despite comparable levels of reported motivation between the control and mental fatigue condition, suggesting that depletion of motivational resources was not a factor impairing task performance. Indeed, citing the work of Barch et al. (1997) and Carter et al. (1998) in which the effects of mentally fatiguing tasks were shown to increase the activity of the ACC, the authors argued that completion of the antecedent cognitive task influenced the perception of central motor command which subsequently impacted on the subject’s perceived exertion and inhibited task performance.

A major departure between closed-loop afferent feedback models and the psychobiological model is the way in which individuals perceive strain during exercise. Whereas closed-loop feedback models rely on the integration of afferent feedback for the generation of perceived exertion; the psychobiological model instead relies on corollary discharge from the motor and premotor regions to somatosensory regions (de Morree, Klein, & Marcora, 2012). In this conception, sense of effort is derived from central interpretation of efferent motor drive rather than afferent feedback. This is supported by evidence from studies examining the effect of local muscle curarisation and weight matching tasks in ipsilateral limbs (Gandevia & Mccloskey, 1977; Gandevia, Mccloskey, & Potter, 1980). Findings from these studies suggest that the increased motor drive required to overcome the partial paralysis of the target limb provides the basis for change in sense of weight and effort. However, more recent findings by Luu, Day, Cole, and Fitzpatrick (2011) suggest that efferent drive and related corollary discharge may not fully explain sense of effort alone. Indeed, the authors demonstrated a role for afferent feedback, stemming from muscle spindles and Golgi tendon organs, through experimental manipulation of type I afferent fibre feedback and partial blockade of motor neuron drive.

Inconsistencies in the interpretation of concepts around the perception of effort and the perception of exertion may contribute to the aforementioned conceptual disparities. For example, Swart and colleagues (2012) demonstrated that effort and exertion can be distinguished from one another and suggested that exertion represented a sense of the physical sensations from the body inferred from afferent feedback whereas sense of effort was related to "psychic" cost of sustaining or increasing exercise work rate (Swart et al., 2012). This interpretation has more recently been supported by Christian, Bishop, Billaut, and Girard (2014) who showed that participants were able to differentiate between effort, peripheral discomfort (analogous with perceived exertion), as well as sensations of breathing and limb discomfort. One possible interpretation of these findings is to suggest that sense of effort and sense of exertion may be generated through subtly different neural pathways.

2.6. Interoception and the Regulation of Exercise Behaviours

2.6.1. Theoretical Basis of Interoceptive Networks during Exercise

Whilst many of the aforementioned psychophysiological models of exercise tolerance incorporate afferent feedback loops as a central tenant in the regulation of muscular work and the emergence of conscious feeling states (e.g., perceived fatigue or exertion), relatively few provide an explicit account of how these phenomena emerge within the interoceptive network. Addressing this limitation, McMorris, Barwood, and Corbett (2018) recently proposed a model of exercise-induced central fatigue based on interoception and motivation. Within their model, predictions of the expected sensory feedback (i.e., prior predictions) are fed forward by the dorsolateral prefrontal cortex (DLPFC) to the anterior insula cortex. During exercise, these prior predictions are compared against afferent sensory inputs from lamina I spinothalamic and medullothalamic pathways. The authors contend that comparison between predicted and actual physiological states (i.e., a prediction error) generates an awareness of the current physiological condition of the body (i.e., percept), which is subsequently forwarded to the ACC and prefrontal cortices (VMPFC and LPFC) for further evaluation and implementation. The model proposes that the LPFC plays an important role in influencing goal-directed behaviour, which is influenced by input from dopaminergic and noradrenergic systems. Phasic activation of dopaminergic and noradrenergic neurons within the PFC is postulated to be necessary for the maintenance of goal-related action (Aston-Jones & Cohen, 2005). Whereas increasing tonic activity of dopaminergic and noradrenergic systems (which respond to increasing interoceptive prediction errors) signals a diminished motivational salience of goal-directed action, thereby directing decision-making processes towards reduced physical exertion or exercise cessation. Consequently, increasing predictions errors (signalling increasing allostatic demand) experienced during exercise are argued to trigger a transition towards greater tonic activity of dopaminergic and noradrenergic systems, which biases LPFC away from the maintenance of goal-directed behaviour.

2.6.2. Current State of Knowledge

Researchers argue that the processing of interoceptive signals is fundamental to the conscious perception of exertion and fatigue experienced during physical activity (Hampson, St Clair Gibson, Lambert, & Noakes, 2001). Findings from imaging studies demonstrate that activation of the insula cortex increases in conjunction with physiological changes during exercise and is positively correlated with changes in perceived exertion during cycling exercise (Williamson, McColl, Mathews, Ginsburg, & Mitchell, 1999). Pronounced activation of anterior and mid insula regions has also been found to occur at the point of task failure during handgrip exercise (Hilty, Jäncke, Luechinger, Boutellier, & Lutz, 2011). Further, Hilty and colleagues (2011), using EEG, have reported an increased lagged phase synchronisation between the insula and primary motor cortex towards the end of volitional exercise, which the authors suggested was indicative of fatigue-related communication between these two regions. Manipulation of metabosensitive afferent signalling from skeletal muscle, as described previously (see Section 2.5.5), has been shown to reliably influence the subjective appraisal of fatigue, pain, and exertion (Amann et al., 2011; Blain et al., 2016; Pollak et al., 2014) and also appears to inhibit cardiovascular and respiratory reflexes during exercise (Amann et al., 2010). Further, studies have demonstrated that increased attention towards interoceptive cues results in increased reports of subjective exertion and fatigue (Fillingim & Fine, 1986; Pennebaker & Lightner, 1980) whereas decreased attention to interoceptive cues results in reduced ratings of perceived exertion and increased work capacity (Mohammadzadeh et al., 2008). Recent evidence by Iodice and colleagues (2019) has further demonstrated that manipulation of auditory heart rate feedback may influence a person's perception of exertion during cycling exercise. Specifically, the authors found that participants reported significantly greater RPE when auditory feedback was faster than actual heart rate compared with conditions of congruent or slower heart rate auditory feedback. Following up on this finding, the authors reported subjective beliefs related to interoceptive awareness (assessed using the MAIA; Mehling et al., 2012) did not influence the effects of the false auditory feedback on RPE.

Individual differences in cardiac interoception may also influence the perception and regulation of exercise work rates. Examining this question, Herbert and colleagues (2007) found that good heartbeat perceivers completed significantly less work during a 15-minute self-regulated exercise task (about 10% less on average) than poor heartbeat perceivers. Physical fitness was not significantly different between groups (p = .85) and is therefore unlikely to have influenced the outcome of the cycling task. Additionally, the authors reported significantly lower elevations in exercise heart rate in the good perceivers despite similar reported perceptions of fatigue between the two groups. Taken together, the authors interpreted their findings as evidence in support of the role interoceptive sensitivity on the perceptual experience and behavioural self-regulation of physical exertion. Conversely, Machado *et al.* (2019) did not find any differences in maximal exercise performance in a graded exercise task between good and poor heartbeat perceivers. This suggests that, whilst manipulation of interoceptive signalling produces reliable changes to exercise perceptions and behaviour, the effect of individual differences in cardiac interoception remains unclear.

A person's cardiac interoceptive accuracy may also influence their physiological responses to exercise. This effect was demonstrated by Pollatos et al. (2007) reporting that good heartbeat perceivers showed significantly greater cardiac reactivity (i.e., increases in heart rate) to an isometric handgrip exercise task compared with poor heartbeat perceivers. This finding was supported by a significant positive partial correlation between change in heart rate and interoceptive accuracy score. Similar findings have been reported in previous studies showing a correspondence between interoception and cardiac reactivity to emotional stimuli (Critchley, Wiens, Rotshtein, Öhman, et al., 2004; Herbert, Pollatos, Flor, Enck, & Schandry, 2010; Pollatos, Kirsch, & Schandry, 2005).

Physical activity status and differences in aerobic fitness may also influence a person's interoceptive characteristics. The earliest known study to examine this link was conducted by Jones and Hollandsworth (1981). The authors reported that male distance runners performed significantly better in a heart rate discrimination task at rest than tennis players (moderately fit), sedentary groups, and also better than female distance runners. However, these differences were reduced during exercise as discriminative accuracy was improved within both the sedentary and moderately fit groups. No significant improvements were observed in the male runners during exercise. This was interpreted as indicating some sort of ceiling effect on performance. However, physical activity in this study was solely quantified using a physical activity questionnaire, which was also the case in a latter study by the same research group (Montgomery et al., 1984). The principal findings in this latter study appeared to somewhat contradict their earlier results, in that interoceptive accuracy was greater in the average fitness group during exercise than the high fitness group but no different at rest. In their interpretation, the authors hypothesised that differences in heart rate discrimination performance between the two studies may have been influenced by the measurement procedure taken when sitting (Jones & Hollandsworth, 1981) versus standing (Montgomery et al., 1984) as well as differences in the exercise protocol, cycling (1981) compared with running (1984). However, it is arguably plausible that subjective self-reported quantification of physical fitness may also have confounded the research findings and this is unlikely to be as robust as other methods of physical fitness assessment, such as the use of indirect calorimetry during graded exercise protocols (Gustavo et al., 2005; Morrow & Freedson, 1994).

Presently, only three study have so far attempted to quantify the relationship between a direct measure of physical fitness (i.e., not self-report) and interoception, with mixed findings (Georgiou et al., 2015; Machado et al., 2019; Perakakis et al., 2017). The study by Georgiou and colleagues (2015) was conducted as part of a larger program investigating physical activity behaviour in children and adolescents. The authors showed a significant, albeit relatively weak, positive correlation between 6-minute running performance and interoceptive accuracy (heartbeat tracking). Additionally, data from the study indicated that children classified as good heartbeat perceivers engaged in higher levels of light physical activity, as measured using physical activity trackers. However, no significant between-groups differences were observed in relation to moderate or vigorous physical activity participation. Similarly, Perakakis and colleagues (2017) have reported that high fitness individuals produce significantly larger heartbeat evoked potentials (a neural correlate of cardiac interoception; Schandry & Montoya, 1996) compared to sedentary individuals. Moreover, exercise training programmes have been shown to result in large increases in trait interoceptive sensibility, as assessed using the Multidimensional Assessment of Interoceptive Awareness questionnaire (Mehling et al., 2018). The influence of training status has also been considered in the context of respiratory interoception. Faull *et al*. (2018) found that endurance athletes demonstrated anticipatory brain activity that positively correlated with resulting breathing perceptions within key interoceptive areas, such as the thalamus, insula, and primary sensorimotor cortices, which was negatively correlated in sedentary controls. However, significant relationships between measures of aerobic fitness and cardiac interoception are not always observed in other studies (Herbert, Ulbrich, & Schandry, 2007; Machado et al., 2019).

Reported differences in heartbeat detection tasks between athletes and sedentary subjects have been suggested to have their origin in the increased stroke volume of athletes, a physiological adaptation provoked by regular exercise (Schandry, Bestler, & Montoya, 1993). This morphological adaptation as well as potentially lower body compositions would provide athletes with an advantage in being able to accurately detect their own heartbeats. Conversely, it is suggested that exercise may represent a form of ‘interoceptive exposure’ where improvements in interoceptive result from exposure to the heightened salience of interoceptive cues experienced during exercise (Georgiou et al., 2015; Montgomery et al., 1984; Sabourin, Stewart, Watt, & Krigolson, 2015).

Other reported studies that have so far investigated the link between interoception and exercise include that of Kollenbaum and colleagues (1996) and more recently Pollatos, Herbert, Kaufmann, Auer, and Schandry (2007). The study of Kollenbaum et al. (1996) did not directly assess interoception via classical cardiac perception tests. Instead, participants were required to adjust cycling intensity to reproduce selected heart rate, blood pressure, and myocardial metabolic parameters. Data from the study showed that subjects could reliably reproduce heart rate with high internal consistency, despite a systematic bias. However, there was no consistency in blood pressure reproduction and only a moderate one in the reproduction of myocardial metabolism. The robustness of this protocol has yet to be examined in other research studies, as such the strength of these findings remains in question. Additionally, there is scant evidence related to other dimensions of interoception (i.e., sensibility and awareness), meaning that understanding of the potential involvement of these different interoceptive dimensions on the regulation of exercise intensity remains unclear.

2.7. Concluding Remarks

To summarise, this chapter covered the relevant aspects within the literature and current understanding around the areas of interoception and exercise. Amongst the topics covered included the neurophysiological basis of interoception, the role of interoception on emotion and behaviour, physiological and behavioural regulation of exercise, and the theoretical implications of interoception on the perceptual and behavioural responses to exercise. Despite the broad implicit arguments put forward in this review, supporting the role of interoception in exercise regulation, relatively scant empirical evidence directly supports these suppositions by examining individual differences for interoceptive sensitivity and exercise. Of the existing evidence, there appears to be some support towards a link between physical fitness and interoceptive sensitivity; an effect of interoceptive ability on exercise regulation; and also has implications on physical activity behaviour. However, there are a number of limitations. For instance, weaknesses in the approach used to describe the link between physical fitness and interoceptive awareness.

2.8. Aims and Hypotheses

This thesis is comprised of four experimental chapters. The aim of the studies within these chapters is to address several of the fundamental gaps in the knowledge surrounding the relationship between interoception, fitness, and exercise. The individual aims and hypotheses for each experimental chapter are detailed below:

Chapter 4: The Relationship between Aerobic Fitness, Physical Activity and Interoception.

> Aim: To examine the effect of aerobic fitness, physical activity status, and body composition on dimensions of cardiac interoceptive accuracy, sensibility, and awareness, assessed using both heartbeat tracking and heartbeat discrimination tasks.
>
> Hypotheses: Physiological markers of aerobic fitness, self-reported physical activity status, and body composition will be positively associated with cardiac interceptive accuracy, sensibility, and awareness for both tracking and discrimination tasks.

Chapter 5: Effect of a 4-week Exercise Intervention on Aerobic Fitness and Interoception.

Aim: To examine the causal relationship between aerobic fitness and interoception using a 4-week exercise intervention.

Hypotheses: The 4-week exercise intervention will significantly improve markers of aerobic fitness. Measures of cardiac interoception (accuracy, sensibility, awareness) will increase after 4-weeks of training. Changes in cardiac interoception will be positively associated with changes in measures of aerobic fitness and negatively correlated with resting heart rate.

Chapter 6: Cardiac Interoception does not Influence Exercise Tolerance during Constant Load Cycling Exercise.

Aim: To examine the relationship between interoceptive ability and tolerance to fixed intensity exercise, assessed using a constant load cycling task.

Hypotheses: Greater interoceptive accuracy will result in a reduced time-to-task failure. Further, more accurate heartbeat perceivers will demonstrate greater changes in cardiac and respiratory dynamics in response to comparable changes in physical activity and metabolic demand.

Chapter 7: The Effect of Cardiac Interoception on the Regulation of Exercise Work Rates and Physiological Responses at Fixed Ratings of Perceived Exertion.

Aim: To investigate the influence of cardiac interoception on exercise behaviour and physiological responses to exercise at fixed ratings of perceived exertion for both light (RPE10) and hard-to-very hard (RPE16) intensity exercise.

Hypotheses: Greater heartbeat perception accuracy will be associated with lower exercising work rates and markers of physiological strain (e.g., lower heart rates) for a given RPE condition.

CHAPTER 3. GENERAL METHODS

3.1. Introduction

This chapter describes the methods, materials, and equipment commonly used in the experimental chapters of this thesis. Any alternative, additional, or modified methods are described within the methods section of the specific experimental chapter. All data were collected in the laboratories at the University of Brighton (Welkin Human Performance Laboratories, Eastbourne, UK).

3.2. Health and Safety

All experimental procedures were conducted according to the University of Brighton's standard operating procedures, health and safety procedures, and risk assessment laboratory guidelines. Accordingly, risk assessments were completed for all experimental studies, accounting for risks and hazards associated with the use of the laboratories, exercise procedures, and invasive techniques such as capillary blood sampling. Biological materials and sharps, such as lancets, were discarded into designated biohazard waste or sharps containers, according to the relevant guidelines. All apparatus was cleaned before and after use. Equipment used for gas collection (i.e., face masks and turbines) were soaked in a biocide solution (Virkon, Day-Impex, Essex, UK) for a minimum of 10-minutes, rinsed with water, and dried before further usage. All other equipment, such as cycle ergometers were cleaned using disinfectant surface spray (Bioguard, UK) or alcohol wipes.

3.3. Ethical Approval

All studies in this thesis were granted favourable ethical approval from the University of Brighton Research Ethics and Governance Committee and conducted in accordance with the guidelines outlined in the Declaration of Helsinki 1964, as revised in 2013, except for registration in a database.

3.4. Participants

Both males and females were recruited for the purpose of this research project. Participants were included into the study if they were: healthy, aged 18-35 yrs, engaged in regular physical activity and accustomed to exhaustive exercise. Individuals were recruited from the University of Brighton student cohort and members of the local community via posters, emails, and social media. Recruitment material included a brief summary of the study and contact details of the lead investigator to invite further information if interested. Prospective participants were provided with a study-specific participant information sheet that: outlined the background to the study, provided details regarding each laboratory visit, as well as an explanation of requirements, risks and benefits associated with participation in the study. Participants were invited to ask questions regarding the study before providing written consent to undertaking the research. Participants were informed that they could withdraw from the study (including withdrawing consent for the use of their data) at any time without providing justification or explanation, and without incurring any penalty or prejudice. Additionally, contact details for the University of Brighton Doctoral College were provided to participants to offer a contact, independent of the research team, to discuss any potential issues or concerns related to the research. Before each study, participants were asked to complete a medical questionnaire and informed consent form. Participants were excluded from the research if they had any recent history of musculoskeletal injury or reported any respiratory, cardiovascular, or haematological morbidities. Additionally, individuals were excluded if they presented with any medical condition that contradicted engagement in maximal exercise. Finally, experimental sessions were terminated if any of the following criteria were encountered:

- At the request of the participant, for which no explanation was required.
- At the discretion of the experimenter, whether it be for equipment issues, or the participant displaying signs of discomfort or illness, including, but not limited to chest pain, dyspnea, nausea, vomiting, generic pain/discomfort, faintness, or dizziness.

The privacy, rights, and dignity of the participants were maintained at all times.

3.5. Confidentiality and Data Protection

All research was conducted in accordance with the Data Protection Act 1998. Data were collected and stored confidentially and anonymously, with participants assigned a numerical identifier. Further, all data were stored on a locked institutional computer with password access restricted to the lead investigator only. All written data and forms will be kept locked and disposed of as confidential waste after a period of ten years.

3.6. Pre-Trial Considerations

Participants were required to refrain from strenuous exercise (48 h), alcohol (24 h), and caffeine (12 h) consumption prior to each visit and were asked to arrive at the laboratory in a rested and hydrated state, at least 2-h postprandial. Each participant undertook testing at the same time of day ± 1 h, to minimise the influence of circadian rhythm on cycling performance (Teo, Newton, & McGuigan, 2011). Participants performed exercise in running trainers and appropriate clothing (i.e., sports shorts, t-shirt).

3.7. Anthropometry

3.7.1. Stature

Stature was measured using a fixed stadiometer (SECA 220 Stadiometer Attachment, Cranlea, Birmingham, UK). Participants were required to stand unshod in the anatomical position facing away from the stadiometer. The stadiometer arm was lowered until it rested horizontally on the most superior aspect of the head. Stature was recorded to the nearest 0.1 cm.

3.7.2. Body Mass

Body mass was recorded to the nearest 0.1 kg using weighing scales (SECA 778 Scales, Cranlea, Birmingham, UK). Participants were required to stand in minimal athletic clothing (t-shirt, shorts, and socks) on the plate until the digital display stabilised.

3.7.3. Body Composition

Skinfold thickness was obtained from the right side of each participant whilst stood in the anatomical position under ambient laboratory conditions. The thickness of each skinfold was measured to the nearest 1-mm from four sites using calibrated Harpenden skinfold callipers (Rosscraft, Canada). Subscapular skinfold was identified by raising 1cm below the inferior angle of the scapular at an approximate 45° angle to the horizontal plane. Triceps skinfold was located on the posterior aspect of the medial triceps at the midpoint between the olecranon process and the acromion process with the hand in a supinated position. The biceps skinfold was located at the anterior aspect of the biceps, at the same level as the triceps skinfold. Iliac crest was measured as a diagonal fold raised immediately above the crest of the ilium on a vertical line from the mid-axilla. Body density was calculated in accordance with Durnin and Womersley (1974) using the following equations dependent on individual participant characteristics.

Equation 1. Calculation of Body Density for Adult Males (Durnin & Womersley, 1974)

$$\text{Body Density} = 1.1610 - 0.0632\text{Log} \sum \text{Iliac Crest, Subscapular, Triceps, Biceps}$$

Equation 2. Calculation of Body Density for Adult Females (Durnin & Womersley, 1974)

$$\text{Body Density} = 1.1559 - 0.0717\text{Log}\sum \text{Iliac Crest, Subscapular, Triceps, Biceps}$$

Following the determination of body density, body fat percentage was calculated according to the method described below.

Equation 3. Calculation of percentage body fat for human populations (Siri, 1956)

$$\text{Percentage Body Fat} = (4.95 - 4.5) \text{ x } 100$$

3.8. Environmental Conditions

All exercise was conducted in ambient conditions maintained at 20-25°C using industrial air conditioning. No control was made for humidity or atmospheric pressure.

3.9. Heartbeat Detection

3.9.1. Set-up

Fingertip pulse oximetry was used to measure pulse, which represents a reliable tool for estimating heart rate at rest (Iyriboz, Powers, Morrow, Ayers, & Landry, 1991). The Nonin OEM development kit was used for pulse oximetry and comprised of a soft sensor oximeter, interface board, and XPOD (XPOD OEM III, Nonin Medical Inc., Plymouth, MN, USA) (Figure 3.1). The development kit was connected to a personal computer (Hewlett Packard, Palo Alto, USA) using a mini-12 connector. A soft sensor was preferred over a hard-plastic clip sensor as it minimises the pressure on the index finger, reducing unwanted sensory feedback on the sensation of a pulse. A medium soft sensor was used in most cases. For testing, the soft sensor was attached to the index finger of the non-dominant hand, the finger was positioned towards the end of the sensor such that the nail bed was directly underneath the light emitting diode, with the hand and arm rested on a soft cushion. Participants were seated throughout the heartbeat detection protocol. Particular attention was given to ensuring that: watches and jewellery were removed from the wrist and hands, legs remained uncrossed, the computer screen was positioned such the participants were unable to view the screen, and minimal ambient noise was present whilst conducting the test.

Interoceptive testing was conducted using a proprietary script with a deployable graphic user interface developed at the University of Sussex and executed using commercially available numerical computer software (MATLAB version 9.2, The MathWorks Inc., Natick, MA, 2017). The script and graphic user interface allowed for the assessment of both the heartbeat tracking and heartbeat discrimination tasks.

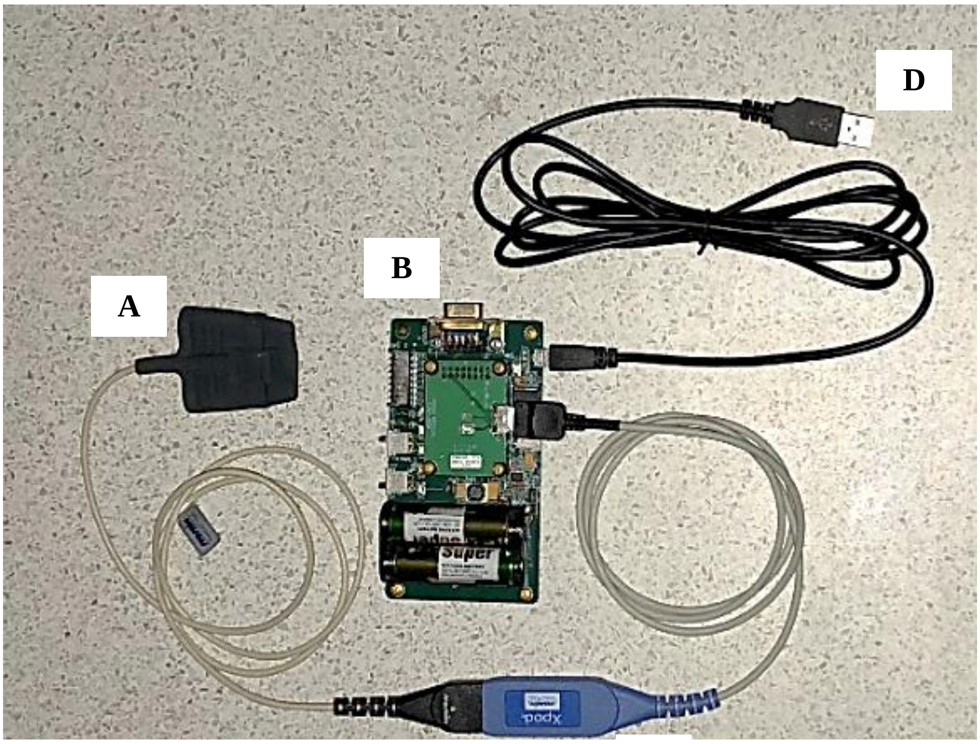
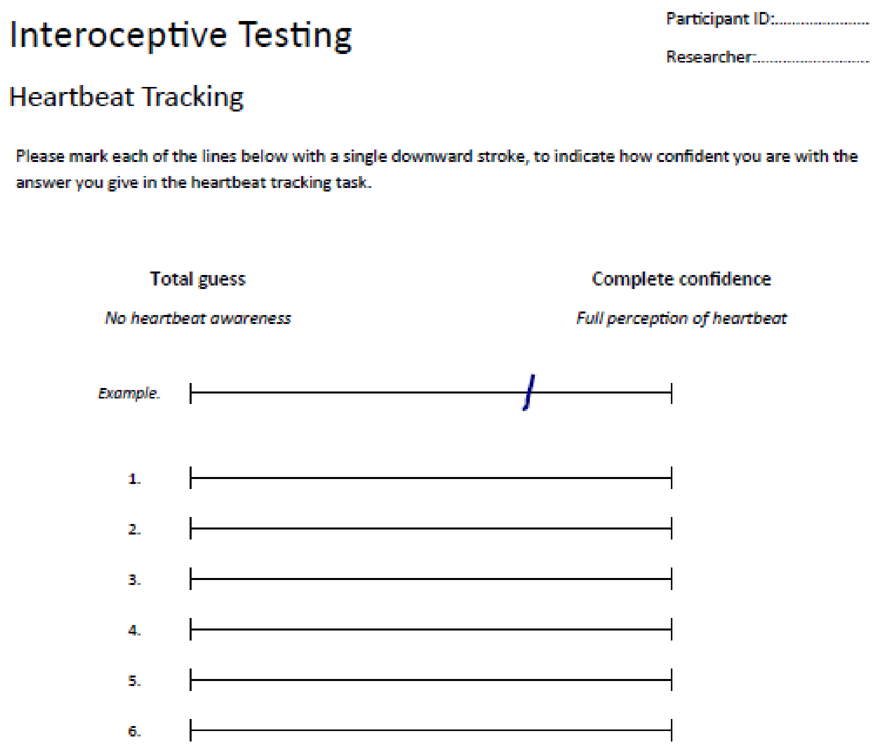


Figure 3.1. Nonin pulse oximeter set-up for heartbeat perception testing. A = soft sensor fingertip pulse oximeter, B = interface board, C = Nonin XPOD, D = mini-12 connector.

3.9.2. Procedure

Prior to testing, participants were instructed on the requirements of the two tasks and familiarised with the confidence rating scale. For both tasks, a trial of 20-s duration was provided for familiarisation. To ensure consistency between all participants, only a single familiarisation trial for each of the tasks was provided. Furthermore, familiarisation to the discrimination task was only performed following completion of the heartbeat tracking task as the audible tones produced during the familiarisation would disclose undesirable information to the participant regarding their heart rate. The confidence scale is a bipolar, continuous visual analogue scale with no intermediate marker points, anchored at opposing ends with verbal indicators of ‘*no confidence at all’* and ‘*complete confidence*’ respectively (Figure 3.2).


Interoceptive Testing

Participant ID:......................

Researcher:..........................

Heartbeat Tracking

Please mark each of the lines below with a single downward stroke, to indicate how confident you are with the answer you give in the heartbeat tracking task.

Total guess — *No heartbeat awareness*

Complete confidence — *Full perception of heartbeat*

Example.

1.

2.

3.

4.

5.

6.

Figure 3.2. Example visual analogue scale (VAS) confidence sheet used to examine cardiac interoceptive sensibility.

For reasons previously described, and in all instances, participants completed the heartbeat tracking task before undertaking the heartbeat discrimination task. For the tracking task, participants were required to silently count the number of heartbeats felt during an undisclosed period indicated by verbal commands of ‘start’ and ‘stop’ produced by the software and PC. At the end of each trial participants were required to report the number of heartbeats felt as well as providing a confidence rating of the accuracy of their perception, denoted by a single vertical pen stroke on the visual analogue scale. In total, each participant completed one familiarisation trial and six experimental trials of 25, 30, 35, 40, 45, and 50 seconds in duration, which were presented in a randomised order. The duration of these trials is made in accordance with original task descriptions (Garfinkel et al., 2015; Schandry, 1981). Although little attention has been given to examining the optimal duration for these trials, Schandry (1981) states that short time windows negate interference from low-frequency cardiac variability on task performance, ensuring that for each trial heart rate remains relatively stable. Further, it is likely that longer trial durations may permit error in heartbeat counting (i.e., losing track of the count), emanating from temporary loss of concentration or boredom.

Participants then completed the heartbeat discrimination task. The discrimination task required participants to make synchronicity judgements between a series of audible tones and the perception of their own heartbeat. Reporting of these judgements was made through simple ‘in sync’ or ‘out of sync’ responses and a subsequent rating of confidence. For synchronous conditions, audible tones were presented at systole (~300-ms after the R-wave); and in non-synchronous conditions, audible tones were presented 250-ms after systole (~550-ms after the R-wave). The respective delays in the presentation of audible tones is in accordance with published findings on synchronicity judgments between audible tones and heartbeat perception (*see* p.40, Wiens & Palmer, 2001). In total, testing was comprised of one familiarisation trial of 20-s duration and 20 experimental trials comprised 10 audible tones per trial.

3.9.3. Analysis

Accuracy in the heartbeat tracking task was assessed by comparing differences between the number of reported heartbeats ($n\text{beats}_{\text{reported}}$) and the number of heartbeats estimated via the pulse oximeter ($n\text{beats}_{\text{recorded}}$) in each trial and examined using the equation below (Equation 4). An overall score for interoceptive accuracy was determined as the mean average of the accuracy scores across all trials.

Equation 4. Calculation of Heartbeat Tracking Accuracy (Hart, McGowan, Minati, & Critchley, 2013).

$$\text{Heartbeat Tracking Accuracy} = 1 - \frac{|n\text{beats}_{\text{recorded}} - n\text{beats}_{\text{reported}}|}{(n\text{beats}_{\text{recorded}} + n\text{beats}_{\text{reported}})/2}$$

In the heartbeat discrimination trial, accuracy was assessed using the number of correct trials (defined as either true positive (hit) or true negative (correct rejection)) relative to the total number of trials (Equation 5).

Equation 5. Calculation of Heartbeat Discrimination Accuracy

$$\text{Heartbeat Discrimination Accuracy} = \frac{\sum(\text{True Positives} + \text{True Negatives})}{\sum \text{Total Trials}}$$

Sensibility for both tracking and discrimination trials was determined using the visual analogue scale for confidence. Scores were determined through visual inspection using an appropriately scaled measurement template. The template is a 'ruler' type 11-point scale from 0 to 10 with minor indentations every 0.2. Scores were recorded to the nearest 0.1. Individual values for confidence were mean averaged within each of the heartbeat perception tasks to give a sensibility measure for both the tracking and discrimination tasks.

Interoceptive awareness was determined as the strength of the relationship between confidence and accuracy. For the tracking task, awareness was calculated using the Pearson correlation coefficient (r) between the accuracy and confidence scores for each individual. Stronger positive correlational values are indicative of greater interoceptive awareness in the heartbeat tracking task. For the discrimination task, interoceptive awareness was determined using receiver operator characteristic (ROC) analysis, performed using SPSS (versions 22-24, IBM, New York, USA). Firstly, correct (true positive and true negative) and incorrect (false positive and false negative) responses were converted to binary numerals (1 = True, 0 = False`) and inputted into the ROC curve analysis as the state variable with confidence scores designated as the dependent variable. Interoceptive awareness was determined using area under the curve (AUC) analysis. Greater positive values are associated with better interoceptive awareness.

3.10. Cardiopulmonary Measurements

3.10.1. Metabolic Gas Analysis

Indirect calorimetry was assessed using expired gases, measured by means of an online gas analysis system (MetaLyzer 3B, Cortex, Germany) with data analysed offline using an associated software package (Metasoft, Cortex, Germany). It's reported that this system demonstrates excellent repeatability when considering values obtained for $\dot{V}O_2$ (r = .97), $\dot{V}CO_2$ (r = 0.96) and $\dot{V}_E$ (r = .95) during graded cycling exercise (Meyer, Georg, Becker, & Kindermann, 2001).

Set-up and calibration of the online gas analysis system were performed in accordance with the manufacturer's instructions for barometric pressure, gas sensors, and flow volume prior to each use. Barometric pressure was obtained from a wall-mounted barometer (Weather Station, Oregon Scientific, Oregon, USA). Gas sensor calibration was performed using a 2-point calibration process of known O_2 and CO_2 concentrations, referred to as Gas 1 and Gas 2, that were sampled until stabilisation of sensors had been achieved. Gas 1 represented gas concentrations observed in ambient air, and Gas 2 reflected the gas concentrations of expired air. Gas 1 (O_2 = 20.93%, CO_2 = 0.05%) was taken directly from the ambient environment. Gas 2 (O_2 = 15%, CO_2 = 5%) was drawn from a contained gas cylinder into a clamp sealed collection bag which was immediately affixed to the sample line. Flow volume calibration required simulated inspiration and expiration via manual syringe (3L, Hans Rudolph, Germany) for 5 acceptable cycles eliciting a flow rate of between 2 and 4 $L.s^{-1}$.

3.10.2. Heart Rate

Heart rate was recorded continuously by short-range telemetry from a moistened chest strap reporting to an electronic wristwatch, which sampled data at 1 Hz (A300 Fitness Watch, Polar Electro Oyo, Temple, Finland).

3.11. Exercise

3.11.1. Cycle Ergometry

Exercise testing was predominantly performed on an SRM cycle ergometer (High Performance Ergometer with Rohloff Gear Hub, SRM, GmbH, Jülich, Germany). The ergometer regulates resistance to pedalling forces using an electromagnetic brake, constraining the dependent variable of either power output or cadence. Power output was measured using a crank-based power meter, sampling at a rate of 2 Hz, and cadence sensor. Zero offset calibration of the power meter was completed prior to every exercise test, in accordance with the manufacturer's instructions. Accuracy of the power meter has previously been reported to ± 1% error, when appropriately calibrated (Abbiss, Quod, Levin, Martin, & Laursen, 2009). Further, Hopker and colleagues (2010) report that the SRM cycle ergometer has a coefficient of variability of 2.9% (95% CI 2.4 - 3.8 %) at lower PO's in untrained individuals (50 – 200 W) and 1.6% (95% CI 1.3 - 2.1 %) at higher PO's in aerobically trained individuals (150 – 300 W).

Participants were allowed to adjust the saddle height, saddle fore and aft, handlebar height, and handlebar reach during their first visit. Individual positions were recorded and replicated for all subsequent exercise tests. A fixed cycling cadence of 80 $r \cdot min^{-1}$ was used for all exercise testing to minimise potential effects on physiological responses, perception of exertion, and changes in cycle efficiency at differing cadences (Jacobs, Berg, Slivka, & Noble, 2013; Löllgen, Ulmer, & Nieding, 1977).

3.11.2. Fast Ramp Graded Exercise Testing (fast-RT)

Participants performed a fast-RT using the cycle ergometer. For studies 1, 3, and 4 (Chapters 4, 6, and 7) the fast-RT consisted of a 3-minute rest period, 5-minute warm-up at 60W, and 2-minute rest period before commencing the graded exercise test at a starting intensity between 80 and 160 W (based on experimenter judgement of the participant's aerobic fitness) with stepwise increases of 20 W at the end of every minute. For study 2 (Chapter 5), participants completed a fast-RT comprised of a 3-minute warm-up at 60W immediately followed by increases in work rate of 20 $W \cdot min^{-1}$. Termination criteria for the tests were as follows: when the participant reached a point of volitional exhaustion; an inability to maintain a cadence above 75 $r \cdot min^{-1}$ for a period of more than 5 seconds, despite strong verbal encouragement; at the request of the participant; or based on any of the termination criteria outlined in section 3.4.

3.11.3. Peak Oxygen Uptake

Peak oxygen uptake ($\dot{V}O_{2\ peak}$) was used to estimate participant's aerobic capacity and intensity for the subsequent testing protocols. Expired gases and f_c obtained from the fast-RT were analysed offline using second-by-second interpolation of the breath-by-breath data. $\dot{V}O_{2\ peak}$ was defined as the highest value obtained from a rolling 15-s average of the data.

3.11.4. Blood Lactate

Blood lactate concentrations ($[La^-]_c$) were obtained from a fingertip capillary blood sample using lithium-heparin coated microvette tubes (CB300, Sarsedt, Germany). Prior to collection, the fingertip was cleaned with an alcohol wipe, left to air dry before being punctured with a single-use lancet (Accu-Chek Safe T-Pro, Roche Diagnostics, West Sussex, UK). Blood samples were analysed for $[La^-]_c$ using an automated, electrochemical lactate and glucose analyser (YSI 2300, Yellow Springs Instruments, Ohio, USA).

3.11.5. Determination of Ventilatory Thresholds

Ventilatory thresholds 1 and 2 (VT_1 and VT_2, respectively) were also identified using the method of ventilatory equivalents (Figure 3.3; Bhambhani & Singh, 1985; Lucia, Hoyos, Perez, & Chicharro, 2000). Accordingly, VT_1 was identified as the first systematic increase in the ventilatory equivalent for oxygen ($\dot{V}_E \cdot \dot{V}O_2^{-1}$) with no concomitant increase in the ventilatory equivalent for carbon dioxide ($\dot{V}_E \cdot \dot{V}CO_2^{-1}$). Confirmation of this threshold was established using the V-slope method examining the departure of $\dot{V}CO_2$

from a line of identity drawn through a plot of $\dot{V}CO_2$ and $\dot{V}O_2$. VT_2 was determined using the criteria of an increase in $\dot{V}_E \cdot \dot{V}CO_2^{-1}$. Identification of these thresholds was made by the lead investigator and corroborated by an independent observer. If there was disagreement, the opinion of a third party was sought.

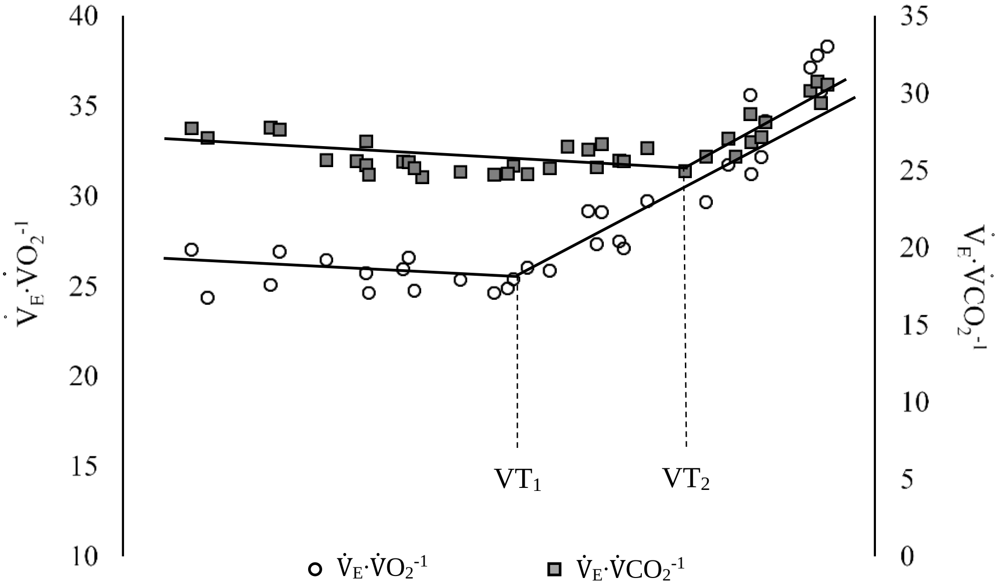


Figure 3.3. Determination of the first (VT_1) and second (VT_2) ventilatory thresholds using the ventilatory equivalent for oxygen ($\dot{V}_E \cdot \dot{V}O_2^{-1}$) and the ventilatory equivalent for carbon dioxide ($\dot{V}_E \cdot \dot{V}CO_2^{-1}$). Solid lines represent bisectional lines of best fit for the ventilatory equivalent data. Dashed lines are used to indicate the identification of the inflection point in the data, which is used to indicate the ventilatory thresholds.

3.11.6. Calculation of Exercise Intensity as a Percentage of Peak Oxygen Uptake

A linear relationship between exercise intensity (PO) and oxygen uptake ($\dot{V}O_2$) has been previously described (Joyner & Coyle, 2008). Based on this assumption, $\dot{V}O_2$ ($L.min^{-1}$) was plotted against the equivalent power output (W), and the slope (*m*) and intercept (*c*) of the linear relationship was identified (Figure 3.4). The maximum recorded $\dot{V}O_2$ ($L \cdot min^{-1}$) was then multiplied by the fraction of the target exercise intensity (e.g., 80% $\dot{V}O_{2\ peak} = 0.8 \cdot \dot{V}O_{2\ peak}$) to give an equivalent $\dot{V}O_2$ value.

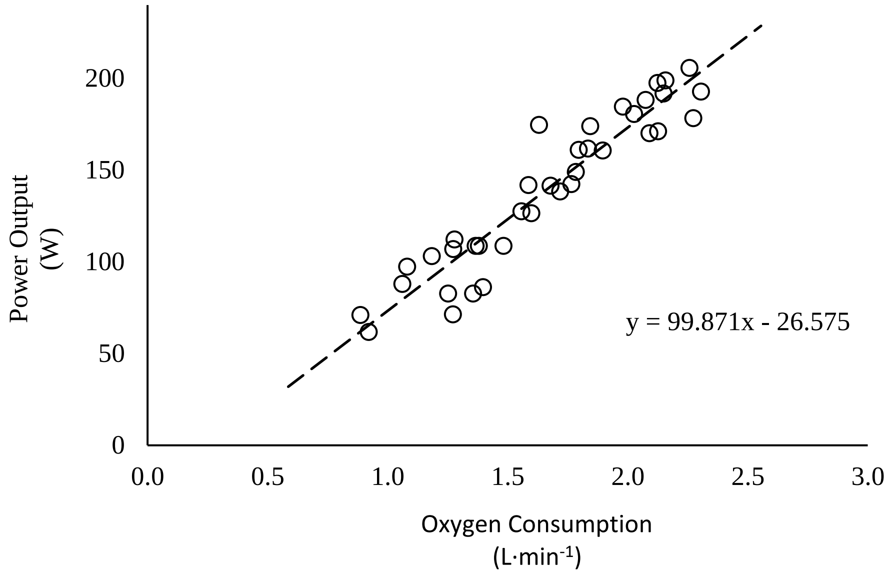


Figure 3.4. The relationship between oxygen consumption and power output for an individual participant. The dashed line represents the line-of-best fit that was used to interpolate exercise intensities at a percentage of $\dot{V}O_{2\ peak}$.

3.12. Perceptual Measurements

3.12.1. Rating of Perceived Exertion

Rating of perceived exertion (RPE) quantifies perceived exertion during exercise using a 15-point Borg scale (Figure 3.5; Borg, 1982). The scale consists of numbered categories with verbal anchors presented for alternate values on the scale as shown in Figure 3.3. As previously described, this 15-point scale for perceived exertion has been validated in healthy adult populations (Chen, 1998). In terms of reliability, test-retest correlation coefficients of 0.72 – 0.97 have previously been reported under various contexts (Lamb, Eston, & Corns, 1999). Taken together, these findings suggest that the 15-point Borg scale is acceptable in terms of validity and reliability as a psychometric tool for assessing participant's perception of physiological strain during whole-body exercise.

RATING OF PERCEIVED EXERTION

6	
7	Very, very light
8	
9	Very light
10	
11	Light
12	
13	Somewhat hard
14	
15	Hard
16	
17	Very hard
18	
19	Very, very hard
20	

Figure 3.5. Borg's (1982) 15-point scale for rating of perceived exertion.

3.13. Statistical Analysis

3.13.1. Data Processing

Processing of data, as well as formatting of figures and tables, was performed using a commercially available spreadsheet programme (Excel 2016, Microsoft Corp., USA). Statistical analysis was performed using SPSS statistical software package (SPSS versions 22-24, IBM Corp, USA).

3.13.2. Power Analysis

The number of participants required for each experimental chapter was determined using G*Power v3.1 in accordance with established guidelines for *a priori* determination (Lakens & Evers, 2014). Effect sizes (see section 3.9.3), relating to the primary dependent variables for each experimental chapter were obtained based upon published data utilising similar experimental designs reporting mean and standard deviation. The required number of participants was calculated based upon conventional α (0.05) and β (0.20) and an effect size obtained from a relevant study.

3.13.3. Descriptive Statistics

Parametric data are presented as mean ± standard deviation (SD). Non-parametric data are presented as median and interquartile range.

3.13.4. Cardiac Interoception Group Allocation

For the purpose of this thesis, accuracy in the heartbeat discrimination task was used as the principal criteria for categorising individuals as ‘good’ (GOOD) or ‘poor’ (POOR) perceivers. The reason for this was twofold. Firstly, the heartbeat discrimination task is more robust to temporal estimation procedures compared with the heartbeat tracking task, which may be a particularly relevant confound in physically active populations who have access to heart rate measuring devices (Desmedt et al., 2020; Phillips et al., 1999). Secondly, accuracy reflects a core interoceptive construct underpinning both sensibility and awareness (Garfinkel et al., 2015). For this thesis, group demarcation was determined according to the median score for the sample, with POOR $\leq \tilde{x} <$ GOOD. This approach is less conservative than signal detection methods used by others (Whitehead et al., 1977), which often allocates a large proportion of individuals as poor perceives due to the stringent *d'* criterion. These differences in group size can result in heterogeneity issues in subsequent comparisons. To account for this more liberal group allocation procedure, and also to negate potential issues related to the dichotomisation of samples (*see* Section 2.3.3), application of a 95% confidence interval (95% CI) was applied to the two groups (GOOD, POOR) in this thesis. Based on 95% CI, participants with heartbeat discrimination accuracy scores located between the median sample score and the adjacent CI boundary were removed from the subsequent between-groups analyses. This procedure ensured that the groups were distinct from each other. Furthermore, the use of the 95% CI criterion is not dependent on researcher judgement (which could emanate from heuristic or visual methodologies). It is also superior to arbitrary numerical methods (e.g., removing a percentage of the sample) as it reflects the specific distribution of the data within each group.

3.13.5. Statistical Significance

Statistical significance was assessed using the typical *p*-value approach. P-values express the probability, when the null hypothesis is true, that the statistical summary would be the same as, or greater than, the observed results. The threshold *p*-value for statistical significance in all experiments within this thesis was set at 5% ($a = 0.05$). This threshold assumes 95% confidence in controlling for Type I error rates.

3.13.6. Tests of Normality and Sphericity of Data

Testing for normality and sphericity were used to examine Gaussian assumptions of the distribution of data across a dataset, aiding the correct determination of approach to statistical assessment (Field, 2013). Normality was assessed using Shapiro-Wilks test. This approach was preferred as it provides a conservative test of normality and is particularly suitable to sample sizes of less than 50 (Razali & Wah, 2011).

Sphericity was examined using Mauchly's test of sphericity. Non-significant results for Mauchly's test allowed for analysis in the ANOVA using 'assumed sphericity' (Field 2013). In cases where significant violations to the assumption of sphericity were observed, Greenhouse-Geisser correction was applied if Mauchly's value was $\leq .75$, Huynh-Feldt correction was used if Mauchly's value was $> .75$ (Field, 2013).

3.13.7. Statistical Tests of Difference

T-testing was used to determine whether the differences between two datasets were statistically significant. Within this thesis, *t*-testing was principally used to examine statistical differences between two different groups of individuals (independent samples). Where data violated the assumption of normality, Mann-Whitney U Test was used to examine differences between two groups.

Analysis of variance (ANOVA) was used to examine a statistical significance between multiple groups and/or factors. Within this thesis, two-way mixed-methods ANOVA was used to examine statistical effects between groups and factors. Details of the factors are provided in the data analysis section of each chapter. Follow-up *post hoc* comparisons were performed on the factors when statistically significant effects were observed in the ANOVA. For *post hoc* analysis, Bonferroni corrected *t*-tests were utilised due to their conservative estimation of the difference between multiple comparisons (Field, 2013). Bonferroni correction controls the familywise type 1 error rate by adjusted the statistical significance by the number of comparisons being performed. The Bonferroni corrections are also the most robust univariate technique should sphericity be violated.

3.13.8. Statistical Tests of Relationship

In this thesis, Pearson's *r* was used to provide a measure of the relationship between two variables that do not violate Gaussian assumptions, whereas Spearman's rho and Kendal's tau were used data violated these assumptions. These *r*-value statistics range between 1 and -1, with strong positive associations between two variables being closer to 1 and strong negative associations being closer to -1. Weak relationships between variables are expressed when the *r*-statistic is close to zero.

Correlations were performed as either: bivariate, partial, or repeated measures correlations. Bivariate correlations represented the simplest form of correlation and examined the relationship between two variables without controlling for any confounding factors. Whereas the partial correlation procedure examined the degree of association between two variables, whilst controlling for the potential effect of a third confounding variable.

Repeated measures correlations were used in Chapter 5 to examine the relationship between the two continuous variables while controlling for the effect of the categorical variable (i.e., the variance between participants) (Bakdash & Marusich, 2017; Bland & Altman, 1995). An adjusted model specification to the method used to model analysis of covariance (ANCOVA) is used to achieve this repeated-measures correlation approach. Repeated-measures correlations were performed in this thesis using the 'rmcorr package' developed by Bakdash and Marusich (2017) and executed in R (R Core Team). The application of repeated measures is advantageous as it facilitates an increased statistical power by allowing for the comparison of multiple data points per participant. Importantly, this approach also overcomes violations to the assumption of independence that is requisite for standard approaches to examining correlations.

Bootstrapping (1000 samples) was performed to provide 95% confidence intervals (95% CI) of the correlational coefficient. 95% CI provides stable estimates of the range of potential values that describe the likely 'true' strength of association between the two measured variables for the population, to a level of 95% confidence.

3.13.9. Effect sizes

Effect sizes provided a measure of the strength of a given phenomenon. In the context of this thesis, effect sizes are examined using standardised statistical measures. For tests of difference, effect sizes reported are partial eta squared (η_p^2), Hedge's *g*, or the *r* equivalent statistic for non-parametric data. For tests of relationship, effect sizes are reported in terms Pearson's correlation coefficient (*r*), Spearman's rho (r_s), or Kendal's tau (τ). This approach is based on the recommendations of Lakens (2013). Interpretation of effect sizes was made in accordance with Cohen's recommendation (Cohen, 1992).

Partial eta squared (η_p^2) was used as a measure of effect size when examining the statistical output from ANOVA (see section 3.9.6). Partial eta squared describes the ratio of variance associated with an effect, plus the effect and its associated error variance. The formula shares similarities with eta squared; however, it is considered a less biased estimator of effect size (Levine & Hullett, 2002). Interpretation of η_p^2 effect sizes was classified as small ($\eta_p^2 \geq 0.01$), medium ($\eta_p^2 \geq 0.06$), and large ($\eta_p^2 \geq 0.13$).

Hedges *g* was used to describe the standardized mean difference of effects for between-subjects designs. Hedges *g* was preferred to other standardised effect size approaches, such as Cohen's *d*, as it provides a more conservative estimate of effect size. This results in a more robust approach to examining effect sizes within small sample sizes ($n \leq 20$; Fritz, Morris, & Richler, 2012). Additionally, the use of pooled weighted standard deviations allows for examination between heteroscedastic samples. Interpretation of *g* was made in accordance with the following: where the effect size was identified as small ($g = 0.2$), medium ($g = 0.5$), and large ($g = 0.8$) based on established recommendations for the comparable Cohen's *d* effect size measure. For data that violated assumptions of normality the *r* equivalent effect size statistic (Equation 6) was used according to the recommendations of Fritz, Morris, and Richler (2012). This effect size is interpreted according to the same criteria as Hedge's *g*.

Equation 6. The formula for the *r*-equivalent effect size statistic. Z = *z*-distribution, N = number of samples.

$$r = \frac{Z}{\sqrt{N}}$$

For correlations, R-value statistics provided by Pearson's correlation coefficient and Spearman's rank correlation coefficient were used to provide an estimate of the strength association (i.e., effect size) between two variables. Interpretation of R-value effect sizes were classified as small ($r \geq 0.1$), medium ($r \geq 0.3$), and large ($r \geq 0.5$).

CHAPTER 4. THE RELATIONSHIP BETWEEN AEROBIC FITNESS, PHYSICAL ACTIVITY AND INTEROCEPTION.

4.1. Abstract

The first study aimed to examine the association between cardiac interoception and aerobic fitness. Twenty-eight physically active participants completed tests to determine cardiac interoception and aerobic fitness and were also assessed for mood state and physical activity status. For statistical analysis, participants were retrospectively allocated to a good (GOOD: N = 10) or poor (POOR: N = 11) cardiac interoception group, based on a median demarcation and 95% confidence intervals using heartbeat discrimination accuracy data. GOOD (i.e., $\dot{V}O_{2\ peak}$ 4.05 ± 0.92 $L{\cdot}min^{-1}$) demonstrated greater aerobic fitness compared with POOR (3.05 ± 0.66 $L{\cdot}min^{-1}$). GOOD were also found to engage in a greater quantity of vigorous physical activity (GOOD: 4400 ± 3165 $METs{\cdot}wk^{-1}$; POOR: 1783 ± 1416 $METs{\cdot}wk^{-1}$), although no significant differences were observed for walking and moderate physical activity ($p > .05$). GOOD also exhibited significantly lower resting heart rates (GOOD: 56 ± 12 $b{\cdot}min^{-1}$; POOR: 75 ± 10 $b{\cdot}min^{-1}$) and lower body compositions (GOOD: 14.7 ± 6.8 % body fat; POOR: 21.5 ± 6.0 % body fat) compared with POOR. Partial correlations further revealed that heartbeat discrimination accuracy exhibited the most robust relationship to markers of aerobic fitness compared with other measures of cardiac interoception obtained from heartbeat tracking and discrimination tasks. No significant differences were observed between GOOD and POOR for mood state. Consequently, the findings of this study support the relationship between aerobic fitness and interoception, particularly when this relationship is assessed according to heartbeat discrimination accuracy.

4.2. Introduction

The term interoception is used to describe the sensation and perception of signals related to the physiological condition of the body (Vaitl, 1996). During interoception, the brain receives inputs from a broad taxonomy of receptors and small diameter afferent neurons which are selectively sensitive to changes in variables such as temperature, pH, and substrate availability, among others (Cameron, 2001). Perception of these changes is often vague and difficult to interpret; nevertheless, the information conveyed within this interoceptive network is strongly implicated in the aetiology of emotional experience

(Dunn, Galton, et al., 2010) and behaviour (Bechara & Damasio, 2005; Bechara et al., 1996; Werner, Duschek, et al., 2009). Therefore, understanding the mechanisms that influence interoception is important in gaining a full understanding of human behaviour.

Interoception is known to differ between individuals, with some demonstrating greater sensitivity to internal physiological signals than others (Garfinkel et al., 2015). Objective assessment of interoceptive sensitivity typically involves the use of either functional imaging data or performance in psychometric tests of awareness of organ-specific activity (Garfinkel et al., 2016; Jones et al., 2015; Schandry, 1981). Predominant among this latter class of interoceptive assessment are tests of cardiac perception. Cardiac perception tests involve the assessment of either: the ability to accurately count the number of heartbeats over an undisclosed period of time (heartbeat tracking task; Schandry, 1981), or the ability to make synchrony judgments between the timing of heartbeats and a series of external cues, such as an audible beep (heartbeat discrimination task; Whitehead, Drescher, Heiman, & Blackwell, 1977).

Several factors are suggested to influence performance in these interoceptive tests (Vaitl, 1996). Included among these is cardiovascular fitness. For instance, Jones and Hollandsworth (1981) reported that adult male distance runners demonstrated better performance in a cardiac perception test than moderately fit and sedentary individuals. A similar finding has also been reported in adolescents, with the subjects categorised within the good interoceptive group having a significantly higher measure of aerobic fitness compared with the poor interoceptive group (Georgiou et al., 2015). It has been argued that the augmented physiological feedback experienced during strenuous or prolonged physical activity improves the awareness and sensitivity to these inputs (Hollandsworth 1979, cited in Montgomery et al., 1984). However, these observations have not always been replicated in other studies (Herbert et al., 2007; Machado et al., 2019; Montgomery et al., 1984).

Understanding of this question has so far been confounded by the indirect approach used to assess aerobic fitness using self-report questionnaires (Jones & Hollandsworth, 1981; Montgomery et al., 1984), field tests (Georgiou et al., 2015), and submaximal performance tests (Herbert, Ulbrich, et al., 2007) which demonstrate weaker validity and reliability compared with direct physiological assessment techniques obtained using indirect calorimetry and graded exercise protocols. For instance, the validity of self-reported measures of physical activity (Mäder, Martin, Schutz, & Marti, 2006) and aerobic fitness (Hagströmer, Oja, & Sjöström, 2006) are considered to be poor compared to criterion measures and subject to reporting bias (Dyrstad, Hansen, Holme, & Anderssen, 2014). Similarly, for field-based assessments, learning effects have been previously reported that may contribute to measurement error in aerobic fitness assessment (Lim, Lambrick, Mauger, Woolley, & Faulkner, 2016; Metaxas, Koutlianos, Kouidi, & Deligiannis, 2005). Consequently, greater certainty is warranted in establishing the strength of the relationship between direct measures of aerobic fitness (i.e., strong face validity) and cardiac interoception.

One explanation for the conflicting findings with regards to the relationship between interoception sensitivity and aerobic fitness may lie in the adaptations associated with aerobic exercise training. Lower resting heart rates and body composition have all been reported to correspond with better interoceptive performance (Knapp-Kline & Kline, 2005; Rouse, Jones, & Jones, 1988). However, these factors are not always solely influenced by levels of chronic physical activity but also by factors such as genetic predisposition (Wang et al., 2009), diet (Vrieze et al., 2010), and age (Kostis et al., 1982). It is also possible that for the heartbeat tracking task, performance in physically active individuals may additionally be biased by prior knowledge of resting heart rate (Ring et al., 2015) gained through the use of heart rate monitoring devices. So, the question remains as to whether aerobic fitness does influence interoceptive parameters, or whether it is merely a biproduct of these other related factors.

This study aimed to overcome these previous limitations and provide a more direct examination of the relationship between aerobic fitness (assessed using indirect calorimetry and a graded exercise task) and interoception (using both heartbeat tracking and heartbeat discrimination tasks). It was hypothesised that greater accuracy in heartbeat perception would be positively associated with markers of aerobic fitness. Testing this hypothesis, differences in aerobic fitness between good and poor heartbeat perceivers were examined first, along with measures of self-reported physical activity and physiological characteristics such as age, gender, body composition, and resting heart rate. Subsequently, follow-up analysis explored the strength of the observed effects, exploring relationships between interoception and aerobic fitness whilst controlling for other physiological covariates related to typical adaptions associated with, but not exclusively contingent on aerobic fitness, such as body composition and resting heart rate.

4.3. Methods

4.3.1. Participants

Following institutional ethical approval, 28 participants (15 males, 13 females; age 23 ± 3 yrs; stature 173 ± 9 cm; mass 69.4 ± 9.6 kg) volunteered to participate in this study. Participants were recruited from the University of Brighton and local sports clubs. All participants were healthy and accustomed to exercise of a maximal nature.

4.3.2. Procedure

Participants visited the laboratory on a single occasion. On arrival, participants were reminded about the purpose and procedures of the study before completing a health history questionnaire, consent form, as well as providing a subjective assessment of typical physical activity using the International Physical Activity Questionnaire (IPAQ) and an assessment of current mood state using the Brunel University Mood Scale (BRUMS).

Participants then undertook the interoceptive assessment protocol following the methods outlined in section 3.9.2. Following interoceptive testing, stature and body mass were obtained according to the procedures outlined in section 3.3. Body density was then estimated using skinfolds measured at four sites: subscapular, biceps, triceps, and iliac crest using the method of Durnin and Womersley (1974), with body composition estimated using the Siri equation (Siri, 1956). Skinfold sites were identified by standardised procedures (Stewart, Marfell-Jones, Olds, & Al., 2011) and measured using skinfold callipers (Harpenden skinfold callipers, Baty International, UK)).

Finally, participants undertook the exercise testing. Testing was performed on an electronically braked cycle ergometer (High Performance Ergometer with Rohloff Gear Hub, SRM, GmbH, Jülich, Germany), which was calibrated in accordance with the methods outlined in section 3.11.1. Participants were instrumented with a heart rate monitor (A300 Fitness Watch, Polar Electro Oyo, Temple, Finland) and face mask connected to an online gas-analysis system (Metasoft, Cortex, Germany) as well as being fitted to the cycle ergometer. The online gas system was calibrated prior to all testing (Section 3.10.1). Participants were reminded of the procedures and requirements of the exercise test and familiarised with the RPE scale (6-20 Borg scale; Borg, 1982). The procedure for the exercise testing consisted of an initial 3-minute rest period sat stationary on the ergometer, a 5-minute warm-up at 60W pedalling at 80 $r \cdot min^{-1}$, a 2-minute rest period, and a graded exercise test to volitional exhaustion. The graded exercise test consisted of a stepwise increase in power output of 20 W at the end of each minute, with initial power output estimated based on the experimenter's judgement of the participants' aerobic fitness (80 - 160 W). Participants were required to maintain a cadence of 80 $r \cdot min^{-1}$ throughout the test. The test continued until one of the following criteria was observed: a reduction in cadence below 75 $r \cdot min^{-1}$ for more than 5-s despite strong verbal encouragement or at the request of the participant. Expired gases were recorded continuously throughout the testing procedure.

4.3.3. Data Analysis

Cardiac Interoception

Measures of accuracy, sensibility, and awareness were determined using both the heartbeat tracking task and heartbeat discrimination task according to the methods outlined in section 3.9.3.

Aerobic Fitness

Participant's aerobic fitness was determined based on the identification of two distinct ventilatory responses observed during the graded exercise test. These ventilatory responses are referred to as the first ventilatory threshold (VT_1) and second ventilatory threshold (VT_2), which were identified according to the methods outlined in section 3.11.5. $\dot{V}O_{2\,peak}$ (Section 3.11.3) and cycling efficiency (Section 3.11.7) were determined in accordance with the methods previously described.

Physical Characteristics

Body composition was determined using the methods outlined in section 3.7.3 and was based on the body density formula of Durnin and Womersley (1974), which accounts for differences in gender and age. Body composition was calculated using the Siri (1956) equation (Section 3.7.3). Finally, body mass index (BMI) was determined as the function of body mass and stature (Equation 7).

Equation 7. Calculation of body mass index (BMI).

$$Body\ mass\ index\ = \frac{body\ mass\ (kg)}{stature\ (m)^2}$$

Mood Scale and Physical Activity Status

Scores for each of the components on the mood scale for BRUMS were categorised into either ‘Anger’, ‘Confusion’, ‘Depression’, ‘Fatigue’, ‘Tension’, and ‘Vigour’. In total there were four components within each category, resulting in a maximum score of 16 for each category.

Physical activity status was calculated based on the International Physical Activity Questionnaire (IPAQ) long-form version, which uses self-report to quantify physical activity across walking as well as moderate-intensity and vigorous-intensity activity domains.

Statistical Analysis

For between-groups analyses, participants were retrospectively allocated as good (GOOD) or poor (POOR) heartbeat perceivers according to a median demarcation of the HBD accuracy data (GOOD > $\tilde{x}$ ≥ POOR). HBD accuracy was selected as the HBD task is considered more robust to temporal estimation bias compared with HBT (Phillips et al., 1999), with accuracy representing the ‘core perceptual construct’ underpinning both confidence and awareness (Garfinkel et al., 2015). The groups were further differentiated by application of 95% confidence intervals (95%CI) to each group, removing participants with accuracy scores located between the sample median value and the adjacent 95%CI boundary. Inclusion of this later approach was employed to minimise a potential limitation associated with dichotomising samples based on continuous variables (Altman & Royston, 2006), namely the issue of characterising participants with scores close to (but on opposite sides) of the cut-off being considered distinctly different from one another (*see* Figure 2.3 for an illustration of this issue).

Data were analysed using the methods described in section 3.13. Further exploration of the relationship between aerobic fitness and cardiac interoception was examined using partial correlations. Partial correlational analysis examined the relationships between interoceptive measures (accuracy, sensibility, and awareness) for both tracking and discrimination tasks against markers of aerobic fitness (PO and $\dot{V}O_2$ at VT_1, VT_2, and Peak) when controlling for age, gender, body composition, and resting heart rate.

4.4. Results

4.4.1. Interoception

Mean accuracy, sensibility, and awareness scores for the heartbeat discrimination task across all participants were: 0.60 ± 0.19, 5.6 ± 2.2, 0.48 ± 0.16 respectively. For the heartbeat tracking task, mean scores for accuracy, sensibility and awareness scores were: 0.78 ± 0.20, 4.2 ± 2.0, 0.37 ± 0.49 respectively. Correlations revealed a significant relationship between sensibility measures ($r_{(28)} = .75$, $p < .01$, 95% CI = [.52, .89]) but no significant relationships for accuracy ($r_{s(28)} = .35$, $p = .07$, 95% CI = [-.05, .65]) or awareness measures ($r_{s(28)} = .09$, $p = .65$, 95% CI = [-.39, .50]) between the tracking and discrimination tasks.

Median demarcation of the data according to heartbeat discrimination accuracy resulted in 12 participants being allocated to GOOD and 16 participants being allocated to POOR. Application of the 95% CI criterion resulted in two participants being removed from GOOD and 5 participants being removed from POOR. Therefore, 10 participants were entered into the subsequent analysis for GOOD (7M, 3F) and 11 for POOR (4M, 7F).

Between groups differences in scores for accuracy, sensibility, and awareness across both heartbeat perception tasks are shown below in Table 4.1. Analysis revealed that GOOD displayed greater discrimination accuracy ($t_{(19)} = 9.2$, $p < .01$, $g = 4.02$) and awareness ($t_{(19)} = 2.2$, $p = .045$, $g = .91$) and were also found to exhibit greater sensibility for both the tracking ($t_{(19)} = 2.2$, $p = .04$, $g = .93$) and discrimination tasks ($t_{(19)} = 2.7$, $p = .02$, $g = 1.09$) compared with POOR. However, no significant differences were observed between groups for either tracking accuracy ($t_{(19)} = 1.0$, $p = .40$, $g = .44$) or tracking awareness ($t_{(19)} = -0.8$, $p = .43$, $g = .34$).

Table 4.1. Measures of cardiac interoception for good (GOOD) and poor (POOR) heartbeat perceiver groups for both heartbeat tracking and heartbeat discrimination tasks.

	Heartbeat Tracking			Heartbeat Discrimination		
	Accuracy	Sensibility	Awareness	Accuracy	Sensibility	Awareness
GOOD	0.79 ± 0.19	5.0 ± 2.1*	0.28 ± 0.58	0.76 ± 0.07*	6.3 ± 1.6*	0.54 ± 0.18*
POOR	0.69 ± 0.24	3.1 ± 1.7	0.48 ± 0.54	0.39 ± 0.12	4.2 ± 2.0	0.37 ± 0.13

* $p < .05$.

4.4.2. Aerobic Fitness

Aerobic fitness measures are reported in Table 4.2. The data showed that, with the exception of $\dot{V}O_2$ at VT_1 ($p = .11$, $g = .73$), values for PO (W) and $\dot{V}O_2$ were significantly greater in GOOD at VT_1, VT_2, and Peak with large-to-very large differences evident for these measures of aerobic fitness (p's < .05; g's > .90). Interestingly, relative PO ($\%PO_{peak}$) were not significantly difference between the two groups at VT_1 ($p = .72$, $g = .16$) and VT_2 ($p = .10$, $g = .87$). GOOD exhibited significantly lower $f_{c\ rest}$ than POOR ($p < .01$, $g = 1.69$) despite no significant differences between the two groups in their $f_{c\ peak}$ ($p = .37$, $g = .34$). Furthermore, no differences were evident between the two groups when considering cycling efficiency, either in terms of gross efficiency ($p = .69$, $g = .15$) or net efficiency ($p = .85$, $g = .10$).

Table 4.2 Aerobic fitness measures for power output (PO) and oxygen consumption (VO_2) at first ventilatory threshold (VT_1), second ventilatory threshold (VT_2), and peak (Peak) as well as measures of cycling efficiency and heart rate for good (GOOD) and poor (POOR) heartbeat perceivers.

		GOOD (N = 10)	POOR (N = 11)	*t*-statistic	*p*-value	Hedge's *g*
VT_1	PO (W)	195 ± 76	132 ± 32	2.4#	.03*	1.11
	PO ($\%PO_{peak}$)	56 ± 10	54 ± 13	0.4	.72	.16
	$\dot{V}O_2$ ($L \cdot min^{-1}$)	2.27 ± 0.77	1.73 ± 0.32	2.1	.047*	.94
	$\dot{V}O_2$ ($mL \cdot kg^{-1} \cdot min^{-1}$)	33 ± 10	27 ± 6	1.7	.11	.73
VT_2	PO (W)	278 ± 63	185 ± 30	4.2#	< .01*	1.93
	PO ($\%PO_{peak}$)	82 ± 4	75 ± 10	1.7	.10	.87
	$\dot{V}O_2$ ($L \cdot min^{-1}$)	3.35 ± 0.60	2.34 ± 0.57	3.9	< .01*	1.68
	$\dot{V}O_2$ ($mL \cdot kg^{-1} \cdot min^{-1}$)	49 ± 8	35 ± 6	4.3	< .01*	1.97
Peak	PO (W)	341 ± 75	247 ± 44	3.5	< .01*	1.54
	$\dot{V}O_2$ ($L \cdot min^{-1}$)	4.05 ± 0.92	3.05 ± 0.66	2.9	< .01*	1.24
	$\dot{V}O_2$ ($mL \cdot kg^{-1} \cdot min^{-1}$)	59 ± 12	45 ± 8	3.0	< .01*	1.37
Cycling Efficiency (%)	Gross	21.5 ± 2.2	21.1 ± 2.9	0.4	.69	.15
	Net	27.1 ± 3.6	26.8 ± 3.0	0.2	.85	.10
Heart Rate ($b \cdot min^{-1}$)	Rest	56 ± 12	75 ± 10	3.9	< .01*	1.69
	Peak	184 ± 11	187 ± 6	0.9	.37	.34

W = watts, $L \cdot min^{-1}$ = absolute oxygen consumption measured in litres per minute, $mL \cdot kg^{-1} \cdot min^{-1}$ = relative oxygen consumption measured in millilitres per kilogram per minute, * $p < .05$ # = non-parametric.

4.4.3. Physical Characteristics

Physical characteristics were examined in terms of age, stature, body mass, BMI, and body composition (Table 4.3). Analysis of the data revealed that participants in GOOD had lower body compositions (p = .03, g = 1.04) were also older (p < .01, g = 1.93) than those in POOR. However, no significant differences were observed for stature, body mass, or BMI between the two groups (p's > .20).

4.4.4. Physical Activity Status

Data for physical activity are reported below (Table 4.3). Self-reported physical activity data indicated that GOOD engaged in greater quantities of vigorous physical activity compared with POOR, with a very large effect size evident for this difference (p = .02, g = 1.09). However, the two groups were not different for other measures of physical activity, which encompassed either walking (p = .17, g = .59) or moderate physical activity (p = .39, g = .37). Furthermore, the total quantity of reported physical activity across all domains was also not significantly different between GOOD and POOR (p = .26, g = .50).

4.4.5. Mood Profiles

Scores for individual items on the Brunel Mood Scale are shown in Table 4.3. Data for the between-groups differences failed to achieve the threshold for statistical significance for any of the individual items including anger (p = .41, r = .16), confusion (p = .64, r = .09), depression (p = .89, r = .03), fatigue (p = .19, r = .25), tension (p = .19, r = .25), and vigour (p = .97, r = .01).

Table 4.3. Physical characteristics, self-reported physical activity data (International Physical Activity Questionnaire: IPAQ), and mood states (Brunel University Mood Scale: BRUMS) for good (GOOD) and poor (POOR) heartbeat perceivers.

		GOOD (N = 10)	POOR (N = 11)	Test statistic	*p*-value	ES
Physical Characteristics	Age (yrs)	24 ± 2	21 ± 1	3.8	< .01*	1.93
	Stature (cm)	175 ± 8	170 ± 9	1.3	.20	.57
	Mass (kg)	69.0 ± 8.6	68.8 ± 12.6	< 0.1	.96	.02
	BMI ($kg \cdot m^{-2}$)	22.5 ± 1.8	23.6 ± 2.6	1.1	.27	.47
	Body Composition (%)	14.7 ± 6.8	21.5 ± 6.0	2.4	.03*	1.04
IPAQ ($METs \cdot wk^{-1}$)	Walking	1388 ± 1228	2401 ± 1926	1.4	.17	.59
	Moderate	1732 ± 985	1278 ± 1334	0.9	.39	.37
	Vigorous	4400 ± 3165	1783 ± 1416	2.5	.02*	1.09
	Total	7520 ± 3874	5462 ± 4142	1.2	.26	.50
BRUMS (a.u.)	Anger	0 (0 - 0)	0 (0 - 0.5)	47.0†	.41	.16
	Confusion	0 (0 - 0)	0 (0 - 0.5)	50.0†	.64	.09
	Depression	0 (0 - 0)	0 (0 - 0)	54.0†	.89	.03
	Fatigue	3.5 (3 - 4.75)	3 (1.5 - 3.5)	36.5†	.19	.25
	Tension	0 (0 - 1)	2 (0.5 - 2)	37.5†	.19	.25
	Vigour	7 (6 - 8.5)	8 (4.5 - 9.5)	54.5†	.97	.01

Test statistic = t-statistic for parametric data or Mann-Whitney U for non-parametric data, ES = effect size (Hedges *g* for parametric data, *r* for non-parametric data), yrs = years, cm = centimetres, kg = kilogram, $kg \cdot m^{-2}$ = kilogram per square metre, $METs \cdot wk^{-1}$ = metabolic equivalent of tasks per week (1 MET ≙ 3.5 $mL \cdot kg^{-1} \cdot min^{-1}$), a.u. = arbitrary units

4.4.6. Correlational analysis

Correlational analyses were performed to examine covariance between measures of aerobic fitness and interoception whilst accounting for confounding variables of age, gender, body composition, and resting heart rate. For this analysis, the two groups were collapsed, and participants that were removed using the 95% CI criterion were reincluded into the dataset (N = 28). The correlational analysis for each control variable is displayed in Tables 4.4 (bivariate), 4.5 (age), 4.6 (gender), 4.7 (% body fat), and 4.8 ($f_{c\ rest}$). Correlations revealed positive relationships between discrimination accuracy and markers of aerobic fitness when controlling for age, gender, and body composition, particularly for fitness parameters obtained at VT_2. Additionally, significant positive relationships for tracking accuracy and peak oxygen consumption ($\dot{V}O_{2\ peak}$) when controlling for age, gender, and body composition but not for other measures of aerobic fitness. Significant positive relationships were also observed for discrimination awareness with PO at VT_2 and Peak when controlling for body composition. No significant correlations were observed for other measures of cardiac interoception. Notably, relationships between all measures of cardiac interoception and aerobic fitness were found to be non-significant when accounting for the influence of $f_{c\ rest}$, indicating that $f_{c\ rest}$ exerted the greatest influence on measures of cardiac interoception.

Table 4.4. Bivariate correlations between measures of aerobic fitness and heartbeat perception. VT_1 = first ventilatory threshold, VT_2 = second ventilatory threshold, PO = power output, $L \cdot min^{-1}$ = oxygen consumption measured in litres per minute, $mL \cdot kg^{-1} \cdot min^{-1}$ = oxygen consumption measured in millilitres per kilogram per minute, * $p < .05$.

	Tracking Accuracy				Tracking Sensibility				Tracking Awareness			
	Correlation	Sig	95% CI Lower	95% CI Upper	Correlation	Sig	95% CI Lower	95% CI Upper	Correlation	Sig	95% CI Lower	95% CI Upper
VT_1 PO	.29	.17	-.02	.57	.01	.97	-.26	.26	.35	.09	.08	.55
VT_1 $L \cdot min^{-1}$	.25	.25	-.19	.53	.00	.98	-.29	.26	.35	.09	.02	.60
VT_1 $mL \cdot kg^{-1} min^{-1}$	.26	.22	-.14	.53	.11	.61	-.21	.41	.25	.23	-.10	.51
VT_2 PO	.24	.25	-.14	.53	.07	.75	-.26	.39	.15	.48	-.27	.52
VT_2 $L \cdot min^{-1}$	.14	.50	-.30	.52	-.02	.93	-.37	.32	.15	.50	-.32	.58
VT_2 $mL \cdot kg^{-1} min^{-1}$	.13	.54	-.34	.49	.08	.70	-.34	.44	.03	.91	-.42	.47
Peak PO	.31	.14	-.05	.61	.12	.56	-.15	.40	.12	.59	-.29	.46
Peak $L \cdot min^{-1}$	.31	.14	-.06	.63	.01	.96	-.26	.29	.01	.97	-.40	.37
Peak $mL \cdot kg^{-1} min^{-1}$	.25	.24	-.14	.58	.07	.75	-.28	.37	-.02	.92	-.40	.36

	Discrimination Accuracy				Discrimination Sensibility				Discrimination Awareness			
	Correlation	Sig	95% CI Lower	95% CI Upper	Correlation	Sig	95% CI Lower	95% CI Upper	Correlation	Sig	95% CI Lower	95% CI Upper
VT_1 PO	.29	.18	-.29	.65	.35	.09	.02	.63	.17	.42	-.43	.63
VT_1 $L \cdot min^{-1}$	.35	.09	-.33	.75	.36	.08	.10	.59	.21	.33	-.47	.66
VT_1 $mL \cdot kg^{-1} min^{-1}$	.42*	.04	-.09	.72	.32	.13	.02	.56	.25	.23	-.41	.67
VT_2 PO	.40	.05	-.16	.74	.40	.05	.10	.65	.30	.15	-.23	.65
VT_2 $L \cdot min^{-1}$	.32	.13	-.24	.74	.32	.13	.01	.60	.18	.41	-.32	.62
VT_2 $mL \cdot kg^{-1} min^{-1}$	.43*	.04	.00	.73	.28	.19	-.09	.57	.25	.25	-.23	.61
Peak PO	.24	.26	-.30	.65	.44	.03	.20	.69	.13	.55	-.39	.56
Peak $L \cdot min^{-1}$	.27	.20	-.23	.65	.32	.13	-.01	.64	.05	.81	-.43	.52
Peak $mL \cdot kg^{-1} min^{-1}$	.42*	.04	.02	.69	.29	.16	-.01	.58	.17	.44	-.34	.55

Table 4.5. Partial correlation between measures of aerobic fitness and heartbeat perception whilst controlling for age. VT_1 = first ventilatory threshold, VT_2 = second ventilatory threshold, PO = power output, $L\cdot min^{-1}$ = oxygen consumption measured in litres per minute, $mL\cdot kg^{-1}\cdot min^{-1}$ = oxygen consumption measured in millilitres per kilogram per minute, * $p < .05$.

	Tracking Accuracy				Tracking Sensibility				Tracking Awareness			
	Correlation	Sig	95% CI		Correlation	Sig	95% CI		Correlation	Sig	95% CI	
			Lower	Upper			Lower	Upper			Lower	Upper
VT_1 PO	.22	.28	-.09	.46	.16	.44	-.37	.56	-.01	.98	-.40	.32
VT_1 $L\cdot min^{-1}$	.19	.35	-.19	.46	.25	.21	-.24	.61	.08	.70	-.29	.40
VT_1 $mL\cdot kg^{-1}min^{-1}$	.35	.08	-.03	.59	.13	.53	-.33	.59	.08	.71	-.40	.42
VT_2 PO	.32	.11	.01	.58	.30	.14	-.17	.66	.05	.82	-.37	.39
VT_2 $L\cdot min^{-1}$	.11	.59	-.22	.47	.38	.05	-.04	.67	.05	.82	-.29	.43
VT_2 $mL\cdot kg^{-1}min^{-1}$	.32	.11	-.04	.61	.30	.14	-.09	.63	.04	.86	-.34	.40
Peak PO	.33	.10	-.05	.58	.27	.19	-.21	.64	.13	.51	-.25	.47
Peak $L\cdot min^{-1}$	.32	.11	-.04	.59	.33	.10	-.21	.71	.21	.29	-.13	.51
Peak $mL\cdot kg^{-1}min^{-1}$	.50*	.01	.15	.70	.22	.27	-.22	.65	.14	.49	-.22	.47

	Discrimination Accuracy				Discrimination Sensibility				Discrimination Awareness			
	Correlation	Sig	95% CI		Correlation	Sig	95% CI		Correlation	Sig	95% CI	
			Lower	Upper			Lower	Upper			Lower	Upper
VT_1 PO	.39	.05	.04	.64	.12	.57	-.37	.48	.35	.08	.04	.64
VT_1 $L\cdot min^{-1}$	.28	.17	-.07	.52	.18	.39	-.34	.57	.17	.41	-.16	.50
VT_1 $mL\cdot kg^{-1}min^{-1}$	.35	.08	-.05	.59	.16	.43	-.32	.56	.26	.21	-.16	.63
VT_2 PO	.59*	>.01	.34	.78	.23	.26	-.16	.58	.35	.08	.05	.62
VT_2 $L\cdot min^{-1}$	.50*	.01	.18	.75	.18	.38	-.20	.51	.22	.29	-.07	.50
VT_2 $mL\cdot kg^{-1}min^{-1}$	.64*	>.01	.32	.85	.20	.32	-.12	.49	.31	.13	-.05	.62
Peak PO	.45*	.02	.11	.71	.15	.45	-.29	.57	.36	.07	.01	.65
Peak $L\cdot min^{-1}$	.39	.05	-.01	.69	.16	.45	-.30	.57	.29	.16	.02	.57
Peak $mL\cdot kg^{-1}min^{-1}$	.51*	>.01	.11	.76	.18	.39	-.17	.48	.35	.08	-.00	.64

Table 4.6. Partial correlation between measures of aerobic fitness and heartbeat perception whilst controlling for gender. VT_1 = first ventilatory threshold, VT_2 = second ventilatory threshold, PO = power output, $L{\cdot}min^{-1}$ = oxygen consumption measured in litres per minute, $mL{\cdot}kg^{-1}{\cdot}min^{-1}$ = oxygen consumption measured in millilitres per kilogram per minute, * $p < .05$.

	Tracking Accuracy				Tracking Sensibility				Tracking Awareness			
	Correlation	Sig	95% CI		Correlation	Sig	95% CI		Correlation	Sig	95% CI	
			Lower	Upper			Lower	Upper			Lower	Upper
VT_1 PO	.15	.47	-.21	.43	.11	.58	-.41	.49	.02	.91	-.42	.33
VT_1 $L{\cdot}min^{-1}$	.12	.57	-.31	.42	.22	.28	-.28	.56	.11	.58	-.27	.44
VT_1 $mL{\cdot}kg^{-1}min^{-1}$	.33	.11	-.12	.60	.07	.75	-.38	.49	.11	.58	-.31	.46
VT_2 PO	.26	.20	-.13	.55	.26	.20	-.23	.58	.10	.63	-.32	.49
VT_2 $L{\cdot}min^{-1}$	<.01	>.99	-.32	.34	.37	.06	-.03	.63	.09	.68	-.30	.52
VT_2 $mL{\cdot}kg^{-1}min^{-1}$	.28	.16	-.10	.57	.25	.23	-.14	.56	.08	.69	-.29	.46
Peak PO	.24	.24	-.22	.55	.24	.24	-.24	.60	.20	.34	-.21	.54
Peak $L{\cdot}min^{-1}$	.16	.45	-.23	.48	.32	.11	-.18	.65	.25	.20	-.20	.58
Peak $mL{\cdot}kg^{-1}min^{-1}$	.44*	.02	.02	.69	.19	.36	-.23	.56	.20	.32	-.17	.55

	Discrimination Accuracy				Discrimination Sensibility				Discrimination Awareness			
	Correlation	Sig	95% CI		Correlation	Sig	95% CI		Correlation	Sig	95% CI	
			Lower	Upper			Lower	Upper			Lower	Upper
VT_1 PO	.39	.05	.04	.64	.12	.57	-.37	.48	.35	.08	.04	.64
VT_1 $L{\cdot}min^{-1}$	.28	.17	-.07	.52	.18	.39	-.34	.57	.17	.41	-.16	.50
VT_1 $mL{\cdot}kg^{-1}min^{-1}$	.35	.08	-/05	.59	.16	.44	-.32	.56	.26	.21	-.16	.63
VT_2 PO	.59*	<.01	.34	.78	.23	.26	-.16	.58	.35	.08	.05	.62
VT_2 $L{\cdot}min^{-1}$	.50*	.01	.18	.75	.18	.38	-.20	.51	.22	.29	-.07	.50
VT_2 $mL{\cdot}kg^{-1}min^{-1}$	.64*	<.01	.32	.85	.20	.32	-.12	.49	.31	.13	-.05	.62
Peak PO	.45*	.02	.11	.71	.15	.45	-.29	.57	.36	.07	.01	.65
Peak $L{\cdot}min^{-1}$	.39	.05	-.01	.69	.16	.45	-.30	.57	.29	.16	.02	.57
Peak $mL{\cdot}kg^{-1}min^{-1}$	.51*	<.01	.11	.76	.18	.29	-.17	.48	.35	.08	-.00	.64

Table 4.7. Partial correlation between measures of aerobic fitness and heartbeat perception whilst controlling for body composition. VT_1 = first ventilatory threshold, VT_2 = second ventilatory threshold, PO = power output, $L \cdot min^{-1}$ = oxygen consumption measured in litres per minute, $mL \cdot kg^{-1} \cdot min^{-1}$ = oxygen consumption measured in millilitres per kilogram per minute, * $p < .05$.

	Tracking Accuracy				Tracking Sensibility				Tracking Awareness			
	Correlation	Sig	95% CI Lower	95% CI Upper	Correlation	Sig	95% CI Lower	95% CI Upper	Correlation	Sig	95% CI Lower	95% CI Upper
VT_1 PO	.15	.47	-.21	.43	.11	.58	-.41	.49	.02	.91	-.42	.33
VT_1 $L \cdot min^{-1}$	.12	.57	-.31	.42	.22	.28	-.28	.56	.11	.58	-.27	.44
VT_1 $mL \cdot kg^{-1}min^{-1}$	.33	.11	-.12	.60	.07	.75	-.38	.49	.11	.58	-.31	.46
VT_2 PO	.26	.20	-.13	.55	.26	.20	-.23	.58	.10	.63	-.32	.49
VT_2 $L \cdot min^{-1}$	<.01	>.99	-.32	.33	.37	.06	-.03	.63	.09	.68	-.30	.52
VT_2 $mL \cdot kg^{-1}min^{-1}$	.28	.16	-.10	.57	.25	.23	-.14	.56	.08	.69	-.29	.46
Peak PO	.24	.24	-.22	.55	.24	.24	-.24	.60	.20	.34	-.21	.54
Peak $L \cdot min^{-1}$	.16	.45	-.23	.48	.32	.11	-.18	.65	.26	.20	-.20	.58
Peak $mL \cdot kg^{-1}min^{-1}$	.44*	.02	.02	.69	.19	.36	-.23	.56	.20	.32	-.17	.55

	Discrimination Accuracy				Discrimination Sensibility				Discrimination Awareness			
	Correlation	Sig	95% CI Lower	95% CI Upper	Correlation	Sig	95% CI Lower	95% CI Upper	Correlation	Sig	95% CI Lower	95% CI Upper
VT_1 PO	.31	.12	-.09	.61	.02	.93	-.49	.40	.37	.07	.08	.66
VT_1 $L \cdot min^{-1}$	.19	.35	-.15	.46	.09	.65	-.46	.46	.17	.42	-.15	.50
VT_1 $mL \cdot kg^{-1}min^{-1}$	.28	.16	-.11	.54	.05	.79	-.43	.44	.28	.17	-.13	.63
VT_2 PO	.54*	<.01	.29	.75	.11	.58	-.33	.46	.40*	.045*	.18	.63
VT_2 $L \cdot min^{-1}$	.42*	.03	.13	.69	.08	.70	-.29	.42	.22	.28	-.03	.51
VT_2 $mL \cdot kg^{-1}min^{-1}$	.60*	<.01	.31	.81	.08	.70	-.25	.37	.34	.09	.04	.60
Peak PO	.36	.07	-.00	.67	.04	.84	-.45	.48	.39*	.049*	.09	.64
Peak $L \cdot min^{-1}$	.24	.24	-.11	.57	.07	.73	-.41	.52	.25	.22	-.03	.57
Peak $mL \cdot kg^{-1}min^{-1}$	.44*	.03	.05	.72	.06	.76	-.32	.36	.39	.05	.08	.68

Table 4.8. Partial correlation between measures of aerobic fitness and heartbeat perception whilst controlling for resting heart rate. VT_1 = first ventilatory threshold, VT_2 = second ventilatory threshold, PO = power output, $L{\cdot}min^{-1}$ = oxygen consumption measured in litres per minute, $mL{\cdot}kg^{-1}{\cdot}min^{-1}$ = oxygen consumption measured in millilitres per kilogram per minute, * $p < .05$.

	Tracking Accuracy				Tracking Sensibility				Tracking Awareness			
	Correlation	Sig	95% CI		Correlation	Sig	95% CI		Correlation	Sig	95% CI	
			Lower	Upper			Lower	Upper			Lower	Upper
VT_1 PO	-.07	.75	-.41	.21	.05	.83	-.51	.49	.02	.93	-.37	.39
VT_1 $L{\cdot}min^{-1}$	-.08	.71	-.39	.19	.16	.44	-.33	.57	.11	.59	-.24	.44
VT_1 $mL{\cdot}kg^{-1}min^{-1}$	.13	.53	-.16	.36	-.09	.67	-.54	.44	.15	.48	-.31	.53
VT_2 PO	.02	.94	-.31	.38	.16	.44	-.30	.54	.08	.69	-.33	.43
VT_2 $L{\cdot}min^{-1}$	-.12	.34	-.53	.26	.30	.15	-.12	.61	.06	.79	-.31	.43
VT_2 $mL{\cdot}kg^{-1}min^{-1}$	.04	.84	-.28	.42	.10	.64	-.30	.51	.10	.65	-.27	.45
Peak PO	<.01	>.99	-.36	.33	.16	.44	-.27	.54	.15	.47	-.23	.53
Peak $L{\cdot}min^{-1}$	-.07	.73	-.54	.33	.28	.18	-.17	.62	.18	.39	-.19	.55
Peak $mL{\cdot}kg^{-1}min^{-1}$	.16	.44	-.24	.51	.08	.70	-.27	.48	.21	.31	-.12	.53

	Discrimination Accuracy				Discrimination Sensibility				Discrimination Awareness			
	Correlation	Sig	95% CI		Correlation	Sig	95% CI		Correlation	Sig	95% CI	
			Lower	Upper			Lower	Upper			Lower	Upper
VT_1 PO	.09	.69	-.21	.31	-.06	.78	-.58	.36	-.03	.91	-.33	.39
VT_1 $L{\cdot}min^{-1}$	-.04	.84	-.36	.16	.03	.91	-.50	.42	-.24	.26	-.49	.10
VT_1 $mL{\cdot}kg^{-1}min^{-1}$	-.04	.87	-.34	.19	-.12	.55	-.60	.31	-.15	.46	-.51	.23
VT_2 PO	.31	.13	-.04	.60	.05	.82	-.40	.43	-.14	.51	-.49	.29
VT_2 $L{\cdot}min^{-1}$	.24	.25	-.16	.58	.07	.74	-.32	.44	-.25	.23	-.57	.18
VT_2 $mL{\cdot}kg^{-1}min^{-1}$	.38	.06	-.11	.73	-.07	.75	-.46	.31	-.23	.27	-.57	.18
Peak PO	.12	.58	-.25	.41	.02	.93	-.40	.40	-.13	.52	-.52	.34
Peak $L{\cdot}min^{-1}$	.04	.85	-.35	.35	.09	.66	-.29	.44	-.25	.24	-.61	.21
Peak $mL{\cdot}kg^{-1}min^{-1}$	.11	.61	-.36	.47	-.06	.78	-.36	.18	-.23	.27	-.60	.25

4.5. Discussion

The current study aimed to assess the relationship between aerobic fitness and measures of interoception. The results supported the primary hypothesis indicating that individuals that were more accurate in perceiving their heartbeats were significantly fitter; as indicated by greater $\dot{V}O_{2\ peak}$, greater PO and $\dot{V}O_2$ at VT_1 and VT_2, and lower $f_{c\ rest}$ than their less interoceptively perceptive counterparts. Partial correlations revealed that this effect was most reliably observed for heartbeat discrimination accuracy, compared with other measures of cardiac interoception, when controlling for potentially confounding demographic factors for age, gender, and body composition. However, the relationship between cardiac interoception and aerobic fitness was not found to be independent of resting heart rate. The data also showed that good heartbeat perceivers had lower resting heart rates and lower body composition and also reported significantly greater engagement in vigorous physical activity compared with poor heartbeat perceivers. No significant group differences were observed for mood profiles.

4.5.1. Contextualising the Interoception Data

The cardiac interoceptive characteristics (as measured using heartbeat tracking and discrimination tasks) of physically active adults have not previously been addressed within the literature. The values for accuracy, sensibility, and awareness obtained from the present cohort (Section 4.4.1) were found to correspond closely with data previously reported for normative adult samples for both heartbeat tracking and heartbeat discrimination tasks (Forkmann et al., 2016; Garber et al., 2011; S. N. Garfinkel et al., 2015; Herman, Rae, Critchley, & Duka, 2019; Rae et al., 2020; Villani, Tsakiris, & Azevedo, 2019). Furthermore, correlational data between comparable measures obtained from the two heartbeat perception tasks (e.g., tracking accuracy vs discrimination accuracy) were largely in agreement with data recently reported in a pre-published meta-analysis (Hickman, Seyedalehi, Cook, Bird, & Murphy, 2020). Specifically, good agreement is found for the positive correlations reported for sensibility measures (meta-analysis reported pooled effect = .60, 95% CI = [.48, .70]) and also the non-significant correlations for interoceptive awareness (meta-analysis reported pooled effect = .09, 95% CI = [-.02, .20], p = .11). Similarly, despite disagreement in the statistical significance of the accuracy measures observed for the present study (r_s = .35, p = .07, 95% CI = [-.05, .65]) and the data reported by Hickman and colleagues (pooled effect = .21, 95% CI = [.13, .29], p < .01) the direction and strength of these relationships also appear in agreement. This suggests that the interoceptive data obtained from physically active populations conform to values previously observed for healthy adult populations.

4.5.2. Effect of Aerobic Fitness on Interoception

The principal finding of the present study supported a positive relationship between aerobic fitness and cardiac interoception, particularly when interoception is examined according to heartbeat discrimination accuracy. Specifically, GOOD were found to produce significantly greater VO_2 and PO at ventilatory thresholds and peak compared with POOR. This extends on existing evidence that had previously examined this relationship predominantly according to heartbeat tracking accuracy alone and also provides a stronger research design than before, by directly measuring both maximal and submaximal physiological parameters of aerobic fitness (Table 4.2). Interestingly, comparing the tracking and discrimination data from this study it was found that measures obtained from the discrimination task, particularly discrimination accuracy, demonstrated stronger and more robust relationships with aerobic fitness measures, particularly when accounting for the influence of variables such as body composition (Tables 4.4 – 4.7). Furthermore, it is notable that the strength of the effects obtained when comparing between GOOD and POOR, based on discrimination accuracy, in this study were also greater than those previously reported when participants are categorised according to performance in the tracking task (Georgiou et al., 2015; Herbert et al., 2007; Machado et al., 2019). This finding offers an insight into the equivocal findings reported across previous studies that have used tracking accuracy to assess this relationship, as weaker effects associated with the tracking task in relation to aerobic fitness may be more challenging to detect.

The disparity in findings reported in previous studies may also be explained by differences in the approaches used to assess aerobic fitness. Early studies, such as Jones et al. (1981) and Montgomery et al. (1984) relied on the use of self-report to subjectively quantify aerobic fitness by which individuals were allocated to different fitness groups. Self-report inventories, such as IPAQ, demonstrate acceptable test-retest repeatability (Craig et al., 2003) and criterion validity when compared to accelerometer data (Sallis & Saelens, 2000) but may demonstrate questionable construct validity when correlated to direct measures of physical fitness and body composition (Hagströmer et al., 2006). Whereas Georgiou et al. (2015) used a field-based approach to estimate aerobic fitness among their cohort, which is a more valid assessment of physical fitness but are still considered to be less accurate than lab-based protocols of indirect calorimetry, particularly due to the influence of learning effects (Metaxas et al., 2005). Consequently, the present study supports the relationship between aerobic fitness and cardiac interoception, suggesting that the strength of this relationship may be greater than previously reported. This finding supports the need for several methodological considerations related to the assessment of both interoception and aerobic fitness when examining this relationship.

4.5.3. Effect of Cardiodynamics on Interoceptive Ability

Cardiac parameters are presumed to influence performance in heart-based tests of interoception. For instance, lower resting heart rates and lower heart rate variability have been shown to correspond with better performance in tests of heartbeat perception (Ehlers & Breuer, 1992; Gaebler, Daniels, Lamke, Fydrich, & Walter, 2013; Knapp-Kline & Kline, 2005; Owens, Friston, Low, Mathias, & Critchley, 2018). This finding was supported in the present study, with GOOD observed to have significantly lower resting heart rates compared to the participants in the POOR. Furthermore, it was shown that the relationship between interoceptive measures and markers of aerobic fitness was not independent of resting heart rate characteristics, suggesting that this physiological factor exerts a substantial influence on a person's heartbeat perception.

Resting heart rates are known to decline with periods of continued exercise training (Blomqvist & Saltin, 1983), with changes in resting heart rate resulting from a combination of either structural changes to the myocardium and vasculature or functional adaptations to the neural systems involved in regulating the heart (Kang, Kim Eon-ho, & Ko, 2016; Melanson & Freedson, 2001). These changes in cardiac function are associated with improved heartbeat perception accuracy (*see* Section 2.3.3) with lower resting heart rates, greater stroke volume, increased measures of myocardial contractile force, and greater momentum of ejected blood mass, which have all been shown to be moderately and positively correlated with heartbeat perception accuracy (Schandry, Bestler, & Montoya, 1993). Ring and colleagues (1994) identified contractility as a particular factor mediating heartbeat perception. Importantly, cardiac contractility is influenced by afterload and preload characteristics, which are a function of the adaptations to myocardial structure commonly observed in aerobically-trained individuals (Fagard, 2003).

The amplitude of the neural signal associated with the processing of incoming sensory input from the heart (heartbeat evoked potential: HEP) are known to be influenced by a person's heart rate characteristics (MacKinnon et al., 2013) and are positively associated with performance in heartbeat perception (Montoya et al., 1993). HEP amplitudes have therefore been investigated as a potential neurophysiological correlate of cardiac interoception. In agreement with the present study, Perakakis and colleagues (2017) demonstrated that HEP amplitude in the occipitoparietal cluster was significantly greater in the physically-trained individuals compared with the sedentary individuals. Consequently, these findings support the influence of resting cardiodynamic characteristics on the ability to accurately detect heartbeats in tasks of heartbeat perception. Consequently, adaptations to the structure and function of the heart associated with regular physical activity appear to be a promising candidate for explaining enhanced performance in tasks heartbeat perception.

4.5.4. Physical Activity and Interoception

These results also showed that GOOD engaged in a significantly greater quantity of vigorous physical activity, but were similar regarding walking, moderate, and overall physical activity compared to poor heartbeat perceivers. This finding contrasted with that of Georgiou et al (2015) who reported that better heartbeat perception corresponded to greater engagement in low, but not moderate or high, intensity physical activity among adolescents. These differences could partly be explained by the methodologies used to examine daily activity, as previous studies have shown significant differences in the quantification of physical activity obtained using self-report compared with an activity-measuring device (Dyrstad et al., 2014; Lee, Macfarlane, Lam, & Stewart, 2011). Despite the contrasting findings, likely related to the different populations (adults vs adolescents), it is important to emphasise that both studies support the links between aerobic fitness and interoception. Therefore, it is perhaps reasonable to argue a generalised effect whereby regular physical activity stimulates adaptations that influence both physical fitness and perception of bodily signals.

The mechanisms underlying the link between physical fitness and interoceptive sensitivity have been discussed hitherto, with contrasting explanations (Georgiou et al., 2015; Montgomery et al., 1984). For instance, Montgomery et al. (1984) postulated that improvement in the ability to accurately perceive interoceptive stimuli result from repeated exposure to increased physiological arousal. Data from studies looking at the acute effects of augmented physiological arousal have demonstrated improved performance in tests of heartbeat perception (Jones & Hollandsworth, 1981; Schandry, Bestler, & Montoya, 1993). Moreover, several neuroimaging studies have shown that the insular cortex is activated during exercise (Hassanpour et al., 2018; Williamson et al., 2014). This brain region is a key neural structure in the processing of interoceptive stimuli (Craig, 2009; Critchley et al., 2004). Importantly, this assertion is supported by evidence whereby a positive association between grey matter density in the right anterior insula and aerobic fitness (Peters et al., 2009). However, Georgiou et al. (2015) suggested an alternative explanation that trait differences in interoception may influence health-based decisions to engage in physical activity. However, the evidence supporting this latter postulate is unclear and should therefore be interpreted with appropriate scrutiny.

4.5.5. Interoception and its Relationship with Physical Characteristics

In the present study, body composition was significantly lower in GOOD compared to POOR. This finding was in accordance with our predictions and is supported by previous research (Jones, Jones, Rouse, Scott, & Caldwell, 1987; Rouse et al., 1988). Importantly, this observation highlights potential issues associated with heartbeat perception tasks as a valid instrument for assessing a person's interoceptive characteristics. Specifically, it is suggested that lower body composition facilitates the somatosensory perception of visceral signals (Murphy, Geary, Millgate, Catmur, & Bird, 2018). This is potentially problematic as somatosensory perceptions are distinct from interoception, with their respective afference signals projecting along different neural pathways and subsequently processed within different cortical regions of the brain (Khalsa, Rudrauf, Feinstein, & Tranel, 2009). Despite these issues, the present study showed that differences in body composition, along with age and gender, could not account for the correlation observed between parameters of aerobic fitness and heartbeat discrimination accuracy, suggesting that the relationship between aerobic fitness and heartbeat discrimination accuracy is independent of these factors.

4.5.6. Effect of Interoception on Mood State

A large body of evidence supports a link between interoception on the experience of feelings and emotion (Barrett, Quigley, Bliss-Moreau, & Aronson, 2004; Dunn, Galton, et al., 2010). For instance, previous studies have reported positive relationships between markers of interoception and subjectively reported measures of anxiety (Critchley, Wiens, Rotshtein, Ohman, et al., 2004; Dunn, Stefanovitch, et al., 2010; Pollatos, Herbert, Kaufmann, et al., 2007), both cardiovascular and cognitive arousal (Herbert et al., 2010; Pollatos, Schandry, Auer, & Kaufmann, 2007), and fatigue (Harrison et al., 2009). However, this effect was not observed within our data. Indeed, no significant differences were observed between good and poor heartbeat perceivers for any of the seven profiled mood states within the Brunel University Mood Scale. The BRUMS questionnaire was selected in this study to examine mood states as it was previously developed for use among in physically-active adolescents and adults and has been validated across several subpopulations (Terry, Lane, & Fogarty, 2003; Terry & Lane, 2000; Hashim, Zulkifli, & Hanafi, 2010). Originally created as a shortened version of the Profile of Mood States (POMS), BRUMS has been used in applied settings in the screening of mood states among athletes (Galambos, Terry, Moyle, & Locke, 2005; Lan, Lane, Roy, & Hanin, 2012).

This study is the first to the author's knowledge to examine the relationship between interoception and reported mood states using the BRUMS questionnaire. Previous studies have typically employed questionnaires that evaluate specific mood states, for instance, The State Anxiety Inventory (Paulus & Stein, 2010). Dunn, Stefanovitch et al. (2010) have suggested that measurement of individual mood states using specific instruments rather than within combined inventories may produce greater measurement sensitivity. Even so, POMS-based questionnaires have previously been used to examine changes in mood states related to changes to interoceptive stimuli and have shown good construct validity, specifically related to the assessment of fatigue (Harrison et al., 2009).

4.5.7. Potential Limitations

The present study was predominantly limited by the cross-sectional research design. This limitation is a pervasive characteristic of all studies that have so far examined the relationship between aerobic fitness and interoception. Consequently, the exact mechanisms underpinning this relationship remain to be elucidated. Researchers have previously stipulated competing arguments suggesting that this relationship may result from either physiological adaptation (i.e., resting heart rate) or increased exposure to heightened interoceptive inputs associated with recurrent engagement in physical activity. The present study indicates support for both of these postulates, with evidence supporting positive associations with both physiological characteristics (i.e., $f_{c\ rest}$) and also engagement in vigorous-intensity exercise. Therefore, the findings of this present support the relationship between interoception and aerobic fitness but do not provide evidence supporting the causal basis of this effect. Consequently, future studies utilising exercise interventions are needed to afford greater clarity on the mechanisms involved.

4.5.8. Future Directions

The present study demonstrated a strong link between aerobic fitness and cardiac interoception in healthy physically active adults. However, further research is warranted to explore these effects across other cardiac interoceptive axes (i.e., respiratory or gastric) to determine whether these effects reflect generalisable changes in interoceptive perception or specific changes to the perception of cardiac afferents. Additionally, research in this area has so far predominantly focussed on these relationships in healthy young adults and adolescents. Consideration of other populations is, therefore, necessary and may be particularly relevant in clinical populations where atypical interoceptive experiences are indicated among the associated factors related to the morbidity (i.e., anxiety disorders, depression, eating disorders, as well as functional disorders related to the persistent experience of fatigue).

4.6. Conclusion

The present study is the first to examine the relationship between cardiac perception and aerobic fitness, directly assessed using indirect calorimetry. The results showed that better heartbeat perceivers were significantly more aerobically fit than poor heartbeat perceivers, supporting the previously presumed link between perceptual sensitivity to cardiac stimuli and aerobic fitness. This key finding suggests that exercise interventions provide a method to alter a person's perception of interoception feedback. Implications of this result extend to sporting contexts where interoceptive stimuli may influence exercise behaviours; as well as in clinical conditions where altered interoceptive perceptions form part of the underlying aetiology. However, further research using is required to substantiate the causal basis of these assertions.

CHAPTER 5. EFFECT OF A 4-WEEK EXERCISE INTERVENTION ON AEROBIC FITNESS AND INTEROCEPTION.

5.1. Abstract

The second study of this thesis aim to examine the effect of a 4-week exercise intervention on markers of aerobic fitness and interoception. Fourteen participants (mean ± SD: age 21 ± 2 years, stature 174 ± 6 cm, mass 69.3 ± 13.7 kg) completed 4 weeks of exercise training (EX). Another fourteen participants (mean ± SD: age 21 ± 2 years, stature 172 ± 8 cm, mass 67.5 ± 12.2 kg) acted as matched controls (paired-match based on peak power output; CON). Before the training intervention (PRE), participants completed: 1) assessment of cardiac interoception and resting heart rate ($f_{c\ rest}$), and 2) a multi-stage graded exercise test (MS-RT) to assess power output (PO) and oxygen consumption ($\dot{V}O_2$) at peak (PO_{peak} and $\dot{V}O_{2peak}$) and at a blood lactate concentration of 3 mmol·L^{-1}. The MS-RT was repeated on three separate occasions after the intervention, with tests separated by 7 days. The best (POST-BEST) and worst (POST-WORST) performances according to time-to-task failure were identified for each individual within the EX group. Participants in CON were matched to participants in EX. For CON, selection of POST-BEST and POST-WORST performance were made for each participant according to the corresponding MS-RT of their matched-pair in EX. The exercise intervention resulted in significant improvements in PO_{peak} for EX (POST-BEST: 277 ± 55 W; POST-WORST: 255 ± 61 W) when compared with PRE (235 ± 45 W) ($p < .05$). PO_{peak} for EX in POST-BEST was also found to be 29% greater compared with CON (215 ± 64 W) ($p < .05$) despite the groups being comparable at PRE (CON: 221 ± 61 W). Conversely, other physiological measures of aerobic fitness, $f_{c\ rest}$, and interoceptive measures remained unchanged ($p > .05$). However, despite these non-significant findings, repeated measures correlations of the data from EX revealed that heartbeat discrimination accuracy was significantly correlated with both $\dot{V}O_{2peak}$ ($r = .49$, $p < .01$) and $f_{c\ rest}$ ($r = -.40$, $p = .03$). These results support the relationships between a person's physiological characteristics and their heartbeat perception accuracy but also indicate that a 4-week exercise intervention was not sufficient to significantly influence cardiac interoception or some markers aerobic fitness.

5.2. Introduction

Interoception reflects a person's perception of the physiological condition of their body (Section 2.1), which has been shown to influence the experience of subjective feeling states (Section 2.4). Importantly, researchers have demonstrated that people vary significantly in their accuracy and awareness of interoceptive afferents, as indicated by performance in tasks of heartbeat perception (e.g., Garfinkel et al., 2015; Ludwick-Rosenthal, Neufeld, & Ludwick-Rosenthal, 1985). Differences in interoception have been shown to be associated with factors such as depression, anxiety, alexithymia, and empathy (Eggart et al., 2019; Montgomery & Jones, 1984; Murphy, Brewer, Hobson, Catmur, & Bird, 2018).

Considering the influence of interoception on psychological well-being, interventions aimed at enhancing interoception offer a potential therapeutic approach for treating symptoms of several psychological and psychophysiological conditions (Khalsa et al., 2018). Studies have shown that interoceptive accuracy may be enhanced through interventions such as biofeedback training (Bornemann & Singer, 2017; Meyerholz, Irzinger, Witthöft, Gerlach, & Pohl, 2019). Further, biofeedback interventions have been shown to improve relaxation (Lewis et al., 2015), reduce anxiety (Prato & Yucha, 2013; Rice, Blanchard, & Purcell, 1993), and also a decrease in heart rate reactivity to aversive stimuli (Peira et al., 2014). However, the practice of directing attention towards interoceptive experience (i.e., meditation, mindfulness, biofeedback) has not always been shown to improve performance tasks of heartbeat perception (e.g., Parkin et al., 2014). Indeed, a recent meta-analysis of 12 studies by Khalsa and colleagues (Khalsa, Rudrauf, Hassanpour, Davidson, & Tranel, 2020) demonstrated that the practice of mindfulness and meditation does not significantly improve cardiac interoceptive awareness when considering studies utilising both cross-sectional and longitudinal designs. Accordingly, alternative approaches to influencing interoception require further consideration.

Exercise engagement and aerobic fitness are also proposed to influence interoception. As described in section 2.3.4, exercise elicits transient increased activation of brain structures associated with the processing of interoceptive signals and has been shown to result in improved heartbeat perception accuracy. Furthermore, several studies support a positive association between aerobic fitness and cardiac interoception (Georgiou et al., 2015; Jones & Hollandsworth, 1981; Perakakis, Luque-Casado, Ciria, Ivanov, & Sanabria, 2017), suggesting that recurrent engagement in physical activity may facilitate greater sensitivity to interoceptive signals. This latter finding was supported in Chapter 4 of this thesis, which showed that good heartbeat perceivers demonstrated greater aerobic fitness than poor heartbeat perceivers (Table 4.4). Further, the findings of Chapter 4 demonstrated that the positive relationships between interoception, particularly for heartbeat discrimination accuracy, and aerobic fitness measures were independent of age, gender, and body composition.

Distinct delineation of the evidence linking aerobic fitness, exercise, and interoception has been further limited by the reliance on descriptive rather than experimental designs. This approach limits the causal assessment of the relationship between these factors, leading to conflicting interpretations of the mechanisms involved. One hypothesis suggests that improved cardiac interceptive accuracy may result from repeated exposure to increased cardio-afferent feedback during exercise, increasing baseline sensitivity to interoceptive signals (Montgomery, Jones, & Hollandsworth, 1984). This concept is analogous with the proposed mechanism supported by biofeedback training approaches (Jones et al., 2015). This process may also be facilitated by the use of heart rate measuring devices that provide real-time biofeedback, which is capable of informing more precise prior beliefs regarding a person's own heart rate at rest and during exercise (Desmedt et al., 2020). Conversely, changes in interoception are also putatively linked to differences in certain physiological states with evidence suggesting a link between greater heartbeat perception accuracy and lower resting heart rates (Knapp-Kline & Kline, 2005), greater stroke volume at rest (Schandry et al., 1993), and lower heart rate variability (Ludwick-Rosenthal et al., 1985; Owens et al., 2018), as well as an inverse relationship with age (Murphy, Geary, et al., 2018) and body composition (Rouse et al., 1988) among healthy adults.

The application of exercise training as an approach to modulate interoception should not only consider its influence on the desired physiological adaptations but also its impact on the accretion of subjective fatigue. The experience of subjective fatigue is also known to influence exercise performance and often occurs following prolonged periods of intensified exercise training (Halson et al., 2002; Hedelin, Kentta, Wiklund, Bjerle, & Henriksson-Larsen, 2000). Importantly, the experience of increased fatigue is associated with the enhanced neural activity of structures within the interoceptive network (Harrison et al., 2009), and this relationship between fatigue and interoception is implicated within nascent theoretical frameworks (Kuppuswamy, 2017; Stephan et al., 2016). Supporting these frameworks, emerging evidence demonstrates that measures of trait interoceptive awareness are typically lower in persons living with chronic fatigue compared with matched controls (Sharp et al., 2021). Furthermore, in exercise contexts, Greenhouse-Tucknott and colleagues (Greenhouse-Tucknott, Butterworth, Wrightson, Harrison, & Dekerle, 2021) have demonstrated that interoceptive awareness may moderate the relationship between fatigue and perception of effort, which has direct implications on performance in externally regulated exercise tasks (Albertus et al., 2005; Hampson et al., 2001; Okano et al., 2015).

Expression of optimal exercise performance typically arises following a period of reduced training load (known as a taper), where fatigue is allowed to diminish whilst maintaining desired physiological adaptations (Bosquet, Montpetit, Arvisais, & Mujika, 2007). However, the optimal duration of this taper period varies considerably, from less than 4-d to more than 28-d, and is dependent on factors such as the intensity and duration of the training period, the characteristics of training undertaken during the taper, as well as consideration of differences between individuals in their responses to these factors (Thomas & Busso, 2005). Identification of optimal performance should therefore be tailored towards the contexts of the individual rather than being standardised towards arbitrary timescales. An individualised approach may also better control for the effect of fatigue on interoception by allowing fatigue to return to baseline levels throughout a tapering protocol.

The aim of the present study was to causally examine the relationship between aerobic fitness and interoception using a 4-week exercise intervention. It was hypothesised that 1) the 4-week exercise intervention would significantly improve markers of aerobic fitness, 2) cardiac interoception would increase after 4-weeks of training, and 3) that changes in cardiac interoception would be positively associated with changes in measures of aerobic fitness and negatively correlated with resting heart rate. Furthermore, in consideration of the impact of fatigue on both exercise performance and also interoception, examination of best and worst performances was explored to ascertain the potential confounding influence of exercise-induced fatigue in this regard.

5.3. Method

5.3.1. Participants

Twenty-eight individuals (18 males, 10 females; age 21 ± 2 years; stature 173 ± 7 cm; body mass 68.4 ± 12.8 kg) volunteered to participate in the study. Participants were undergraduate students from the University of Brighton. Participants completed a medical health questionnaire and provided written informed consent prior to testing (Section 3.4). All experimental procedures were approved by the University of Brighton Research Ethics & Governance Committee (Section 3.3). Participants were instructed to report to the laboratory in a fully rested and well-hydrated state, to avoid vigorous activity within the previous 24 h and to refrain from alcohol (24 h) and caffeine consumption (12 h) prior to testing.

5.3.2. Experimental Design

The study utilised a matched-pairs design with repeated measures, consisting of three distinct phases: pre-training (PRE: 2-weeks), training (4-weeks), and post-training (POST: 3-weeks). PRE provided an assessment of the participant's baseline characteristics, including aerobic fitness, resting heart rate, and interoception. Participants were allocated to either a training group (EX) or a control group (CON), matched against peak power output (PO_{peak}) obtained in the first physiological assessment. During the training phase, EX completed a 4-week exercise intervention, whilst CON maintained normal physical activity. For POST, participants were assessed on three occasions, separated by a 7-day period, commencing within two days of the final training session. All testing was performed in the same laboratory setting under controlled environmental conditions with participants undertaking testing at the same time of day (± 1 h) and on the same day of the week. Equipment was calibrated prior to all testing as previously described in section 3.10.1 and section 3.11.1.

5.3.3. Protocol

Phase 1: Pre-Training

Participants visited the laboratory on two separate occasions separated by 7 days. For the first visit, stature and body mass were obtained (Sections 3.7.1 – 3.7.2) and a fast ramp exercise test (fast-RT) was used to determine peak power output (PO_{peak}). The fast-RT consisted of a 3-minute cycling warm-up at 60 W followed by an increase in work rate of 20 $W \cdot min^{-1}$, with testing conducted on an electronically braked cycle ergometer (High Performance Ergometer with Rohloff Gear Hub, SRM, GmbH, Jülich, Germany). Participants were required to maintain a pedalling cadence of 80 $r \cdot min^{-1}$. The exercise was terminated according to the criteria previously described (Section 3.11.2). Fractions of PO_{peak} were used to determine the exercise intensities for the multi-stage incremental ramp test (MS-RT).

For visit 2, resting heart rate was obtained in a dimly lit, quiet lab-space using during a 10-minute 3-lead ECG recording. ECG electrodes (Kendall foam electrodes, Covidien, Canada) were placed as follows: RA (white) lead under the right clavicle along the mid-clavicular line, LA (black) electrode under the left clavicle along the mid-clavicular line, and LL (green) placed over the fifth intercostal space on the left side of the rib cage along the mid-clavicular line. All electrode sites were prepared in accordance with manufacturer's guidelines. ECG leads were connected to a PowerLab (15T, ADInstruments, Dunedin, New Zealand) and linked to a personal computer (Hewlett Packard, Palo Alto, USA) via USB cable. Once instrumented, participants were then seated and remained undisturbed for two minutes before commencing ECG recording, to ensure heart rate returned to resting levels. Participants then completed the interoception testing as outlined previously (Section 3.9.2). Subsequently, participants commenced the MS-RT (Figure 5.1). Participants were instrumented with a heart rate monitor (A300, Polar Electro Oyo, Temple, Finland) and a face mask, connected online metabolic system (MetaLyzer, Cortex, Germany). The exercise was performed on a manually braked cycle ergometer (874E, Monark Exercise AB, Vansbro, Sweden) fitted with power measuring cranks (Gossamer Powermeter, SRM, GmbH, Jülich, Germany). The test began with 105-s resting on the ergometer before the work rate was increased to 40% PO_{peak}. Each 3-min stage was preceded by a 15 s of unweighted cycling and followed by a 60-s recovery period. PO was increased by 10% PO_{peak} with each stage. The exercise was terminated according to the same criterion as the fast-RT. Heart rate, expired gases, and cycle ergometry data were sampled continuously throughout the test. A fingertip capillary blood sample was taken (Section 3.11.4) and a rating of perceived exertion was recorded in the final 20-s of each stage (RPE 6-20 scale; Borg, 1982).

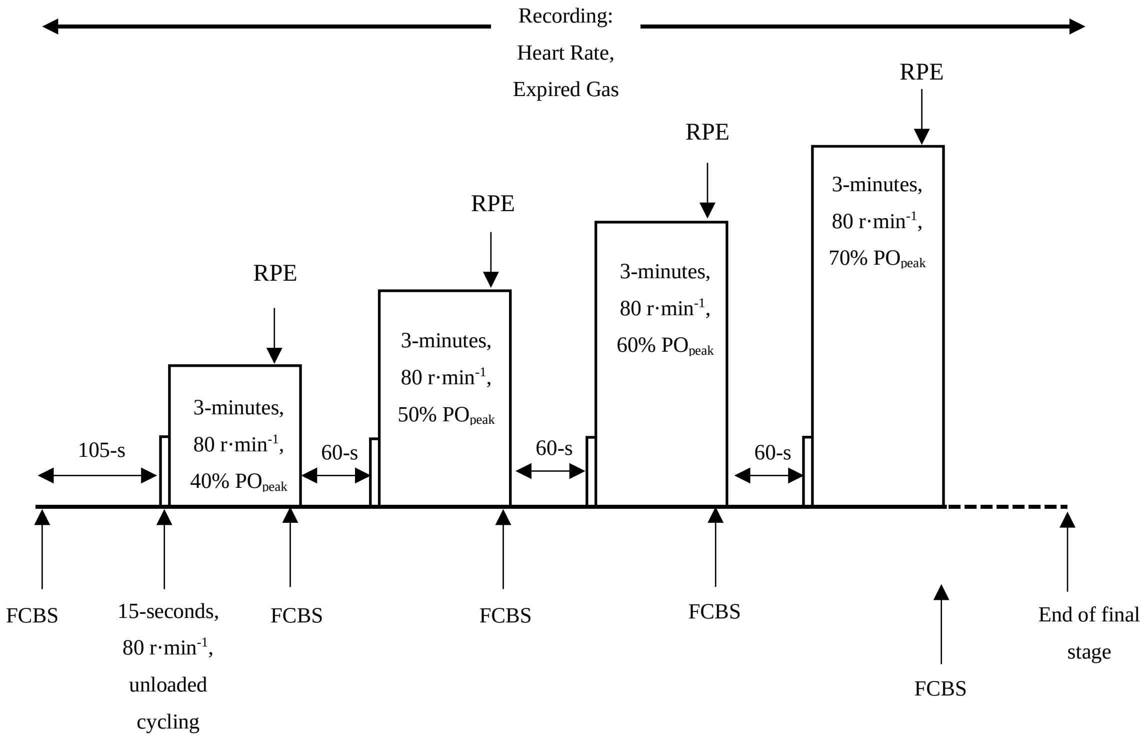


Figure 5.1. Schematic for multi-stage ramp test (MS-RT). FCBS = fingertip capillary blood sample, RPE = rating of perceived exertion, % PO_{peak} = percentage of peak power output, r·min-1 = revolutions per minute.

Phase 2: Training

EX completed a four-week intervention of high-intensity cycling exercise, comprised of 13 sessions as follows Week-1: 3-sessions, Week-2: 3 sessions; Week-3: 4 sessions; Week-4: 3 sessions plus first POST assessment. Each session consisted of two 15-minute blocks at 70% of the PO_{peak} (obtained from the MS-RT) with a 5-minute passive recovery between blocks. Sessions began with a 6-minute warm-up, as 3-minutes at 35% of PO_{peak} (50% of training block intensity) and 3 minutes of 52.3% PO_{peak} (75% of training block exercise intensity). All cycling exercise was completed on a Monark 874E Ergometer. Participants maintained 80 r·min^{-1} cadence throughout, with intensity determined through changes in the weight placed on the ergometer cradle. Heart rate was recorded at rest ($f_{c\ rest}$) and throughout the two blocks of exercise, with $f_{c\ end}$ determined as the f_c obtained at the end of the second 15-minute block. RPE $_{end}$ and $[La^-]_{c\ end}$ were also obtained at the end of the second 15-minute block.

Phase 3: Post-Training

POST commenced at the end of the final week of the training phase, with the first assessments completed 36-48hrs following the final training session. Participants completed an identical assessment protocol as described in the second visit of PRE, including a 10-minute ECG, interoception testing, and MS-RT. This testing battery was completed on three separate occasions each separated by 7 days.

During POST, EX maintained a reduced training load comprised of 2 sessions$\cdot$wk^{-1}. The sessions consisted of identical warm-up procedures as previously described followed by a single 15-minute exercise block at 70% PO_{peak}. The training was scheduled to ensure 48-h recovery between sessions and 36-48 h recovery before the MS-RT assessments. Participants in CON maintained normal physical activity behaviour during this period.

5.3.4. Data Analysis

Exercise Testing Data

For the fast-RT, data for PO was analysed using rolling 30-s averages, with PO_{peak} defined as the highest 30-s average.

For the MS-RT, breath-by-breath data for expired gases were converted to second-by-second and averaged over the final 30-s of each stage (Metalyser software, Cortex, Germany). $\dot{V}O_{2\,peak}$ was defined as the highest 30-s average. Heart rate data were averaged over the final 5-s of each stage, PO data was taken as the average over the duration of each stage. Capillary blood samples were analysed to determine blood lactate concentration $[La^-]_c$ using a glucose-lactate analyser, in accordance with section 3.11.4. Determination of PO, f_c, and $\dot{V}O_2$ values for $[La^-]_c$ values at 3 mmol$\cdot$L^{-1} were based on linear interpolation. Cycling efficiency was calculated using the expired gas data for the first stage of the MS-RT (40% PO_{peak}).

Interoception Data

Performance in the heartbeat detection tests was determined as previously described (Section 3.9.3).

Best and Worst Performance

Identification of the best (POST-BEST) and worst (POST-WORST) performances of the three post-training MS-RT assessments were determined for each individual in EX, with performance based on the exercise duration in the MS-RT. Participants in CON were subsequently allocated POST-BEST and POST-WORST according to their corresponding matched-pair.

5.3.5. Statistical Analysis

All data were examined for assumptions of parametric distribution, sphericity, and tests of equality of variance according to the methods outlined in section 3.13.5.

Two-way (2x3) mixed methods ANOVA on factors for Group (EX, CON) and Performance (PRE, POST-BEST, POST-WORST) were used to examine measures of aerobic fitness, exercise performance, and interoception. *Post hoc* analysis was performed using Bonferroni-corrected pairwise comparisons. Repeated-measures correlations were performed as described in section 3.13.7 to examine intra-individual linear relationships for changes in aerobic parameters (PO_{peak}, $\dot{V}O_{2\ peak}$, $f_{c\ rest}$) and changes in cardiac interoceptive measures for PRE, POST-BEST, and POST-WORST.

5.4. Results

5.4.1. Group Characteristics

The baseline characteristics for the two groups are shown in Table 5.1. Age violated assumptions of normality in both EX ($W = .47$, $p < .01$) and CON ($W = .86$, $p = .01$), which was not resolved following log-transformation, so the age difference between the two groups was consequently examined using Mann-Whitney *U* test. Analysis revealed that the groups did not significantly differ in terms of age, stature, or body mass at baseline. However, there were descriptive differences in the distribution of males and females between the two groups (EX: 11 M, 3 F (79% M); CON: 7 M, 7 F (50% M)).

Table 5.1. Baseline characteristics for the training group (EX) and control group (CON).

Variable	EX	CON	*p*-value	ES
Age	20 (20 – 20.75)	21 (20 – 22.50)	.25	.08 ^{r}
Stature (cm)	174 ± 6	172 ± 8	.63	.23 ^{g}
Body Mass (kg)	69.3 ± 13.7	67.5 ± 12.2	.72	.14 ^{g}

Abbreviations: ES = effect size, cm = centimetres, kg = kilogram, g = effect size for parametric data (Hedge's *g*), *r* = effect size for non-parametric data.

5.4.2. Training Responses

Changes in $f_{c\ rest}$, $f_{c\ end}$, RPE $_{end}$ and $[La^-]_{c\ end}$ are shown in Figure 5.2. Analysis of these changes revealed the both $f_{c\ end}$ ($t_{(13)}$ = 3.9, p < .01, g = 1.44) and RPE $_{end}$ ($Z_{(13)}$ = 3.2, p < .01, r = .86) were reduced in EX from the first training session to the last training session of the 4-week exercise intervention. Conversely, both $f_{c\ rest}$ ($t_{(13)}$ = 2.0, p = .07, g = .42) and $[La^-]_{c\ end}$ ($t_{(13)}$ = 1.9, p = .09, g = .82) remained statistically unchanged following the exercise intervention, despite a large effect for the change in $[La^-]_{c\ end}$.

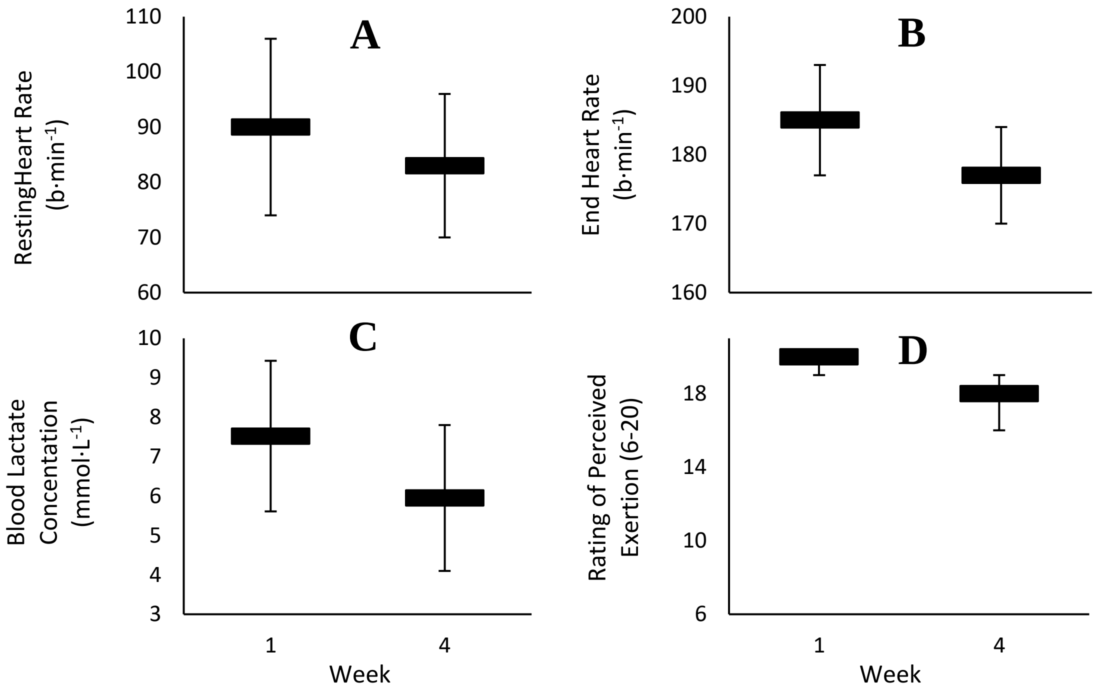


Figure 5.2. Physiological and perceptual responses of the exercise training group (EX) to the 4-week exercise intervention, obtained for the first (week 1) and last (week 4) training session. Physiological measures included: A) resting heart rate, B) end heart rate, C) end blood lactate concentration, and D) end rating of perceived exertion.

5.4.3. Aerobic Fitness and Exercise Performance

Data for PO, $\dot{V}O_2$, f_c, and cycling efficiency for both peak and at a blood lactate concentration of 3 mmol·L^{-1} are shown in Table 5.2. Resting heart rate data is also included.

Analysis of the data revealed that EX improved their PO_{peak} by ~18% from PRE to POST-BEST ($p < .01$) and by 9% from PRE to POST-WORST ($p < .01$). PO_{peak} for POST-BEST was also found to be significantly greater than POST-WORST ($p = .04$). For CON, however, PO_{peak} was not significantly different between PRE, POST-BEST, and POST-WORST ($p > .76$). Comparison between the two groups further revealed that PO_{peak} for POST-BEST was significantly greater in EX ($p = .01$) despite differences in PO_{peak} being non-significant between groups for both PRE ($p = .45$) and POST-WORST ($p = .14$). However, no significant effects were found for $\dot{V}O_2$ at peak or 3 mmol·L^{-1} ($p > .05$), indicating that the changes in exercise performance were likely related to other factors.

The ANOVA revealed group-wise differences for gross cycling efficiency ($F_{(1,\ 18)} = 11.043$, $p < .01$, $\eta_p^2 = .38$), indicating that EX (19.0 ± 2.0 %) exhibited greater efficiency compared with CON (15.8 ± 2.0 %). Conversely, no significant PRE *vs* POSTs differences ($F_{(2,\ 36)} = .20$, $p = .82$, $\eta_p^2 = .01$) or interaction effect were observed ($F_{(2,\ 36)} = 1.07$, $p = .35$, $\eta_p^2 = .06$) suggesting that the exercise intervention itself did not significantly influence cycling efficiency in EX.

No significant effects were observed in the ANOVA for any other fitness parameters ($p > .05$).

Table 5.2. Measures of aerobic fitness for the training group (EX) and control group (CON) for baseline (PRE) as well as best performance (POST-BEST), and worst performance (POST-WORST) in the post-training assessments.

Group	EX			CON		
	PRE	POST-BEST	POST-WORST	PRE	POST-BEST	POST-WORST
Peak						
PO (W)	235 ± 45	277 ± 55*†	255 ± 48	221 ± 61	215 ± 64	224 ± 62
$\dot{V}O_2$ ($L \cdot min^{-1}$)	3.13 ± 0.70	3.25 ± 0.68	3.22 ± 0.56	3.01 ± 0.81	2.94 ± 0.79	2.92 ± 0.73
f_c ($b \cdot min^{-1}$)	191 ± 7	192 ± 7	191 ± 7	188 ± 10	188 ± 11	190 ± 9
$[La^-]_c$ ($mmol \cdot L^{-1}$)	8.80 ± 0.88	8.96 ± 1.95	9.09 ± 2.64	7.58 ± 1.64	7.94 ± 1.46	7.22 ± 1.60
3 $mmol \cdot L^{-1}$						
PO (W)	147 ± 35	167 ± 43	177 ± 41	138 ± 27	153 ± 43	156 ± 43
PO (PO_{peak})	62 ± 8	63 ± 21	69 ± 10	61 ± 23	61 ± 19	68 ± 14
PO (%PO_{peak})	69 ± 13	63 ± 21	69 ± 10	65 ± 14	61 ± 19	67 ± 13
$\dot{V}O_2$ ($L \cdot min^{-1}$)	2.15 ± 0.53	2.35 ± 0.49	2.22 ± 0.50	1.97 ± 0.47	2.22 ± 0.59	2.34 ± 0.62
f_c ($b \cdot min^{-1}$)	157 ± 20	156 ± 12	154 ± 23	162 ± 13	162 ± 14	158 ± 10
Efficiency						
Gross (%)	17.9 ± 3.5	18.9 ± 2.4	19.9 ± 2.9	16.4 ± 2.8	16.9 ± 4.0	16.6 ± 5.3
Net (%)	24.7 ± 6.0	25.2 ± 8.2	25.3 ± 5.0	21.5 ± 4.9	22.0 ± 5.5	23.1 ± 6.2
Resting Heart Rate						
$f_{c\ rest}$ ($b \cdot min^{-1}$)	72 ± 12	72 ± 10	69 ± 10	78 ± 11	76 ± 8	77 ± 12

Abbreviations: PO = power output, W = watts, $\dot{V}O_2$ = rate of oxygen consumption, $L \cdot min^{-1}$ = litres per minute, f_c = heart rate, f_c rest = resting heart rate, $b \cdot min^{-1}$ = beats per minute, $[La^-]_c$ = blood lactate, $mmol \cdot L^{-1}$ = millimoles per litre, RPE = rating of perceived exertion, a.u. = arbitrary units, * denotes significant difference between PRE and POST-BEST for EX ($p < .05$), † denotes significant difference between EX and CON for POST-BEST ($p < .05$).

5.4.4. Interoception

Data for heartbeat tracking and heartbeat discrimination tasks are shown in Table 5.3 with statistical outputs for the ANOVA's reported in Table 5.4. Analysis of the cardiac interoception data showed no significant effects within the ANOVA for all comparisons, except for the factor of Performance (i.e., comparing between PRE, POST-BEST, POST-WORST) on heartbeat discrimination accuracy ($F_{(2, 52)} = 3.476$, $p = .04$, $\eta_p^2 = .12$). *Post-hoc* analysis revealed that heartbeat discrimination accuracy was greater for POST-WORST (0.58 ± 0.17) compared with both PRE (0.48 ± 0.22; $p = .04$) and also POST-BEST (0.52 ± 0.21; $p = .046$). However, exploratory analysis of this effect within each group indicated that heartbeat discrimination accuracy did not differ between time-points for either EX or CON (Table 5.3 – 5.4), suggesting that this effect of factor (Performance) was not influenced by changes particular to either group.

Table 5.3. Measures of interoception in the training group (EX) and control group (CON) at baseline (PRE) as well as best performance (POST-BEST) and worst performance (POST-WORST) following the 4-week training intervention.

Group	EX			CON		
	PRE	POST-BEST	POST-WORST	PRE	POST-BEST	POST-WORST
Tracking						
Accuracy	0.72 ± 0.32	0.68 ± 0.22	0.72 ± 0.21	0.62 ± 0.31	0.75 ± 0.17	0.71 ± 0.20
Sensibility	5.1 ± 3.0	5.3 ± 2.2	4.9 ± 2.3	3.5 ± 2.4	3.9 ± 2.6	3.9 ± 2.5
Awareness	0.36 ± 0.51	0.53 ± 0.37	0.22 ± 0.42	0.17 ± 0.49	0.28 ± 0.43	0.21 ± 0.42
Discrimination						
Accuracy	0.50 ± 0.19	0.55 ± 0.20	0.62 ± 0.24	0.46 ± 0.13	0.50 ± 0.21	0.54 ± 0.19
Sensibility	6.1 ± 2.2	5.6 ± 2.6	5.4 ± 3.0	4.0 ± 2.6	4.7 ± 3.3	4.2 ± 3.5
Awareness	0.36 ± 0.51	0.49 ± 0.21	0.57 ± 0.23	0.49 ± 0.17	0.43 ± 0.20	0.54 ± 0.21

Table 5.4. ANOVA statistical output for heartbeat tracking and heartbeat discrimination measures comparing factors for Group (EX, CON), Performance (PRE, POST-BEST, POST-WORST), and the Interaction.

Factor	Group			Performance			Interaction		
	F-value	*p*-value	η_p^2	*F*-value	*p*-value	η_p^2	*F*-value	*p*-value	η_p^2
Tracking									
Accuracy	0.025	.88	< .01	0.583	.56[#]	.02	1.676	.20[#]	.06
Sensibility	2.333	.14	.08	0.647	.53	.02	0.153	.86	< .01
Awareness	2.890	.10	.10	1.813	.17	.07	1.090	.34	.04
Discrimination									
Accuracy	0.958	.34	.04	3.476	.04*	.12	0.156	.86	< .01
Sensibility	2.431	.13	.09	0.186	.83	< .01	0.471	.63	.02
Awareness	0.296	.59	.01	2.431	.10	.09	0.291	.75	.01

* $p < .05$, # Greenhouse-Geisser corrected

5.4.5. Correlational Analysis

Examination of the intra-individual correlation coefficients revealed a significant positive relationship between heartbeat discrimination accuracy and $\dot{V}O_{2\ peak}$ (Figure 5.3a; $r_{(25)}$ = .49, p = .01, 95%CI = [.11, .74]) as well as a significant negative relationship for heartbeat discrimination accuracy and $f_{c\ rest}$ (Figure 5.3b; $r_{(27)}$ = -.40, p = .03, 95%CI = [-.67, -.02]). Correlation coefficients for all other comparisons were observed to be below the threshold for statistical significance (p > .05).

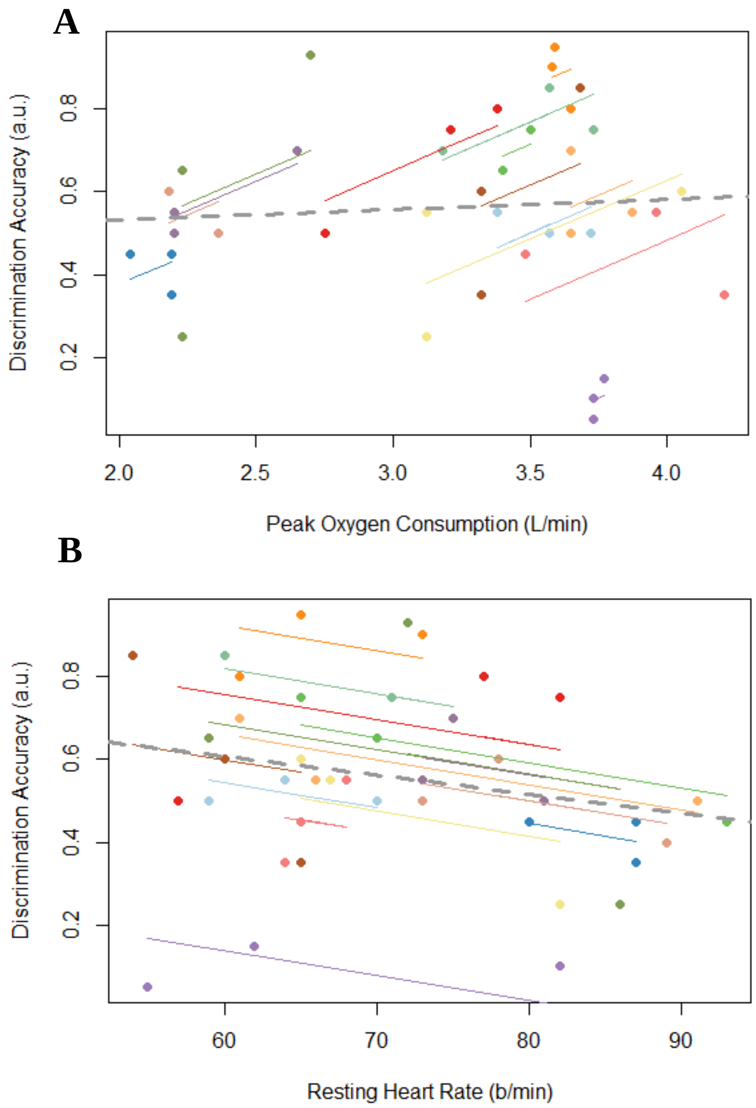


Figure 5.3. Intra-individual correlations for heartbeat discrimination accuracy with A) peak oxygen consumption, and B) resting heart rate.

5.5. Discussion

The present study is the first to examine the efficacy of an exercise training intervention on changes in both aerobic fitness and interoception. The data indicated that the exercise intervention significantly improved PO_{peak} in the training group but did not significantly influence other markers of aerobic fitness or resting heart rate. Measures of interoception also remained statistically unchanged following the exercise intervention. This suggests that intervention within this experiment was not effective when examining the potential relationship between changes in aerobic fitness and changes in cardiac interoception.

5.5.1. Effect of Training Intervention on Performance and Aerobic Fitness

Although challenging to directly compare the effectiveness of the exercise intervention with previous studies - due to differences in initial training status, assessment protocol, and factors linked to the intervention itself - the 18% improvement in PO_{peak} (for POST-BEST) was observed to be at the upper limit of the expected improvements in PO_{peak} (4 to 20 %) which are reported in similar studies (Astorino et al., 2017; Duffield, Edge, & Bishop, 2006; Esfandiari, Sasson, & Goodman, 2014; S. Seiler, Jøranson, Olesen, & Hetlelid, 2013; Weston et al., 1997). The large improvement in PO_{peak} in the current study may be allied to the approach used to identify optimal performance following the training intervention rather than comparing outcomes at a singular standardised time-point. Optimal exercise performance is known to typically occur between 1- and 4-weeks following periods of intensive exercise training; but with notable inter-individual variability in the time-course of this response (Bosquet et al., 2007; Mujika et al., 2000; Thomas, Mujika, & Busso, 2008). This response variability may be influenced by differences in the level of fatigue accumulated during the training period (Thomas & Busso, 2005), which under certain contexts may reflect a state of non-functional overreaching or overtraining where maladaptive responses to an exercise training stimulus are observed (e.g., Le Meur et al., 2013). Further, hereditary factors may influence the trainability of aerobic fitness components such as $\dot{V}O_{2\,max}$ (Bouchard et al., 1999), which is linked to the expression of certain physiological phenotypes (Bae, Kang, Lee, & Lee, 2007; Bouchard & Rankinen, 2001).

Surprisingly, despite the substantial improvement in PO_{peak}, no significant changes were observed for $\dot{V}O_{2\,peak}$, cycling efficiency, or submaximal values for $\dot{V}O_2$ and PO at 3 $mmol \cdot L^{-1}$ blood lactate concentration. This is in contrast with data from previous exercise training studies, demonstrating improvements in PO_{peak} alongside changes in $\dot{V}O_{2\,peak}$ and submaximal exercise capacity (Duffield et al., 2006; S. Seiler et al., 2013). For instance, Seiler and colleagues (2013) reported an increase of 6.5% in $\dot{V}O_{2\ peak}$ and 16% in PO at 4 mmol·L^{-1} corresponding to an improvement of 8.5% in PO_{peak} following a similar 7-week exercise intervention in recreational cyclists. Improvements in $\dot{V}O_{2\ peak}$ (7.5%) has also been observed after a 3-week exercise intervention alongside a 5.2% increase in PO_{peak} (Astorino et al., 2017). Moreover, Carter, Jones, and Doust (1999) reported improvements of 9.9% for $\dot{V}O_{2\ peak}$ and 9.5% for $\dot{V}O_2$ at 3 mmol·L^{-1} following a 6-week exercise intervention using a continuous interval training intervention. This discrepancy might be a consequence of the training intervention itself, with differences in volume, intensity, and frequency of training known to influence the time course of physiological adaptations (Costill et al., 1991; Guellich & Seiler, 2010; Helgerud et al., 2007). Adaptations to the training interventions showed large-to-very large reductions in both $f_{c\ end}$ (p < .01, g = 1.44) and $[La^-]_{c\ end}$ (p = .09, g = .82) (Figure 5.2) indicating an increased work capacity at exercise intensities above the lactate threshold. As shown below, these changes corresponded with marginal reductions in $[La^-]_c$ over the first 6 stages of the MS-RTs for the post-training tests (Figure 5.4), which may have facilitated the observed improvements in performance despite non-significant differences in PO and VO_2 at 3 mmol·L^{-1}, or $\dot{V}O_{2\ peak}$. Importantly, peak values for both RPE and $[La^-]_c$ were not found to be significantly different between MS-RTs, suggesting that motivational factors could not account for differences in these findings (Table 5.2).

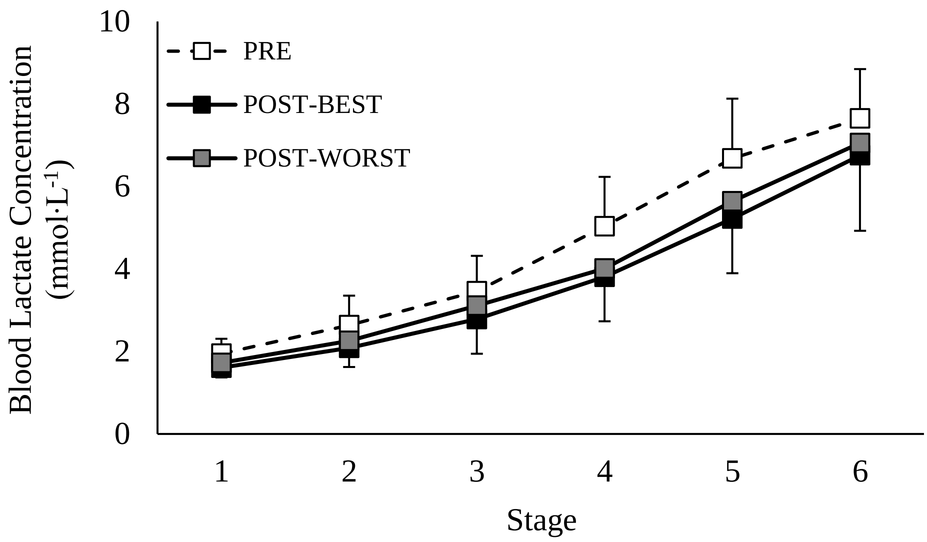


Figure 5.4. Changes in blood lactate concentration during a multi-stage graded exercise test obtained for pre-training (PRE) and for best (POST-BEST) and worst (POST-WORST) performances for the exercise training group (EX) in the post-training assessments.

5.5.2. Effect of Training Intervention on Cardiac Function

Resting heart rate remained unchanged following the exercise intervention. This finding is surprising given the large body of published evidence demonstrating significant reductions in $f_{c\ rest}$ in both healthy and clinical populations (Carter, Banister, & Blaber, 2003; Furlan et al., 1993; Goodman, Liu, & Green, 2005; Shibata et al., 2012; Stein, Michielli, Diamond, Horwitz, & Krasnow, 1980). Short-term changes in cardiac function to exercise training typically occurs in relation to increased plasma volume (hypervolemia), evident within 2-4 weeks of exercise training (Goodman et al., 2005). Hypervolemia enables augmented venous return (Kanstrup & Ekblom, 1982) and also attenuates baroreceptor sensitivity (Green, Jones, & Painter, 1990; Thompson, Tatro, Ludwig, & Convertino, 1990), thereby increasing stroke volume that may result in a concomitant reduction in $f_{c\ rest}$. Additionally, short-term effects of exercise have been shown to increase the parasympathetic input to the heart, contributing to a decrease in $f_{c\ rest}$ (Carter, Banister, & Blaber, 2003). However, these effects are not always observed following periods of intensified training when symptoms of non-functional overreaching or overtraining are present (Mourot et al., 2004).

5.5.3. Interoceptive Response to Exercise Training

Interoception was also not influenced following the 4-week training intervention in the present study, suggesting that short-term exercise interventions may not be sufficient to result in stable (trait-based) changes in a person's cardiac interoceptive characteristics. This finding is in disagreement with previous studies demonstrating improvements in reported interoceptive sensibility (using questionnaires) following exercise interventions (Mehling et al., 2018; Sabourin et al., 2015). Differences in these findings may reflect the methods used to assess interoception compared with the present study (i.e., questionnaire-based assessment of interoceptive sensibility vs. accuracy, sensibility, and awareness measures obtained in heartbeat perception tasks). Indeed, Garfinkel, Seth, Barrett, Suzuki, and Critchley (2015) have previously reported that questionnaire-based measures of interoception (Porges, 1993) demonstrated poor correspondence to more objective state-based measures of interoceptive accuracy, sensibility, and awareness, suggesting that these approaches may examine conceptually different aspects of interoceptive beliefs and experiences. Consequently, exercise training may result in greater trait-based beliefs (as indicated using body perception questionnaires) but does not appear to influence performance in an objective assessment of interoception or state-based interoceptive sensibility (i.e., VAS for confidence during heartbeat perception tasks).

Conversely, the current data was in accordance with studies showing that interoceptive accuracy is not altered following interventions involving: increased state anxiety (Stevens et al., 2011), mindfulness meditation (Khalsa et al., 2008), or stress (Fairclough & Goodwin, 2007). These findings have been interpreted to suggest that individual differences in the perception of interoceptive stimuli may be underpinned by certain trait attributes that are resistant to change, particularly in the context of short-term interventions such as the training intervention used in the present study. Conversely, Ainley and colleagues (2013; 2012) have demonstrated that interoceptive accuracy is malleable in situations of heightened self-awareness using: mirror self-observation, viewing photographs of self, and reading self-relevant words. Similarly, more recent studies using biofeedback training have shown improvements in markers of interoception (Farb, Segal, & Anderson, 2013; Peira et al., 2014). The capacity to influence interoceptive perceptions has been identified as a potential target candidate for the treatment of several psychological and psychophysiological conditions (Domschke, Stevens, Pfleiderer, & Gerlach, 2010; Khalsa et al., 2015; Paulus & Stein, 2010; Stephan et al., 2016; Wiebking et al., 2015). Identifying effective interventions is proposed as a potentially powerful clinical tool for the treatment of such morbidities (Khalsa et al., 2018). However, the lack of effect found in the present study demonstrates that manipulation of interoceptive characteristics remains challenging and requires further investigation to identify effective treatment interventions.

A major confounding factor in the interpretation of the interoception data of this study was the failure to induce significant changes in the physiological markers of aerobic fitness within the present cohort. These results demonstrate that short-term ($\leq$ 4 weeks) recurrent exposure to exercise stimulus alone is not sufficient to induce changes in interoception among healthy populations Nevertheless, the exploratory correlational analysis indicated the presence of intra-individual relationships for heartbeat discrimination accuracy with both $\dot{V}O_{2\,peak}$ (r = .49) and $f_{c\ rest}$ (r = -.40) (Figure 5.3). These correlational findings support the previous observations reported in Chapter 4, which demonstrated that heartbeat discrimination accuracy was most strongly associated with markers of aerobic fitness, compared with other measures of cardiac interoception. Furthermore, differences in $f_{c\ rest}$ have been reported to be negatively associated with performance (accuracy) in tasks of heartbeat perception (Chapter 4, Knapp-Kline & Kline, 2005; Schandry et al., 1993) and it's suggested that cardiac dynamics reflect a core construct in cardiac interoception (Forkmann et al., 2016).

Previous studies have suggested a possible relationship between interoception and aerobic fitness; however, the observational nature of this data has precluded causal inferences around the underlying mechanisms (Jones & Hollandsworth, 1981; Machado et al., 2019; Montgomery, Jones, & Hollandsworth, 1984; Perakakis, Luque-Casado, Ciria, Ivanov, & Sanabria, 2017). The findings from this study, in accordance with Chapter 4, provide notable insight into the nature of these effects, supporting the importance of physiological conditions of the body in the perception of heartbeats, suggesting that these effects may be driven by the strength (precision) of bottom-up sensory inputs. This contrasts with previous notions that engagement in exercise improves cardiac interoception principally through a process of augmented interoceptive exposure, leading to greater precision in the brain's modelling of expected interoceptive inputs (Hollandsworth, 1979 cited in Montgomery et al., 1984).

In accordance with predictive coding models of the brain, Ainley *et al*. (2016) suggest that perception of heartbeats occurs when the characteristics of ascending sensory inputs (termed prediction error) from the heart are not fully accounted for by the brain's prior expectations (termed priors). Importantly, relative precision afforded to both the priors and the prediction errors are considered as factors in the brain's resolution of the differences in these two components, with greater relative precision in the prediction error precluding a reconciliation of these differences at lower orders of the cortical hierarchy (Parr & Friston, 2018). The findings from this study support the notion that physiological characteristics, such as lower $f_{c\ rest}$ (which is associated with greater stroke volume and ejected blood momentum; Schandry, Bestler, & Montoya, 1993) afford greater precision to bottom-up prediction errors, aiding the detection of heartbeats. This suggests that physiological adaptations associated with exercise training may facilitate a more accurate perception of heartbeats. Conversely, based on the findings of this study, it is not clear whether the short-term exercise intervention influenced the relative precision afforded to priors particularly as certain psychophysiological states (such as fatigue) are thought to result in their reduced precision through a loss in the brain's held efficacy of its modelling of physiological states (Stephan et al., 2016). Consequently, the present study complements the existing literature by providing support to the view that factors related to functional or structural physiological characteristics may influence cardiac interoception but does not provide evidence to ascertain a role for exercise in improving the brains modelling of bodily states through a form of augmented 'interoceptive exposure'.

5.5.4. Limitations

Despite the aim of this study, to examine the causal basis of the relationship between cardiac interoception and markers of aerobic fitness, the nature of the findings obtained from the data can only be considered as providing observational rather than experimental evidence for this effect. This may be partly explained by the modest sample size of the study, which has implications on the statistical power to detect a significant effect. Further, the relatively high initial fitness of the present cohort may have also contributed to the lack of experimental effect, as changes in measures of cardiorespiratory fitness are typically more modest in trained compared with sedentary populations (Seiler & Tønnessen, 2009). The effect of differences in baseline resting heart rate between the two groups (EX, CON) was a further confounding factor that may have contributed to the null findings reported. This issue occurred despite the paired samples approach to group allocation based on measures of aerobic fitness. Consequently, future studies may wish to consider allocation based on resting heart rate rather than other physiological metrics. Further, this study failed to obtain reliable self-reported measures of daily physical activity (outside of the training intervention). Therefore, it is unclear whether the null effects in EX were a consequence of potential compensatory reductions in physical activity in other domains. Consequently, interpretation of these findings should be considered with appropriate caution. As a result of these limitations there remains a need for studies that elicit positive changes in aerobic fitness parameters in order to effectively examine its relationship with cardiac interoception.

5.5.5. Future Research

Future research should extend on the present study investigating the effect of different exercise interventions over longer periods to ascertain the efficacy of exercise as a tool to influence interoceptive processing. Additionally, exploration of the effect of exercise on changes in interoceptive processing across different physiological systems, such as respiratory interoception, is required to gain a more complete perspective of the interaction between physical activity and the processing of homeostatic afferent signals.

5.6. Conclusion

The current study is the first to examine the causal link between exercise, aerobic fitness, and interoception. The results of the study suggest that short-term exercise interventions involving high-intensity long-interval training may not be an effective tool for influencing interoception when aerobic fitness parameters remain unchanged. This occurred despite significant intra-individual relationships between markers of interoception and aerobic fitness. This finding is interesting because it suggests that recurrent exposure to heightened interoceptive feedback may not be sufficient to influence the generalised processing interoception within healthy, active populations. However, additional research is required to better understand the relationship between physical activity, aerobic fitness, and interoception.

CHAPTER 6. CARDIAC INTEROCEPTION DOES NOT INFLUENCE EXERCISE TOLERANCE DURING CONSTANT LOAD CYCLING EXERCISE.

6.1. Abstract

The third study of this thesis aimed to examine the influence of cardiac interoception on exercise tolerance in a constant load cycling task. Twenty-six physically active participants completed tests to determine cardiac interoception and aerobic fitness (GXT) and subsequently completed a constant load cycling task at 80% of the peak power output observed in the GXT. For statistical analysis, 15 participants were retrospectively allocated to a good (GOOD: N = 7) or poor (POOR: N = 8) cardiac interoception group, based on median demarcation and 95% confidence intervals using heartbeat discrimination accuracy data. The findings indicated GOOD (467 ± 121 s) and POOR (406 ± 91 s) did not differ in their time-to-task failure (T_{lim}) ($p = .29$). Additionally, T_{lim} was not significantly correlated with any measures of cardiac interoception (i.e., accuracy, sensibility, awareness) for either tracking or discrimination tasks ($p > .05$). Finally, a comparison of the physiological responses and ratings of perceived exertion were found to not be significantly different between GOOD and POOR at any of the measured time points ($p > .05$). Therefore, the results of this study indicate that differences in cardiac interoception do not influence exercise tolerance or the physiological and perceptual responses to whole-body high-intensity constant-load exercise.

6.2. Introduction

Constant-load exercise tasks represent a common approach to examining the limits of human physical performance. These tasks can be implemented to examine the performance of either isolated muscle groups or whole-body exercise capacity. The data obtained from these tasks support a robust relationship between physical performance intensity and the duration of the performance, which can be represented graphically as a hyperbolic decay in work rate over time (Hill, 1993). These decays in performance have been reliably attributed to a loss of force-generating capacity in skeletal muscle resulting from either intramuscular metabolic disturbances (Allen, Lamb, & Westerblad, 2008) or corticospinal inhibition of motor efferents (Weavil & Amann, 2018). Whilst description of the mechanisms underlying this relationship have predominantly focussed on physiological factors determining performance (Jones & Burnley, 2009; Thomas, Elmeua, Howatson, & Goodall, 2016; Walsh, 2000) limitations to physical performance also include subjective perceptual attributes, such as the increased perception of effort or increasingly negative affective states (Hartman, Ekkekakis, Dicks, & Pettitt, 2019; Marcora & Staiano, 2010). Indeed, previous studies have demonstrated that both prior physical activity (Greenhouse-Tucknott, Wrightson, Raynsford, Harrison, & Dekerle, 2020) or prolonged cognitive activity (Marcora, Staiano, & Manning, 2009) may results in heightened perceptions of fatigue, leading to reduced motor performance in a previously non-active part of the body, but without reducing the neuromuscular system's capacity to produce force. Additionally, high intra-subject coefficients of variation observed for motor performance (i.e., reduced time-to-task failure) in constant load tasks (variability ranging from 2.8 to 31.4 %; McLellan, Cheung, & Jacobs, 1995) further indicate a possible role for non-physiological determinants (i.e., behavioural factors) on physical performance.

Subjective perceptions related to physical exertion are argued to emerge from cortical representations of both efferent and afferent inputs. Related to efferent inputs, corollary discharge from the motor and premotor cortical regions have been shown to contribute to the appraisal of effort and perceived heaviness (Gandevia, Enoka, McComas, Stuart, & Thomas, 1995; Zénon et al., 2015). Conversely, afferent inputs, particularly those related to the physiological condition of the body (i.e., interoception), are considered to provide important information that informs a person's subjective appraisal of the allostatic demands that are experienced during physical activity (e.g., Rauch, St. Clair Gibson, Lambert, & Noakes, 2005), which are thought to be represented subjectively as a person's perception of exertion (Fontes et al., 2015; Okano et al., 2015; Williamson et al., 2014). Importantly, individual differences in interoceptive characteristics, demonstrated through psychometric assessment, suggest that sensitivity to visceral stimuli can differ substantially between persons (Ludwick-Rosenthal & Neufeld, 1985). Consequently, individuals may perceive comparable levels of acute physiological strain to differing degrees. This stance is supported by the observations reported by Herbert and colleagues (2007), who demonstrated that individuals performing better in a task of heartbeat counting (i.e., greater interoceptive accuracy) completed significantly less work during a self-paced exercise task, yet reported comparable levels of fatigue to their less interoceptively accurate counterparts at the end of the task. Broader support from studies of pain perception also indicates that interoceptive sensitivity is positively associated with the magnitude of reported pain sensation (Weiss, Sack, Henningsen, & Pollatos, 2014). However, Machado and colleagues (2019) reported that cardiac interoceptive accuracy did not influence either exercise tolerance (performance in a graded exercise task to exhaustion) or rating of perceived exertion at the heart rate variability threshold during a graded exercise task.

Interoceptive feedback may also affect autonomic responses to physiological changes. This effect occurs in the first instance through bottom-up input of second-order neurons projecting to brainstem sites (Dampney, 1994; Smith, Abdala, Rybak, & Paton, 2009). Structures within these subcortical sites form part of the so-called interoceptive network and are directly involved in the autonomic regulation of cardiac, respiratory, and vascular functions. However, studies also support the notion that the cardiovascular system may be regulated by top-down cortical input. Neuroimaging data reveals that the insular cortex, anterior cingulate gyrus, and amygdala play a crucial role in the regulation of the central autonomic nervous system (Beissner, Meissner, Bar, & Napadow, 2013). Interestingly, differences in perceptual sensitivity to interoceptive stimuli have been reported to influence cardiovascular responses. This includes studies demonstrating greater changes in heart rate in good heartbeat perceivers in response to isometric exercise (Pollatos, Herbert, et al., 2007) and also the presentation of emotionally evocative images and mental stress (Herbert et al., 2010). These findings suggest that a person's interoceptive sensitivity may influence their physiological responses to changes in allostatic demands, which are likely to be observed both during and following (i.e., heart rate recovery) bouts of physical activity.

The purpose of this study was to directly examine the relationship between interoceptive ability and tolerance to fixed intensity exercise, assessed using a constant load cycling task. It was hypothesised that greater interoceptive ability would result in a reduced time-to-task failure (Herbert et al., 2007); as greater sensitivity to interoceptive stimuli would result in greater perceptions of exertion for comparable magnitudes of physiological strain. Finally, it was hypothesised that more accurate heartbeat perceivers would demonstrate greater changes in cardiac and respiratory dynamics in response to comparable changes in physical activity and metabolic demand (i.e., fixed work rates at equivalent relative exercise intensities).

6.3. Methods

6.3.1. Participants

Following institutional ethical approval, 26 participants (13 males, 13 females; age 24 ± 3 yrs; stature 173 ± 9 cm; mass 69.7 ± 12.0 kg) volunteered to participate in this study. Participants were undergraduate students from the University of Brighton. Participants completed a medical health questionnaire and provided written informed consent prior to testing (Section 3.4). All experimental procedures were approved by the University of Brighton Research Ethics & Governance Committee (Section 3.3). Participants were instructed to report to the laboratory in a fully rested and well-hydrated state, to avoid vigorous activity within the previous 24 h and to refrain from alcohol (24 h) and caffeine consumption (12 h) before testing.

6.3.2. Procedure

Experimental Procedure

Participants visited the laboratory on two separate occasions. During the first visit, participants undertook the cardiac interoceptive assessment and completed a graded exercise test to establish an objective marker of aerobic fitness. In the second visit, participants completed the constant-load exercise protocol at fixed cycling intensity equal to 80% of the peak power output (PO_{peak}) observed at the end of the graded exercise test. All testing was performed in the same laboratory setting under controlled environmental conditions with participants undertaking testing at the same time of day (± 1 h) and on the same day of the week. Equipment was calibrated prior to all testing as previously described in sections 3.10.1 and 3.11.1.

Assessment of Cardiac Interoception and Aerobic Fitness

During the first visit, participants were reminded about the purpose and procedures of the study upon arrival. Participants then undertook the cardiac interoceptive assessment as previously described (Section 3.9.2) before having stature and body mass recorded (Section 3.7). Testing was performed on an electronically braked cycle ergometer (High Performance Ergometer with Rohloff Gear Hub, SRM, GmbH, Jülich, Germany). Participants were instrumented with a heart rate monitor (A300 Fitness Watch, Polar Electro Oyo, Temple, Finland) and a face mask connected to an online gas-analysis system as well as being fitted to the cycle ergometer. The exercise test was conducted following the method and termination criteria outlined in section 3.11.2. Power output (PO), heart rate (f_c), and expired gases were recorded continuously throughout the test. RPE was obtained in the final 15-s of each stage using the 6-to-20 Borg scale (Borg, 1982). Values for PO_{peak} (highest 30-s average) were used to determine the exercise intensity for the constant load task.

Constant-Load Exercise Task

During the second visit, participants completed the constant load exercise protocol. Participants were first fitted to the cycle ergometer before being instrumented with a heart rate monitor and face mask connected to an online gas analysis system. Participants were then reminded of the procedures and requirements of the exercise task. The exercise task began with a 3-minute resting sample of expired gases and f_c before commencing a 5-minute warm-up at 60 W and 80 r·min^{-1}. At the end of the warm-up, participants again rested on the ergometer for a further 2-minutes before beginning a period of unloaded cycling at the target cadence for the exercise task (80 r·min^{-1}) for a further 15s. The exercise test began immediately succeeding the end of the unloaded cycling phase. Participants were required to cycle for as long as possible at the target cadence at an external workload equal to 80% PO_{peak}, observed as the highest 30-second average power output during the fast-RT. Heart rate and expired gases were recorded continuously throughout the duration of the task, with f_c recorded for a further 60-seconds post-exercise test to examine heart rate recovery ($f_{c\ recovery}$). RPE was obtained from the participants in the final 15s of the first 4-minutes of the test and again at the end of the test to identify RPE at the termination of exercise. Termination criteria for the test were set according to an observed reduction in cadence below 70 r·min^{-1} for more than 10-s despite strong verbal encouragement.

6.3.3. Data Analysis

Cardiac Interoception

Measures of accuracy, sensibility, and awareness were determined according to the methods outlined in section 3.9.3.

Aerobic Fitness

The participant's aerobic fitness was determined based on the identification of two distinct ventilatory responses observed during the graded exercise test. These ventilatory responses are referred to as the first ventilatory threshold (VT_1) and second ventilatory threshold (VT_2), which were identified according to the methods outlined in section 3.11.5. Peak values for PO, $\dot{V}O_2$, and f_c were determined as the highest 30-s average obtained from the test.

Constant-Load Exercise Task

Performance in the constant load task was based on task duration (T_{lim}) which was recorded using the cycle ergometer output to the nearest 0.5-s prior to the termination of the test. Cardiorespiratory parameters $\dot{V}O_2$, $\dot{V}_E$, V_T, f_b, RER, and f_c were first averaged over the final 15-s of each minute during the first 4-minutes as well as the final 15-s of the test. For $\dot{V}O_2$, $\dot{V}_E$, V_T, values were normalised for each participant, relative to peak values observed in the fast-RT.

Inclusion Criteria

For statistical purposes, participants were excluded from the final analysis if they failed to achieve a minimum T_{lim} of 4-minutes before exercise termination in the constant-load task. Further, T_{lim} identified as being extreme outliers (*z*-score deviation from the mean > 3.29 (99^{th} percentile)) were also excluded from the final dataset.

Statistical Analysis

All data were examined for assumptions of parametric distribution, sphericity, and tests of equality of variance according to the methods outlined in section 3.13.5. Examination of group characteristics between GOOD and POOR for interoception measures as well as differences in age, stature, body mass, $f_{c\ rest}$, $f_{c\ peak}$, $\dot{V}O_{2\ peak}$, and PO_{peak} were completed using independent samples *t*-tests.

For the constant load task, between-groups differences in T_{lim} were assessed using independent samples *t*-test, which was also used to assess differences in $f_{c\ recovery}$. A two-way (2 x 5) mixed methods ANOVA on factors for Group (GOOD, POOR) and TIME

(1-min, 2-min, 3-min, 4-min, and endpoint) were used to examine physiological and perceptual measures obtained during the task. *Post-hoc* analysis was performed using Bonferroni-corrected pairwise comparisons. Bivariate correlations were performed to explore relationships between cardiac interoceptive measures and T_{lim}. Finally, partial correlations were performed on $f_{c\ recovery}$ and cardiac interoceptive measures, controlling for markers of aerobic fitness (PO_{peak}, $\dot{V}O_{2\ peak}$).

6.4. Results

6.4.1. Group Characteristics

Based on the inclusion criteria for performance in the constant load task, two participants were excluded from analysis for failing to achieve a minimum performance standard of 4 minutes before exercise termination (T_{lim}: 115 s and 208 s, respectively). Further, one participant was identified as an extreme outlier in the dataset based on T_{lim} (1278-s, *z*-score = 4.15) and was also excluded from the final dataset. Subsequently, application of the median demarcation and 95% CI criterion for interoception group membership resulted in the removal of a further eight participants from the dataset, resulting in a total of 15 participants (8 poor perceivers [POOR], 7 good perceivers [GOOD]) were included into the final analysis.

Demographic data for the two groups are shown below (Table 6.1). The data revealed that stature ($t_{(13)} = 2.6$, $p = .02$, $g = 1.27$) and body mass ($t_{(13)} = 2.4$, $p = .03$, $g = 1.15$) were greater for GOOD compared with POOR. These effects likely reflected the descriptive differences in gender distributions of the two groups, with a greater proportion of female participants in POOR compared with GOOD. No differences were observed between the two groups with respect to age ($t_{(13)} = 0.3$, $p = .76$, $g < .01$).

Table 6.1. Demographic characteristics for good (GOOD) and poor (POOR) heartbeat perceivers.

	GOOD (N = 7)	POOR (N = 8)	*t*-statistic	*p*-value	Hedge's *g*
Gender	5M, 2F	2M, 6F	-	-	-
Age (yrs)	23 ± 3	23 ± 2	0.3	.76	< .01
Stature (cm)	178 ± 7	168 ± 8	2.6	.02*	1.27
Body Mass (kg)	74.7 ± 8.7	62.8 ± 10.6	2.4	.03*	1.15

Data presented as mean ± SD, yrs = years, cm = centimetres, kg = kilogram, * $p < .05$

Cardiac Interoception and Aerobic Fitness

Between-groups differences in scores for accuracy, confidence, and awareness across both heartbeat perception tasks are shown below in Table 6.2. Analysis of the groups revealed significant differences in terms of discrimination accuracy ($t_{(13)} = 7.6$, $p < .01$, $g = 3.86$). However, no significant differences were observed between the groups for any other measures of interoceptive sensitivity.

Aerobic fitness characteristics for the two interoception groups are also shown in Table 6.2. Analysis of the data revealed that GOOD produced significantly greater PO's at VT_1 ($t_{(15)} = 2.3$, $p = .04$, $g = 1.12$), VT_2 ($t_{(15)} = 2.4$, $p = .03$, $g = 1.17$) and Peak ($t_{(15)} = 2.5$, $p = .03$, $g = 1.21$) compared with POOR. No significant differences were observed for any of the other measured variables; however, large effect sizes were evident for the $\dot{V}O_2$ values at VT_1 ($g = .85$), VT_2 ($g = .86$), and Peak ($g = .89$) between the two groups.

Table 6.2. Group characteristics for good (GOOD) and poor (POOR) heartbeat perceivers related to measures of cardiac interoception and physiological parameters.

		GOOD (N = 7)	POOR (N = 8)	*t*-statistic	*p*-value	Hedge's *g*
Interoception Tracking (SU)	Accuracy	0.69 ± 0.23	0.52 ± 0.31	1.2	.26	.58
	Sensibility	5.4 ± 2.3	5.2 ± 2.7	0.3	.75	.08
	Awareness	0.18 ± 0.29	0.11 ± 0.68	0.8	.46	.12
Interoception Discrimination (SU)	Accuracy	0.72 ± 0.09	0.28 ± 0.12	7.6	< .01*	3.86
	Sensibility	5.8 ± 1.7	4.43 ± 2.33	1.5	.16	.63
	Awareness	0.53 ± 0.22	0.41 ± 0.14	1.8	.10	.62
VT_1	PO (W)	205 ± 74	139 ± 32	2.3	.04*	1.12
	PO (% PO_{peak})	64 ± 12	57 ± 10	1.1	.30	.61
	$\dot{V}O_2$ ($L \cdot min^{-1}$)	2.33 ± 0.77	1.83 ± 0.25	1.8	.10	.85
	$\dot{V}O_2$ ($mL \cdot kg^{-1} \cdot min^{-1}$)	31 ± 9	30 ± 6	0.4	.69	.12
VT_2	PO (W)	258 ± 75	186 ± 38	2.4	.03*	1.17
	PO (% PO_{peak})	80 ± 7	77 ± 8	0.5	.62	.38
	$\dot{V}O_2$ ($L \cdot min^{-1}$)	3.08 ± 0.99	2.41 ± 0.41	1.9	.08	.86
	$\dot{V}O_2$ ($mL \cdot kg^{-1} \cdot min^{-1}$)	42 ± 12	38 ± 5	0.7	.49	.42
Peak	PO (W)	321 ± 79	242 ± 41	2.5	.03*	1.21
	$\dot{V}O_2$ ($L \cdot min^{-1}$)	3.83 ± 1.11	3.03 ± 0.52	1.8	.09	.89
	$\dot{V}O_2$ ($mL \cdot kg^{-1} \cdot min^{-1}$)	51 ± 14	48 ± 6	0.6	.59	.27
Heart Rate ($beats \cdot min^{-1}$)	Rest	62 ± 17	71 ± 18	1.4	.19	.48
	Peak	181 ± 11	188 ± 5	1.6	.16	.79

Data presented as mean ± SD, SU = standardised units, VT_1 = first ventilatory threshold, VT_2 = second ventilatory threshold, W = watts, $L \cdot min^{-1}$ = litres per minute, $b \cdot min^{-1}$ = beats per minute, * $p < .05$

6.4.2. Time-to-Task Failure

<u>Task Performance</u>

The average PO during the constant load task was 250 ± 62 W for GOOD and 191 ± 34 W for POOR. This corresponded to 98 ± 10 % and 104 ± 11 % of the PO at VT_2 (% PO_{VT2}) for GOOD and POOR respectively. Mean PO were found to be not significantly different between the two groups (e.g., % PO_{VT2}; $t_{(13)} = 1.2$, $p = .26$, $g = .54$). T_{lim} for both groups is shown in Figure 6.1. Analysis of the data indicated that that the two groups were not significantly different for T_{lim} ($t_{(13)}$ = 1.1, p = .29, g = .19). Similarly, total work completed for the constant load task was also found to be non-significantly different between GOOD (120.3 ± 56.8 kJ) and POOR (78.3 ± 23.2 kJ) despite evidence for a large effect ($t_{(13)}$ = 1.8, p = .11, g = .94).

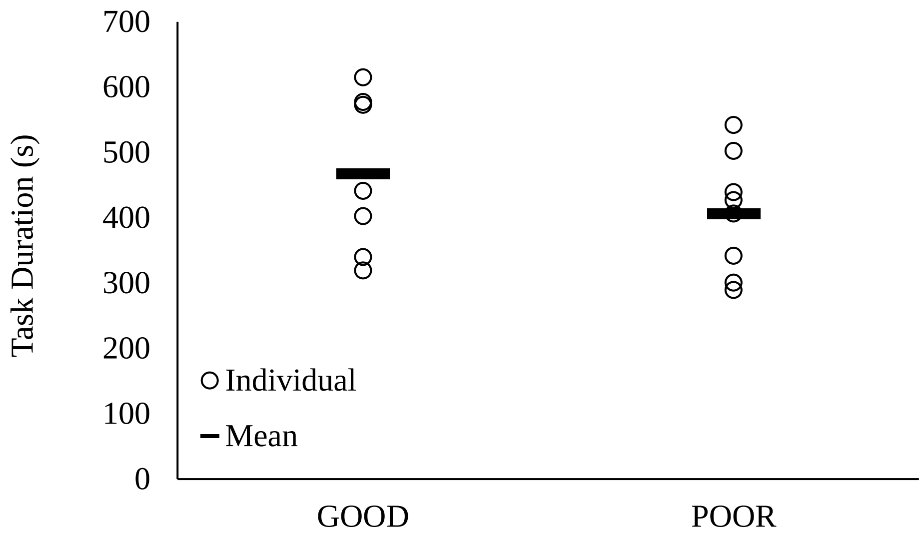


Figure 6.1.
Task duration (s) during a constant-load task at 80% of peak power output for good (GOOD) and poor (POOR) heartbeat perceivers.

Considering the observed differences in gender distribution of the two groups, exploratory analysis comparing male (468 ± 118 s) and female (405 ± 94 s) indicated that T_{lim} was not significantly different between the two genders despite a moderate ES for the difference ($t_{(13)}$ = 1.1, p = .27, g = .56). Finally, correlational analysis comparing T_{lim} with measures of relative exercise intensity, described in terms of $\%PO_{VT1}$ ($r_{(15)}$ = - .475, p = .07, 95%CI = [-.04, 22]), $\%PO_{VT2}$ ($r_{(15)}$ = - .311, p = .26, 95%CI = [-.00, 20]), and $\%PO_{peak}$ ($r_{(15)}$ = - .496, p = .06, 95%CI = [-.02, 16]) indicated that performance was not significantly associated with the relative intensity of the constant-load task (Figure 6.2).

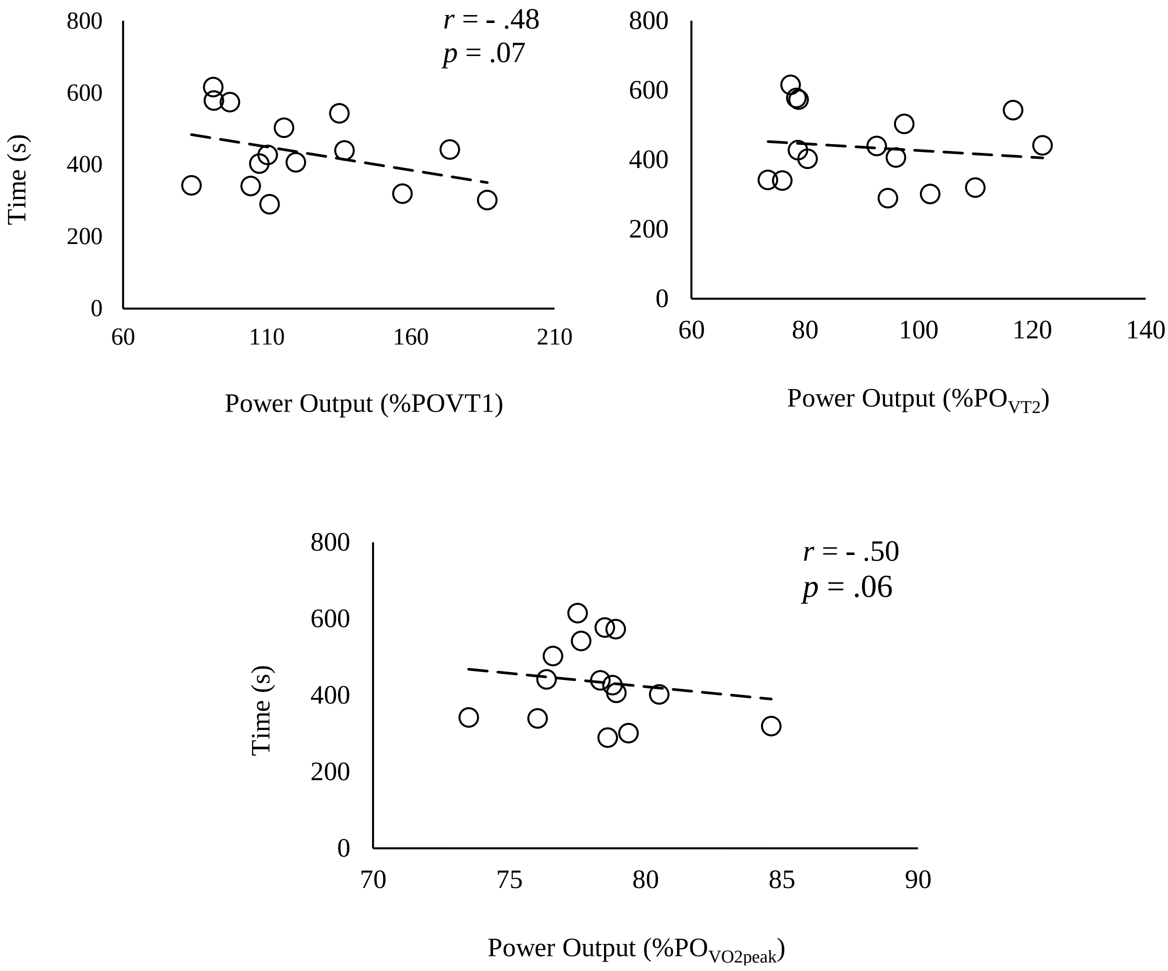


Figure 6.2. Relationship for the time-to-task failure during a constant-load cycling task at 80% of peak power output with (a) power output relative to the power output at the first ventilatory threshold (%PO$_{VT1}$), (b) power output relative to the power output at the second ventilatory threshold (%PO$_{VT2}$), (c) power output relative to the power output at peak oxygen consumption (%PO$_{VO2peak}$).

Physiological Responses

$\dot{V}O_2$, $\dot{V}_E$, V_T, f_b, and RER are shown together below (Figure 6.3). The normalised data (relative to peak values) for $\dot{V}O_2$, $\dot{V}_E$, V_T were not significantly different between the two groups ($p > .19$, $\eta_p^2 < .14$). Similarly, the ANOVA also indicted that RER was not different between GOOD and POOR in the task ($F_{(1, 13)} = 4.293$, $p = .06$, $\eta_p^2 = .25$). However, a main effect of time was observed for $\dot{V}O_2$ ($F_{(1.232, 16.017)} = 113.666$, $p < .01$, $\eta_p^2 = .90$), $\dot{V}_E$ ($F_{(1.351, 17.561)} = 86.235$, $p < .01$, $\eta_p^2 = .87$), V_T ($F_{(1.499, 19.483)} = 37.242$, $p < .01$, $\eta_p^2 = .74$), f_b ($F_{(1.845, 23.981)} = 124.080$, $p < .01$, $\eta_p^2 = .91$), and RER ($F_{(1.536, 19.972)} = 69.706$, $p < .01$, $\eta_p^2 = .84$). *Post hoc* analysis of the significant main effect of time revealed significant differences between all timepoints for $\dot{V}O_2$, $\dot{V}_E$, and f_b. V_T was significant for minutes 1 and 2 ($p < .01$) only. Similarly, f_b was significantly different at all time points ($p < .01$) except for between minutes 2 and 3 ($p = .15$). RER was significantly different between minutes 1 and 2 ($p < .01$) and minutes 2 and 3 ($p < .01$) only. Conversely, analysis of the interaction effect between group and time failed to reveal any significant differences between the two groups across any of the measured variables described.

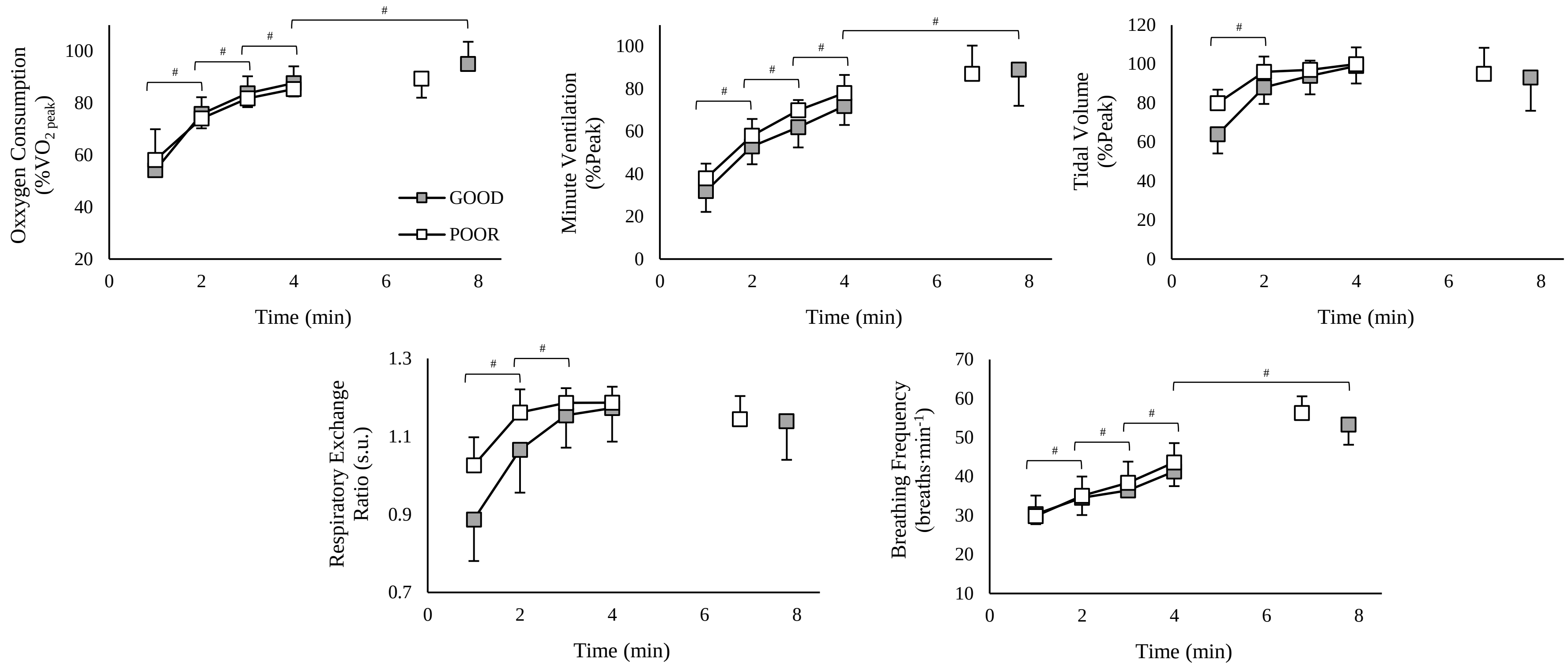


Figure 6.3. Differences between good (GOOD) and poor (POOR) heartbeat perceivers on the physiological responses during a constant load cycling task at 80% PO_{peak}. A: oxygen consumption ($\dot{V}O_2$). B: minute ventilation ($\dot{V}_E$). C: tidal volume (V_T). D: respiratory exchange ratio (RER). E: breathing frequency (f_b). Data presented as mean ± SD. For $\dot{V}O_2$, $\dot{V}_E$, and V_T data were normalised based peak values obtained from a graded exercise test. SU = standardised units. # Significant effect of time ($p < .05$).

Heart rate responses during the constant load task are shown in Figure 6.4. Data for time effects violated assumptions of sphericity ($W_{(5)}$ = .158, p = .01) and were accounted for using Greenhouse-Geisser correction factor (ε = .652). The ANOVA revealed that f_c increased significantly over time ($F_{(2.610, 33.929)}$ = 249.606, p < .01, η_p^2 = .95) with *post hoc* analysis indicating significant differences in f_c for all time-point (p's < .01). Conversely, no significant effects were observed for the main effect of group ($F_{(1,13)}$ = 1.134, p = .90, η_p^2 < .01) or the interaction between group and time ($F_{(9.122, 33.929)}$ = 2.230, p = .11, η_p^2 = .15).

Post-exercise $f_{c\ recovery}$ revealed reductions of 44 ± 19 b·min^{-1} for GOOD and 28 ± 5 b·min^{-1} for POOR over the first minute following the end of the task. An independent samples t-test indicated that $f_{c\ recovery}$ was reduced to a significantly greater extent in GOOD than POOR ($t_{(15)}$ = 2.4, p = .03) with a large magnitude of the difference between the two groups (g = 1.14). However, examining the strength of this relationship, when accounting for the potential confounding effect of differences in aerobic fitness (as seen in Table 6.2), partial correlational analysis indicated that the relationship between heartbeat discrimination accuracy and $f_{c\ recovery}$ was not significant when considering $\dot{V}O_{2\ peak}$ (r = .31, p = .29, 95% CI = [-.17, .76]).

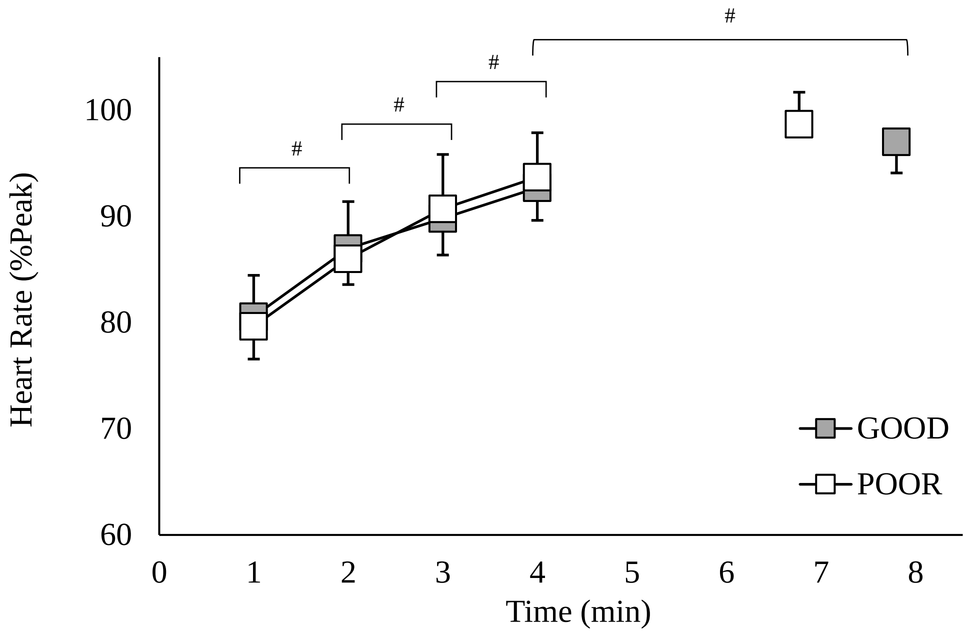


Figure 6.4. Heart rate responses (% peak heart rate recorded in a graded exercise task) for good (GOOD) and poor (POOR) heartbeat perceivers during a constant load task at 80% PO_{peak}. Data presented as mean ± SD. # Significant effect of time (p < .05).

<u>Perceptual Responses</u>

Changes in RPE during the constant load task are shown in Figure 6.5. Analysis of the data indicated that RPE scores increased significantly over time ($F_{(1.696, 22.047)} = 106.478$, $p < .01$, $\eta_p^2 = .89$) but were not significantly different for either the main effect of group ($F_{(1, 13)} = 3.020$, $p = .11$, $\eta_p^2 = .19$) or the interaction between group and time ($F_{(3, 39)} = .641$, $p = .59$, $\eta_p^2 = .05$). *Post hoc* analysis of the main effect of time revealed significant differences between all timepoints ($p < .01$).

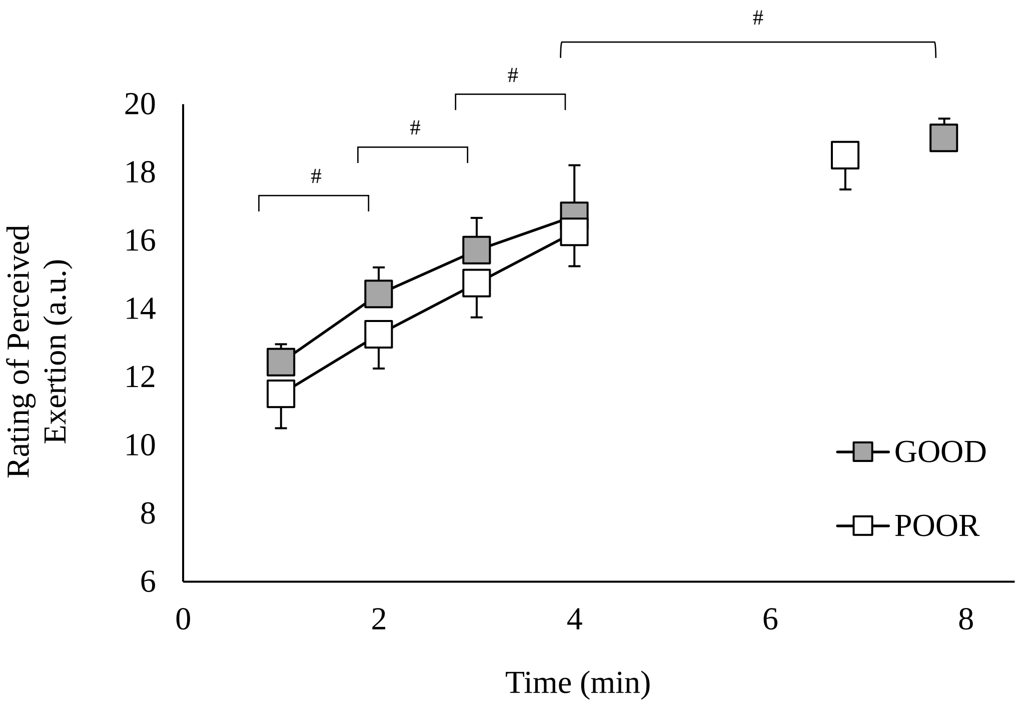


Figure 6.5. Rating of perceived exertion (RPE) for good (GOOD) and poor (POOR) heartbeat perceivers during a constant load task at 80% PO_{peak}. Data presented as mean ± SD. a.u. = arbitrary units. # Significant effect of time.

6.4.3. Exploratory Correlations

For exploratory analysis, the eight participants removed following interoceptive group membership allocation (see Section 6.4.1) were reincluded into the dataset. Correlational analysis revealed that T_{lim} exhibited non-significant relationships with all measures of cardiac interoception (Figure 7.5) including: tracking accuracy ($r_{(23)}$ = .38, p = .08, 95% CI = [.05, .63]), tracking sensibility ($r_{s(23)}$ = .06, p = .80, 95% CI = [-.39, .50]), tracking awareness ($r_{(23)}$ = .15, p = .51, 95% CI = [-.30, .51]), discrimination accuracy ($r_{(23)}$ = .27, p = .22, 95% CI = [-.21, .61]), discrimination sensibility ($r_{(23)}$ = .27, p = .22, 95% CI = [-.26, .62]), discrimination awareness ($r_{(23)}$ = -.01, p = .95, 95% CI = [-.51, .47]).

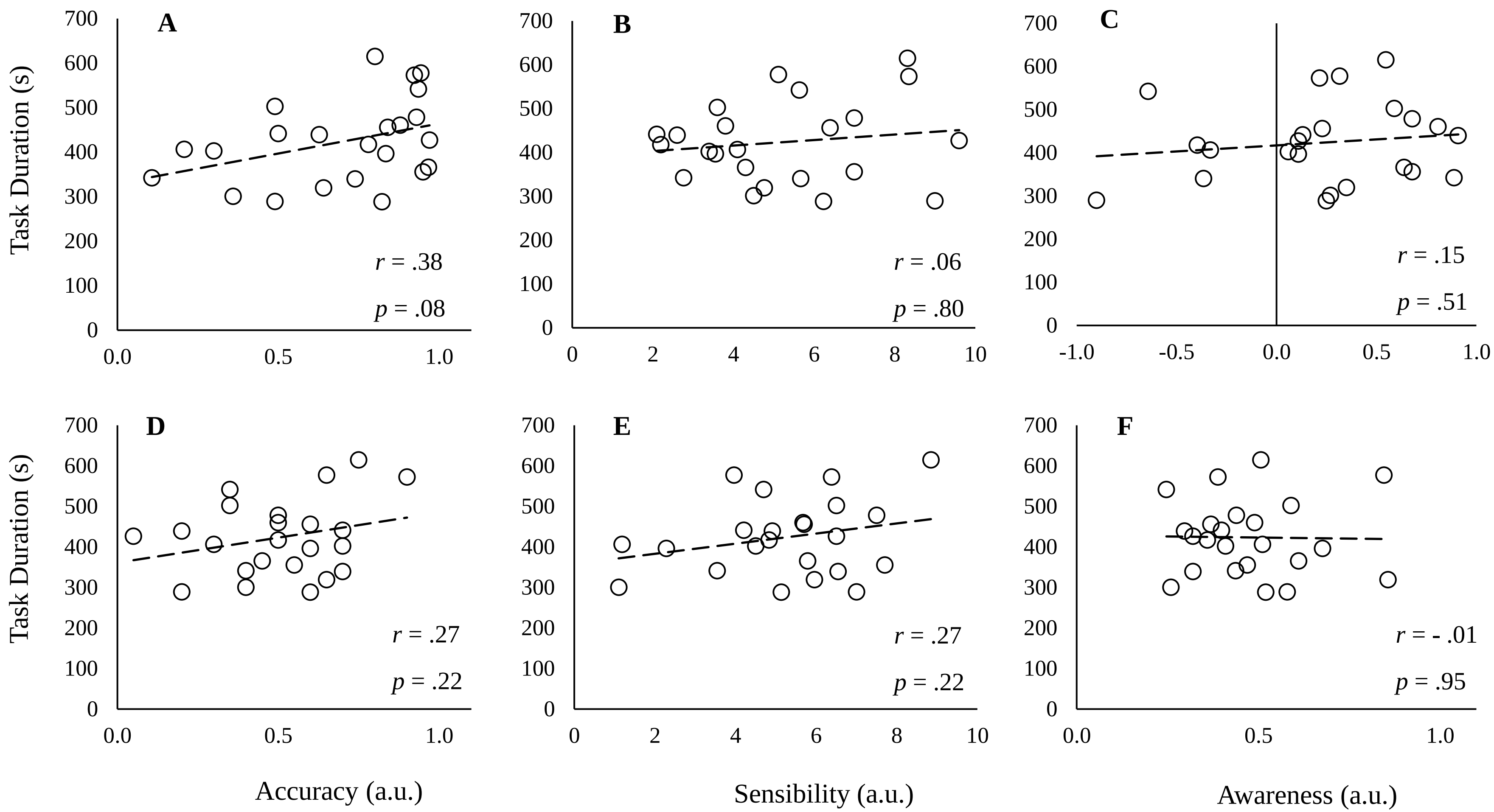


Figure 6.6. Relationship between the time-to-task failure during a constant-load cycling task at 80% of peak power output and (A) heartbeat tracking accuracy, (B) heartbeat tracking sensibility, (C) heartbeat tracking awareness, (D) heartbeat discrimination accuracy, (E) heartbeat discrimination sensibility, (F) heartbeat discrimination awareness.

6.5. Discussion

This is the first study to examine the influence of cardiac interoception on exercise tolerance during a constant load cycling task. The results of this study indicated that individual differences in cardiac interoception did not influence exercise tolerance during the constant load task, with good (GOOD) and poor (POOR) heartbeat perceivers demonstrating comparable time-to-task failure (T_{lim}) at 80% PO_{peak}. Furthermore, an examination of the data between GOOD and POOR indicated that both the physiological data (e.g., heart rate, oxygen consumption) as well as RPE data were not significantly different between the two groups, suggesting that differences in cardiac interoception did not influence these parameters.

6.5.1. Contextualising the Time-to-Task Failure Data

Time-to-task failure was notably shorter among the present cohort compared with previous studies examining exercise tolerance at 80% PO_{peak} (Egaña, Green, Garrigan, & Warmington, 2006; Goodall, González-Alonso, Ali, Ross, & Romer, 2012; Marcora et al., 2009; Sidhu, Cresswell, & Carroll, 2012). For instance, Marcora and colleagues (2009) reported T_{lim} at 80% PO_{peak} was 754 ± 339 s, which was ~73% greater than the average duration observed in the present study, but notably with substantially larger variations in performance between participants (45% CV compared with 25% CV for this study). Interestingly, both of these studies examined performance in samples comprised of male and female participants. Examining the effect of gender on performance, Egaña, Green, Garrigan, and Warmington (2006) reported that males cycled ~170% longer to T_{lim} when cycling at 80% PO_{peak} than females. However, this effect (Section 7.4.1) was not observed in the present study despite differences in the gender distributions of the two groups (Table 6.1). Differences in these findings are therefore likely to reflect differences in the relative exercise strain obtained using arbitrary workloads (i.e., 80% PO_{peak}) which may reflect very different magnitudes of physiological strain, particularly when described in terms of biological markers such as lactate or ventilatory thresholds. Related to this observation, the short duration of T_{lim} observed in the present study, alongside the non-significant relationships observed between T_{lim} and measures of relative exercise intensity (i.e., %PO at VT_1, VT_2, and Peak; Figure 6.2), indicates that the relative exercise intensity was likely to reflect a more severe exercise intensity than in previous comparable studies, with a potentially important contribution of anaerobic energy pathways influencing T_{lim} (Housh, Housh, & Bauge, 1990).

6.5.2. Effect of Interoception on Exercise Tolerance

The current study demonstrates that individual differences in cardiac interoception did not influence exercise tolerance during a constant-load exercise task. Support for this finding is obtained from the observation the GOOD and POOR (based on heartbeat discrimination accuracy) were not significantly different in their T_{lim} (Figure 6.1) and correlational analysis further demonstrated T_{lim} was not significantly associated with any of the measured constructs of cardiac interoception in this study (Figure 6.6). This finding contrasts with previous observations that have suggested that greater cardiac interoceptive accuracy is associated with reduced physical work rates, despite comparable levels of subjective fatigue (Herbert et al., 2007), although differences in the approaches to assessing interoception (e.g., Herbert et al., 2007 used the heartbeat tracking task with group demarcation based on 85% accuracy score) and exercise tolerance may have contributed to these discrepancies, which may affect the comparability of the respective findings.

Independent of a person's cardiac interoceptive characteristics, previous studies have demonstrated that enhanced attention towards interoceptive cues, through manipulation of environmental cues (Pennebaker & Lightner, 1980) or direction of attentional focus towards physical symptoms (Fillingim & Fine, 1986), results in (a) greater rating of subjective fatigue during treadmill walking, and (b) reductions in running distance during self-paced exercise despite comparable ratings of fatigue at submaximal intensities. Importantly, these previous studies have typically examined exercise behaviour in self-paced exercise tasks. By contrast, Machado and colleagues (2019) demonstrated comparable findings to the present study using a graded exercise task, whereby good and poor perceivers (based on heartbeat tracking accuracy) were not found to significantly differ in their performance. Comparing the differences in the findings between these different studies raises two potential considerations related to the influence of cardiac interoception on exercise behaviour. Firstly, cardiac interoception may exert greater influence in closed-loop (i.e., known endpoint), self-paced exercise tasks because of the opportunity for interoceptive feedback to influence pacing (e.g., Herbert et al., 2007; Pennebaker & Lightner, 1980) compared with open-loop externally prescribed exercise tasks where exteroceptive information (for instance a visual display of a set PO or cadence) is provided to regulate output (e.g., Machado et al., 2019) and secondly, differences in the relative exercise intensity may also influence differences in the observed findings, with the self-paced tasks being performed at lower relative exercise intensities compared with the respective open-loop externally prescribed tasks.

6.5.3. Cardiac Interoception and Perceived Exertion

The results for this study also indicated that cardiac interoception did not influence the participant's subjective RPE during exercise. Changes in RPE throughout the exercise task were found to be comparable between GOOD and POOR, with no differences in the reported values at any of the measures timepoints (Figure 6.5). This finding is noteworthy as RPE is thought to emerge, at least in part, from the processing of afferent sensory inputs related to the physiological condition of the body (Hampson, St Clair Gibson, Lambert, & Noakes, 2001) that are processed within the insular cortex (Williamson et al., 1999). It is therefore surprising that differences between a person's sensitivity to their body at rest (as indicated by measures of heartbeat perception accuracy) did not influence sensitivity to changes in physiological strain with both groups demonstrating comparable shifts in physiological parameters during the constant load task (Figures 6.3 and 6.4).

One interpretation of this conflicting finding is to propose that cardiac interoceptive sensitivity may not solely influence the factors which underlie the perception of exertion. The RPE scale was developed as a gestalt measure of perceived somatic stress (G. A. Borg, 1970), which likely integrates information across multiple interoceptive axes (e.g., cardiac, respiratory, thermal, metabolic, and chemo-sensitive channels). While RPE is strongly correlated with changes in heart rate during exercise (Chen, Fan, & Moe, 2002) the contribution of other interoceptive axes should also be considered. For instance, Christian and colleagues (2014) identified perceived 'breathing difficulty' as the primary perceptual component associated with effort perception in hypoxia, with no difference in peripheral or limb discomfort (for a given level subjective of effort) between hypoxia and normoxia. Comparably, cutaneous thermal afferents have been also shown to influence the perception of effort in hot environments (Roussey et al., 2018). Measures of interoceptive sensitivity indicate that although performance for cardiac and gastric interoceptive axes show good correspondence (Herbert, Muth, Pollatos, & Herbert, 2012; Whitehead & Drescher, 1980), the relationship between cardiac and respiratory interoceptive accuracy is less clear (Harver et al., 1993; Pennebaker et al., 1985 cited in Vaitl, 1996), despite evidence of a shared metacognitive component (interoceptive awareness) across these two axes (Garfinkel et al., 2016). This suggests that measures of cardiac interoception are unlikely to provide an appropriate proxy for expressing the multitude of interoceptive inputs experienced during exercise. Consideration of the particular interoceptive channel should be applied depending on the specific allostatic demands generated by the exercise task (e.g., examining respiratory interoception to assess latent sensitivity to breathing difficulty during exercise in hypoxia).

PE may also be generated from the processing of neural inputs emerging through distinctly non-interoceptive pathways. For instance, sense of effort, which describes the perceptual experience of how “hard, heavy or strenuous a task is” (Marcora, 2010), has been shown to emerge through the central interpretation of efferent motor drive and related corollary discharge rather than afferent feedback (de Morree et al., 2012; Zénon et al., 2015) and may have been a factor in participant's perception of exertion. Furthermore, the relationship between RPE and physiological markers of strain are modifiable according to expectations regarding task duration (Eston et al., 2012) and within the contexts of head-to-head competition (Corbett, Barwood, Ouzounoglou, Thelwell, & Dicks, 2012). RPE also appears to be modifiable by psychological appraisal. For instance, motivational self-talk has been shown to alter the relationship between exercise intensity and RPE, improving performance for both self-paced (Barwood, Corbett, Wagstaff, McVeigh, & Thelwell, 2015) and fixed intensity exercise (Blanchfield, Hardy, De Morree, Staiano, & Marcora, 2014). Taken together, these findings suggest that both psychological factors and non-interoceptive sensory inputs represent important mediating factors in the perception of exertion. Therefore, sensitivity to interoceptive signals may simply represent one partial aspect of a person’s appraisal of their perceived exertion during exercise.

Alternatively, the results of this study could indicate that greater interoceptive sensitivity at rest may not reflect sensitivity to changes to interoceptive inputs during states of augmented arousal. For instance, previous studies using pharmacological manipulation of cardiac arousal have been used to show that heartbeat perception accuracy improves with increases in heart rate (Khalsa, Rudrauf, Sandesara, Olshansky, & Tranel, 2009; Khalsa, Rudrauf, Hassanpour, Davidson, & Tranel, 2020). Similarly, transient improvements in heartbeat perception accuracy have also been shown to occur following engagement in physical activity (Jones & Hollandsworth, 1981). However, these improvements in heartbeat perception accuracy appear to be greater among poor heartbeat perceivers, with minimal augmentation among good perceivers. Consequently, elevations in physiological arousal may act to minimise the observed differences in interoceptive sensitivity that are characteristic of individuals at rest, suggesting that the experience of physical exertion is likely to be equivocal between good and poor heartbeat perceivers, at least during heavy or severe exercise intensity domains.

6.5.4. Effect of Interoception on the Physiological Responses to Exercise

The present study did not find evidence to suggest that cardiac interoception influences physiological responses to the constant-load exercise task or heart rate recovery following exercise cessation (*see* p. 146). By contrast, previous studies have demonstrated that more accurate heartbeat perception is associated with greater cardiac reactivity in response to physical exertion in an isometric exercise task (Pollatos, Herbert, et al., 2007) and also to increased emotional arousal (Pollatos et al., 2005). These discrepancies are likely to also reflect the potential influence of differing magnitudes of arousal induced through the respective interventions. The level of physiological arousal induced in the present study is demonstrably greater than the intensity of physiological arousal induced via localised isometric contraction of the forearm musculature and also arousal experienced from emotional picture presentation. This effect, therefore, supports the notion that substantial elevations in arousal are likely to diminish individual differences in interoceptive characteristics, which putatively also influence the regulation of autonomic reflexes (e.g., cardiac function). The relationship between heartbeat perception and autonomic function is thought to be underpinned within the insular cortex (Hassanpour et al., 2018). Firstly, the insular cortex is involved in the processing of cardio-afferent feedback (Verberne & Owens, 1998) and that better heartbeat perceivers exhibit greater heartbeat-evoked potential (HEP) amplitudes within this region (Pollatos & Schandry, 2004), which are associated with better performance in heartbeat perception tasks (Critchley, Wiens, Rotshtein, Öhman, et al., 2004; Schandry & Montoya, 1996). Furthermore, dysfunction of cardio-autonomic regulation has been reported in stroke patients with observed damage to the insular cortex, particularly within the right hemisphere (Meyer et al., 2004). Consequently, whilst inputs emerging from within the interoceptive network may influence the regulation of autonomic reflexes, differences in interoceptive characteristics (i.e., heartbeat perception) do not appear to affect the response of these physiological systems under contexts of substantial changes in arousal.

6.5.5. Potential Limitations

Interpretation of the findings of this study should be considered in the context of the limitations of the results. Firstly, although the findings (interpreted in the context of previous studies) indicate that increasing physiological arousal acts to diminish the differences in physiological and perceptual effects reported between good and poor heartbeat perceivers at rest, this could not be explicitly established using a singular constant-load exercise task at 80% PO_{peak}. Relatedly, the nature of the exercise task when considered both in terms of the arbitrary exercise intensity (i.e., 80% PO_{peak} rather than being relative to clearly defined exercise intensity domains) and also the limitation on participants capacity to regulate their exercise work rates may be considered to be tertium factors that may have influenced the observed findings of this study. Further, the intensity of the exercise may have been too severe to enable the detection of a mediating effect for cardiac interoception on exercise tolerance, as rapid and substantial changes in physiological stasis were likely to be easily perceived regardless of resting interoceptive sensitivity. Finally, the application of the cardiac group membership inclusion criteria resulted in a relatively large proportion of the current sample being removed from the between-groups analysis, which may have potentially limited the statistical power to draw meaningful inferences from the data.

6.5.6. Future Directions

Further research is necessary to investigate the influence of interoceptive sensitivity on exercise performance and behaviour under different contexts. Specifically, examining potential effects during self-paced exercise such as time-trial protocols to explore the impact of interoceptive sensitivity on pacing behaviours. An additional research avenue is to explore the inter-relationship between interoceptive sensitivity and cardiodynamic responses to exercise-induced stress. This may be potentially relevant in studying cardiodynamic responses to prolonged periods of intensive exercise training, where cardio-autonomic dysfunction is often relevant as a physiological marker of overtraining in athletes (Le Meur et al., 2013), and atypical interoceptive perceptions are hypothesised to occur in clinical forms of fatigue (Hanken, Eling, & Hildebrandt, 2014; Manjaly et al., 2019; Stephan et al., 2016).

6.6. Conclusion

The present study examined the influence of interoceptive sensitivity on exercise tolerance as well as physiological and perceptual responses during high-intensity exercise. The results suggest that interoceptive sensitivity does not influence time-to-task failure nor did it result in any differences in heart rate or respiratory adaptations to changes in allostatic demand. Further research is required to examine whether this effect is influenced by the relative intensity of the exercise task.

CHAPTER 7. THE EFFECT OF CARDIAC INTEROCEPTION ON THE REGULATION OF EXERCISE WORK RATES AND PHYSIOLOGICAL RESPONSES AT FIXED RATINGS OF PERCEIVED EXERTION.

7.1. Abstract

The aim of the third study was to examine the effect of cardiac interoception on self-regulated exercise behaviour using a fixed-RPE based protocol. Twenty-four physically active participants completed tests to determine cardiac interoception and markers of aerobic fitness followed by two 20-minute self-paced exercise tasks at a fixed RPE conducted over separate visits (target RPE of 10 or 16; 6-20 Borg scale, Borg, 1962). Power output (PO), respiratory breath-by-breath exchanges and heart rate (f_c) were measured throughout the fixed-RPE tasks. For statistical analysis, participants were retrospectively allocated to a good (GOOD: n = 9) or poor (POOR: n = 11) cardiac interoception group, based on both median demarcation and 95% confidence intervals of the heartbeat discrimination accuracy data. Aerobic fitness parameters were not significantly different between the two groups for PO_{peak} (GOOD: 308 ± 73 W, POOR: 256 ± 40 W, p = .06), $\dot{V}O_{2\ peak}$ (GOOD: 3.71 ± 0.99 L·min^{-1}, POOR: 3.18 ± 0.51 L·min^{-1}, p = .13), or $f_{c\ peak}$ (GOOD: 182 ± 13 b·min^{-1}, POOR: 184 ± 13 b·min^{-1}, p = .67). For the fixed RPE tasks, comparison of the changes in PO, f_c, and RER from the RPE10 to RPE16 condition were significantly greater in GOOD (PO: 42 ± 18 Δ%Peak; POOR: 20 ± 19 Δ%Peak; f_c: 21 ± 10 Δ%Peak; POOR: 15 ± 12 Δ%Peak; RER: 0.13 ± 0.10 Δs.u.; POOR: 0.09 ± 0.09 Δs.u.). These differences were in-part attributable to a lower relative PO (relative to PO at the first ventilatory threshold; GOOD: 48 ± 21 %PO_{VT1}; POOR: 75 ± 34 %PO_{VT1}), f_c (GOOD: 58 ± 3 %Peak; POOR: 66 ± 2 %Peak) and RER (GOOD: 0.86 ± 0.07 s.u.; POOR: 0.96 ± 0.06 s.u.) observed in GOOD over the first 5-minutes of the RPE10 condition. Cardiac interoception therefore appears to influence judgements related to the selection of optimal exercise work rates during self-paced tasks, particularly at low exercise intensities.

7.2. Introduction

Perceived exertion is considered to be a gestalt phenomenon, integrating information from the periphery (i.e., muscles, cardiovascular, and respiratory) along with central nervous system inputs (i.e., cognitive, motivational, attentional, memory) to provide a singular index of perceived physical strain (Hutchinson & Tenenbaum, 2006). Using Borg's scale for rating of perceived exertion (RPE; Borg, 1982), researchers have demonstrated that perceived exertion increases linearly with duration during constant-load exercise, that exercise termination coincides with reporting of the highest sustainable RPE (e.g., Noakes, Snow, & Febbraio, 2004). Additionally, RPE is also modifiable under different contexts when sensory information from either internal bodily states or the external environment are manipulated (Brownsberger et al., 2013; De Oliveira Pires & Hammond, 2012; Flood, Waldron, & Jeffries, 2017; Hampson et al., 2001; Dave Parry & Micklewright, 2014). During self-paced exercise, researchers suggest that interpretation of RPE is an important factor determining ongoing pacing behaviour alongside expectations of the task demands (i.e., remaining duration) (de Koning et al., 2011; Tucker, 2009).

Researchers suggest that neural processing of physiological afferents contributes to the emergence of perceived exertion (see section 2.5.4). As previously described (Section 2.2), the signalling and processing of these physiological afferents occur largely within the interoceptive network. Evidence from studies manipulating the transduction (e.g., simulation of receptors for type III/IV afferent neurons; Pollak et al., 2014; Schlader, Simmons, Stannard, & Mündel, 2011), transmission (e.g., spinal blockade of type III/IV afferent neurons; Amann, Sidhu, Weavil, Mangum, & Venturelli, 2015; Blain et al., 2016), and processing (e.g., increased cortical excitability of the insula by transcranial direct current stimulation; Okano et al., 2015) of these interoceptive signals demonstrate support for their role in the emergence of perceived exertion and its relationship to muscular work and allostatic demand during exercise. Moreover, researchers have reported that individual differences in the intensity of a person's 'preferred' exercise work rate is related to their perceptual accuracy in tests of cardiac interoception, with greater interoceptive accuracy being associated with lower exercise work rates in a 15-minute cycling task despite comparable ratings of fatigue post-exercise (Herbert, Ulbrich, et al., 2007). Further, studies have demonstrated that increased attention towards interoceptive cues results in increased reports of subjective exertion and fatigue (Fillingim & Fine, 1986; Pennebaker & Lightner, 1980) whereas decreased attention to interoceptive cues results in reduced ratings of perceived exertion and increased work capacity (Mohammadzadeh et al., 2008).

Several studies have demonstrated that aerobically fit individuals are also typically more accurate at perceiving their heartbeats than sedentary individuals (Chapter 4; Georgiou et al., 2015; Jones & Hollandsworth, 1981). Considering the proposed link between greater interoceptive sensitivity with an increased experience of exercise-induced fatigue (Herbert, Ulbrich, et al., 2007), the positive relationship between aerobic fitness and interoceptive accuracy presents a plausibly counterintuitive argument as it suggests a potential for reduced exercise tolerance among aerobically trained populations compared with moderately physically active and sedentary groups. However, Chapter 6 of this thesis did not find support for differences in exercise tolerance related to heartbeat perception accuracy during a constant-load cycling task at 80% PO_{peak}. This suggests that cardiac interoception alone does not influence sensitivity to the physiological strain experienced during heavy-to-severe intensity exercise. Instead, sensitivity to interoceptive afferents may be involved in the optimisation of pacing behaviour during exercise. For instance, spinal blockades of interoceptive afferent pathways show that pacing behaviour is substantial altered in the absence of afferent feedback, leading to greater peripheral neuromuscular fatigue at the end of a self-paced time trial task (Amann et al., 2009; Blain et al., 2016). Consequently, researchers have suggested that optimal pacing behaviour relies on the continual processing of afferent feedback to optimise performance and manage ongoing allostatic demand (Marino, 2004).

Fixed-RPE based protocols provide a useful tool to examine the factors influencing self-paced exercise behaviour (Swart, Lamberts, St Clair Gibson, et al., 2009). In this task, participants voluntarily adjust their work rates to achieve and then maintain a constant RPE. Using this protocol, researchers have demonstrated that work rate decreases as a linear function of exercise duration during exercise at a fixed RPE of 16, representing *hard-to-very hard* exertion (Swart et al., 2009; Tucker, Marle, Lambert, & Noakes, 2006). Moreover, the rate of this decline has been shown to be sensitive to experimental manipulations of physiological strain during exercise. For instance, Tucker and colleagues (2006) demonstrated a significantly greater rate of decline in hot compared to normothermic conditions. Similarly, Browne and Renfree (2013) demonstrated that declines in PO during a cycling task at RPE16 were significantly reduced (21%) when participants were supplemented with sodium bicarbonate. It has been further demonstrated that centrally acting agents (amphetamine; Swart et al., 2009) as well altered thermal perception (L-methanol mouth-rinsing; Flood, Waldron, & Jeffries, 2017) also reduce the rate of decline in power output during exercise at a fixed RPE of 16. Interestingly, these effects have not been extensively explored at other RPE's, which raises further questions regarding potential intensity-dependent effects of regulating exercise behaviour (i.e., pacing strategies) according to RPE.

Despite the usefulness of fixed-RPE based protocols as a framework for examining self-paced exercise behaviour, relatively little is known about the influence of intrinsic factors on the regulation of muscular work within such protocols, specifically differences in cardiac interoception. The aim of this study was to investigate the influence of cardiac interoception on exercise behaviour and physiological responses to exercise at fixed ratings of perceived exertion for both *light* (RPE10) and *hard-to-very hard* (RPE16) intensity exercise. In accordance with the literature outlined above, it was hypothesised that more accurate heartbeat perception would be associated with lower exercising work rates and markers of physiological strain for a given RPE condition. The inclusion of two different prescribed exercise intensities (RPE10 versus RPE16) was undertaken to permit the examination of intensity-dependent effects.

7.3. Methods

7.3.1. Participants

Following ethical approval (see Section 3.3) and collection of informed consent (see Section 3.4), 24 individuals (14 males, 10 females; age 23 ± 3 years, stature 172 ± 9 cm, mass 68.7 ± 10.3 kg) volunteered to participate in the study. Participants were recruited from the University of Brighton. All participants were physically active and accustomed to exercise of a maximal nature.

7.3.2. Experimental Design

Participants visited the laboratory on three separate occasions. During the first visit, participants undertook an assessment of cardiac interoception and completed a graded exercise test to establish aerobic fitness. In the two subsequent visits, participants completed a 20-minute self-regulated exercise task at an RPE of either 10 (*light*) or 16 (*hard to very-hard*), presented in a randomised order. Calibration of equipment was completed prior to all visits as previously described for both the online gas-analysis system (Section 3.10.1; MetaLyzer 3B, Cortex, Germany) and cycle ergometer (Section 3.11.1; High-Performance Ergometer with Rohloff Gear Hub, SRM, GmbH, Jülich, Germany).

7.3.3. Assessment of Aerobic Fitness and Cardiac Interoception

On arrival at the laboratory, the participant's body mass and stature were obtained (see Section 3.7) and cardiac interoception was assessed (see Section 3.9). Subsequently, participants completed the graded exercise test. Participants were instrumented with a heart rate monitor (A300 Fitness Watch, Polar Electro Oyo, Temple, Finland) and a face mask connected to an online gas-analysis system as well as being fitted to the exercise bike. The exercise test was conducted in accordance with the methods and termination criteria outlined in section 3.11.2. Power output (PO), heart rate (f_c), and expired gases were recorded continuously throughout the test. RPE was obtained in the final 15s of each stage using the 6-to-20 Borg scale (Borg, 1982). Following completion of the exercise test and allowing for sufficient recovery, participants completed an 8-minute familiarisation of the fixed-RPE protocol at a rating of 13 on the Borg scale (Section 3.12.1).

7.3.4. Fixed-Rating of Perceived Exertion Tasks

During visits 2 and 3, participants completed the fixed-RPE exercise task. Participants were fitted to the same cycle ergometer and instrumented with a heart rate monitor and face mask connected to the online gas analysis system. Participants were reminded of the procedures and requirements of the exercise task, including a description of the Borg scale and the required level of exertion corresponding to either RPE10 or RPE16. The task began with identical warm-up procedures as the ramp test, consisting of a 3-minute resting sample of expired gases and heart rate before a 5-minute warm-up at 60 W (80 $r \cdot min^{-1}$) and 2-minutes passive recovery. For the fixed-RPE tasks, the cycle ergometer was set to isokinetic mode, maintaining pedalling cadence at 80 $r \cdot min^{-1}$. Participants were required to self-regulate exercise intensity by altering the effort produced through the pedals. In turn, the ergometer in its programmed setting increased or decreased resistive torque accordingly. Standardized feedback was provided every ~2-minutes to remind participants to maintain the desired RPE. Heart rate, expired gases, and PO were recorded continuously throughout the exercise task. Participant’s RPE was obtained every five minutes to assess adherence to the task constraints.

7.3.5. Data Analysis

Cardiac Interoception

Cardiac interoception was analysed in accordance with the methods outlined in section 3.9.3.

Aerobic Fitness

Breath-by-breath data was converted to second-by-second (Metalyser software, Cortex, Germany) and analysed across rolling 30-s averages.

Participant's aerobic fitness was determined using the methods previously described (Sections: 3.11.3, 3.11.5, 3.11.7).

RPE Clamp Task

Data for PO was calculated for absolute (W) and relative values. Relative POs were contextualised against average trial PO (%Trial$_{mean}$), PO at ventilatory thresholds (%PO$_{VT1}$ for RPE10, %PO$_{VT2}$ for RPE16), and peak PO observed in the graded exercise test (%PO$_{peak}$). $\dot{V}O_2$, RER, and f_c were also calculated relative to peak values identified in the graded exercise test. Data were then averaged over sequential 1-minute periods for the first 5 minutes of exercise, and then 5-minute epochs from minute 5 onwards. This approach was used to reflect the changing nature of $\dot{V}O_2$ kinetics during the early stages of exercise, whereby dynamic changes in $\dot{V}O_2$ responses are observed in the first 3-5 minutes of exercise followed by a more stable (steady-state or slow) component thereafter (Jones & Burnley, 2009). Finally, the change from RPE10 to RPE16 was calculated for the dependent measures relative to peak (PO, $\dot{V}O_2$) and absolute (PO (PO$_{abs}$), f_c, RER) to compare differences between the two groups.

Statistical Analysis

Statistical analysis was completed using SPSS 25 (IBM Corp, USA). Data were examined for assumptions of parametric distribution and tests of equality according to the methods outlined in section 3.13.5.

The sample was divided into good (GOOD) and poor (POOR) heartbeat perceivers according to the methods outlined previously (see Section 4.4.1). Group characteristics for stature, mass, age, aerobic fitness, and cardiac interoception were examined using independent samples *t*-tests.

For the fixed-RPE data, task adherence was examined using Friedman's test on the RPE data to determine differences between the two groups. Data for each minute of the first 5 minutes of the fixed-RPE tasks were examined using 2-way (2 x 5) (GROUP x TIME) mixed methods ANOVA. Analysis of the 5-minute epochs was examined using 2-way (2 x 3) (GROUP x TIME) mixed methods ANOVA and are reported with respect to the final minute of each epoch (e.g., minute 10, minute 15, minute 20). *Post hoc* analysis was performed using Bonferroni-corrected pairwise comparisons. Exploratory analysis, relationships between relative changes in PO (average PO throughout the duration of the trial, normalised to participants $\%PO_{peak}$) from RPE10 to RPE16 conditions were compared with measures of cardiac interoception (accuracy, sensibility, awareness) for both heartbeat perception tasks (tracking, discrimination) were assessed using Kendal's τ following observation that change in mean trial $\%PO_{peak}$ violated assumptions of normality ($W_{(20)} = .900$, $p = .04$).

Parametric data are presented as mean ± SD and non-parametric data are presented as median (lower quartile – upper quartile). Effect sizes were examined as previously described (Section 3.13.8).

7.4. Results

7.4.1. Group Characteristics

Application of the median demarcation and 95% CI criterion for interoception group membership resulted in the removal of four participants from the total sample (two participants each from GOOD and POOR). This resulted in a total of 20 participants (11 POOR; 9 GOOD) being included in the final analysis.

Group characteristics are shown in Table 7.1. No significant differences were found for age, stature, or body mass (*p's* $\geq .27$). For cardiac interoception, GOOD were more accurate in their HBD as a result of the grouping criteria ($p < .01$) and also demonstrated greater confidence in HBT compared with POOR ($p = .02$). HBD awareness was marginally non-significant between groups ($p = .06$) after accounting for violations to the assumption of equality ($F = 6.717$, $p = .02$), despite a large effect size for this difference ($g = .95$). Parameters for aerobic fitness were also found to be non-significantly different between the two groups; however, PO_{peak} ($p = .06$, $g = .87$), PO_{VT1} ($p = .06$, $g = .91$) and PO_{VT2} ($p = .06$, $g = .86$) demonstrated large effect sizes despite being marginally non-significant.

Table 7.1. Group characteristics for good (GOOD) and poor (POOR) heartbeat perceivers related to measures of interoceptive sensitivity and physiological parameters.

		GOOD (N = 9)	POOR (N = 11)	Test statistic	*p*-value	Hedge's *g*
Demographic Characteristics	Age (yrs)	22 (21-26)	22 (21-22.5)	61.5^{U}	.37	.45
	Stature (cm)	174.3 ± 9.7	170.2 ± 7.7	1.1	.31	.45
	Mass (kg)	71.7 ± 9.7	66.2 ± 11.6	1.2	.27	.49
	Sex	5M, 4F	6M, 5F	-	-	-
Interoception Tracking (SU)	Accuracy	0.72 ± 0.21	0.67 ± 0.24	0.4	.66	.21
	Sensibility	5.3 ± 2.1	3.0 ± 1.9	2.6	.02*	1.11
	Awareness	0.25 ± 0.30	0.40 ± 0.58	0.7	.49	.30
Interoception Discrimination (SU)	Accuracy	0.72 ± 0.08	0.42 ± 0.10	7.4	< .01*	3.14
	Sensibility	5.9 ± 1.5	4.6 ± 1.8	1.8	.10	.74
	Awareness	0.56 ± 0.21	0.40 ± 0.11	$2.1^{\#}$	.06	.95
Peak	PO (W)	308 ± 73	256 ± 40	2.0	.06	.87
	$\dot{V}O_2$ ($L \cdot min^{-1}$)	3.71 ± 0.99	3.18 ± 0.51	1.6	.13	.67
	$\dot{V}O_2$ ($mL \cdot kg^{-1} \cdot min^{-1}$)	51 ± 13	48 ± 5	0.5	.64	.30
VT_1	PO (W)	190 ± 71	141 ± 27	2.0	.06	.91
	PO ($\%PO_{peak}$)	61 ± 12	57 ± 9	0.8	.41	.37
	$\dot{V}O_2$ ($L \cdot min^{-1}$)	2.22 ± 0.71	1.83 ± 0.30	1.7	.12	.71
	$\dot{V}O_2$ ($mL \cdot kg^{-1} \cdot min^{-1}$)	30 ± 8	29 ± 5	0.3	.77	.15
VT_2	PO (W)	249 ± 67	203 ± 35	2.0	.06	.85
	PO ($\%PO_{peak}$)	81 ± 6	77 ± 11	0.9	.37	.42
	$\dot{V}O_2$ ($L \cdot min^{-1}$)	3.01 ± 0.79	2.55 ± 0.58	1.5	.17	.65
	$\dot{V}O_2$ ($mL \cdot kg^{-1} \cdot min^{-1}$)	41 ± 11	38 ± 5	0.9	.40	.35
Heart Rate ($b \cdot min^{-1}$)	Rest	59 ± 17	69 ± 10	1.6	.14	.71
	Peak	182 ± 13	184 ± 13	0.4	.67	.15

Abbreviations: SU = standardised units, PO = power output, W = watts, $\dot{V}O_2$ = oxygen consumption, $L \cdot min^{-1}$ = litres per minutes, $b \cdot min^{-1}$ = beats per minute, * Significant difference between groups p < .05. # t-statistic corrected for violations to Levene's Test for Equality of Variances.

7.4.2. RPE Clamp Task

Task Adherence

The reported RPE values were found to be non-significantly different between the two groups, suggesting that the perceived effort exerted by both groups was comparable (Table 7.2, p > .15). Furthermore, median values for RPE matched the target RPE for both groups across all time points, except for minute 5 in the RPE16 condition.

Table 7.2. Rating of perceived exertion during fixed-RPE tasks (RPE10 and RPE16) for good (GOOD) and poor (POOR) heartbeat perceivers.

Condition	Group	Time (min)			
		5	10	15	20
RPE10 (a.u.)	GOOD	10 (9 - 10)	10 (10 - 10)	10 (10 - 10)	10 (10 - 10)
	POOR	10 (10 - 11)	10 (10 - 10.5)	10 (10 - 10)	10 (10 - 10)
RPE16 (a.u.)	GOOD	14 (13 – 15)	16 (15 – 16)	16 (16 – 17)	16 (16 – 16)
	POOR	15 (15 – 15.5)	16 (16 – 16)	16 (16 – 16)	16 (16 – 16)

Abbreviations: a.u. = arbitrary units.

Exercise Behaviour

PO data for RPE10 and RPE16 are shown in Figure 7.1 and Figure 7.2, respectively. The change in PO from RPE10 to RPE16 is shown in Figure 7.3 (PO_{abs} and $\%PO_{peak}$). Summary of the ANOVAs is presented in Tables 7.3 (RPE10), 7.4 (RPE16), and 7.5 (difference between RPE10 and RPE16).

For RPE10, the analysis revealed significant TIME effects for all measures of PO over the first 5-minutes but not for minutes 10-20 (Table 7.3). *Post hoc* analysis revealed that PO was greater at minute 1 compared with minute 3(PO_{abs}, p = .04) and minute 4 ($\%Trial_{mean}$, p = .04). GROUP effects were also found over the first 5-minutes for $\%Trial_{mean}$ (GOOD: 103 ± 11; POOR: 116 ± 11), $\%PO_{VT1}$ (GOOD: 48 ± 28; POOR: 75 ± 28), and $\%PO_{peak}$ (GOOD: 28 ± 14; POOR: 43 ± 17) (p's < .05). No significant GROUP effect was found for minutes 10-20. Interaction effects (GROUPxTIME) also failed to achieve statistical significance (Table 7.3).

Table 7.3. Summary of the main effects within the ANOVA for measures of power output in the RPE10 condition. ANOVAs are presented separately by analysis of the first 5-minutes (minutes 1-5, 1-min averages) and the final 15-minutes (minutes 10-20, 5-min averages).

minutes 1-5	GROUP			TIME			GROUPxTIME		
	F	*p*	η_p^2	*F*	*p*	η_p^2	*F*	*p*	η_p^2
PO_{abs}	0.7	.42	.04	4.8	.02*	.21	1.2	.30	.06
$\%Trial_{mean}$	6.2	.02*	.26	5.8	.01*	.24	0.7	.54	.04
$\%PO_{VT1}$	4.5	.047*	.20	4.0	.03*	.18	1.1	.36	.06
$\%PO_{peak}$	4.6	.046*	.20	3.7	.04*	.17	1.1	.33	.06

minutes 10-20	GROUP			TIME			GROUPxTIME		
	F	*p*	η_p^2	*F*	*p*	η_p^2	*F*	*p*	η_p^2
PO_{abs}	0.0	.92	.00	1.2	.31	.06	4.6	.02*	.20
$\%Trial_{mean}$	6.2	.02*	.02	2.0	.15	.10	3.8	.03*	.18
$\%PO_{VT1}$	2.3	.14	.12	1.6	.21	.08	3.7	.03*	.17
$\%PO_{peak}$	1.9	.18	.10	1.5	.23	.08	4.4	.02*	.20

*$p < .05$

For RPE16, a significant effect of GROUP was found for PO_{abs} for both minutes 1-5 (GOOD: 214 ± 38 W, POOR: 156 ± 46 W) and minutes 10-20 (GOOD: 198 ± 37 W, POOR: 142 ± 45 W) (*p*'s = .01) with no significant effects found for other measures of PO. No significant effect of TIME was found for any measure of PO for either minutes 1-5 or minutes 10-20 (Table 7.4). However, significant interaction effects (GROUPxTIME) were found for all measures of PO (*p*'s < .05) over the first 5-minutes but not for minutes 10-20 (Table 7.4), suggesting that the two groups adopted differing pacing strategies over the initial 5-minutes of the RPE16 task (Figure 7.2). *Post hoc* analysis revealed that PO differed between the two groups for minute 2 (PO_{abs}), minute 3 (PO_{abs}, $\%Trial_{mean}$, $\%PO_{peak}$), minute 4 (PO_{abs}, $\%Trial_{mean}$, $\%PO_{peak}$), and minute 5 (PO_{abs}, $\%PO_{peak}$).

Table 7.4. Summary of the main effects within the ANOVA for measures of power output in the RPE16 condition. ANOVAs are presented separately by analysis of the first 5-minutes (minutes 1-5, 1-min averages) and the final 15-minutes (minutes 10-20, 5-min averages).

minutes 1-5	GROUP			TIME			GROUPxTIME		
	F	*p*	η_p^2	*F*	*p*	η_p^2	*F*	*p*	η_p^2
PO_{abs}	9.7	.01*	.35	1.1	.31	.06	5.8	.02*	.24
$\%Trial_{mean}$	0.0	.98	.00	1.5	.24	.08	5.6	.02*	.24
$\%PO_{VT2}$	0.0	.92	.00	1.8	.20	.09	5.9	.02*	.26
$\%PO_{peak}$	2.1	.16	.11	1.6	.23	.08	6.7	.01*	.27

minutes 10-20	GROUP			TIME			GROUPxTIME		
	F	*p*	η_p^2	*F*	*p*	η_p^2	*F*	*p*	η_p^2
PO_{abs}	9.5	.01*	.34	1.1	.32	.06	1.6	.23	.08
$\%Trial_{mean}$	0.0	.98	.00	1.1	.33	.06	0.8	.40	.04
$\%PO_{VT2}$	0.0	.90	.00	0.0	.89	.00	1.1	.36	.06
$\%PO_{peak}$	3.3	.09	.15	0.5	.51	.03	1.2	.30	.06

*$p < .05$

Finally, the change in PO from RPE10 to RPE16 a significant effect of GROUP was found for PO_{abs} (minutes 1-5 and minutes 10-20) and $\%PO_{peak}$ (minutes 1-5 only) (p's < .05) (Table 7.5). No significant effect of TIME was found for either measure. However, a significant interaction (GROUPxTIME) effect was found for both PO_{abs} and $\%PO_{peak}$ (minutes 1-5 and minutes 10-20) (Table 7.5). *Post hoc* analysis revealed that the two groups differed in their POabs for all time points except for minute 1 (Figure 7.3A). For $\%PO_{peak,}$ *post hoc* analysis indicated that the groups differed at all time-point except for minute 1 and minute 20 (Figure 7.3B).

Table 7.5. Summary of the main effects within the ANOVA for the change in power output between RPE10 and RPE16. ANOVAs are presented separately by analysis of the first 5-minutes (minutes 1-5, 1-min averages) and the final 15-minutes (minutes 10-20, 5-min averages).

minutes 1-5	GROUP			TIME			GROUPxTIME		
	F	*p*	η_p^2	*F*	*p*	η_p^2	*F*	*p*	η_p^2
POabs	10.5	.01*	.37	0.2	.96	.01	4.9	.00*	.21
%POpeak	6.2	.02*	.26	0.1	.91	.00	4.8	.02*	.21

minutes 10-20	GROUP			TIME			GROUPxTIME		
	F	*p*	η_p^2	*F*	*p*	η_p^2	*F*	*p*	η_p^2
POabs	10.7	.00*	.37	0.2	.77	.01	6.6	.01*	.27
%POpeak	7.0	.20	.28	0.0	.91	.00	5.1	.02*	.22

*$p < .05$

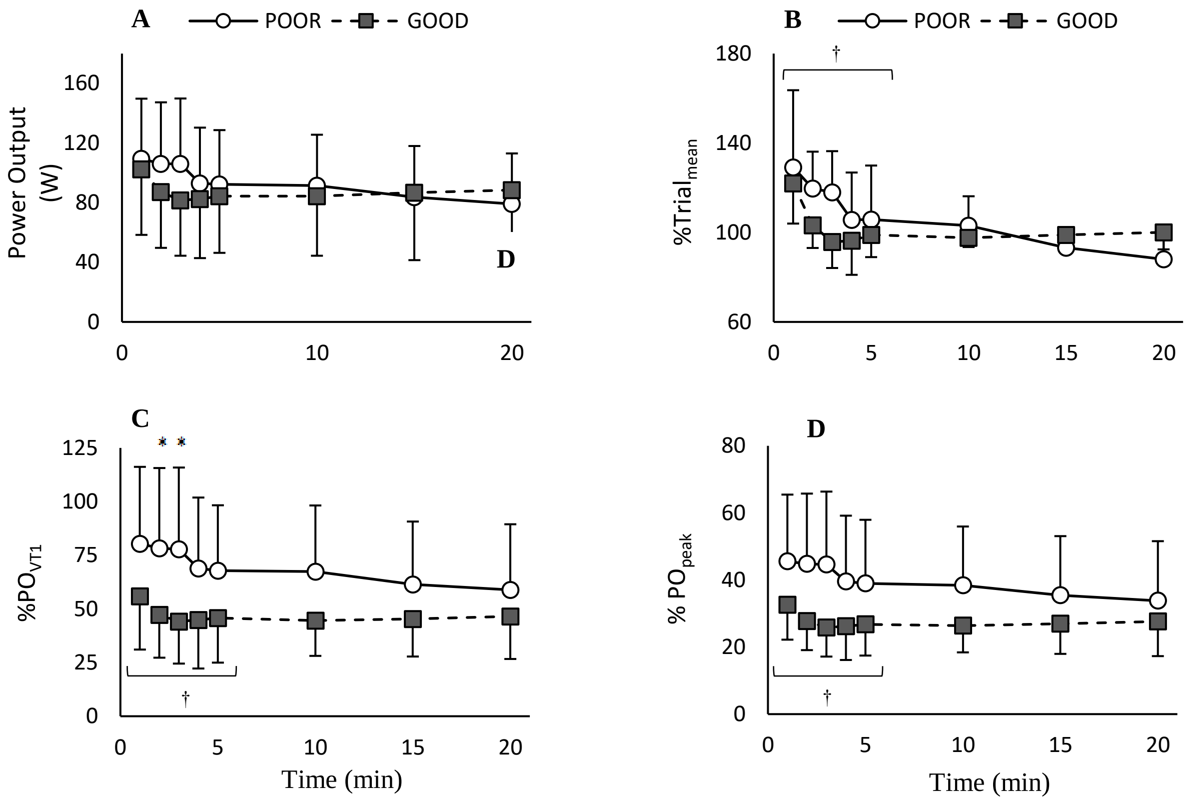


Figure 7.1. Power output (PO) responses during the 20-minute self-regulated exercise task at light rating of perceived exertion (RPE10) for both good (GOOD) and poor (POOR) heartbeat perceivers. PO represented in absolute terms (A), normalised to participants average PO over the duration of the trial (B), normalised to the participants peak PO obtained in the graded exercise test (C), and normalised to participants PO at the first ventilatory threshold (D). † denotes significant GROUP effect. * denotes significant *post hoc* differences between groups for the GROUPxTIME interaction effect. Main effects for TIME and GROUPxTIME omitted for clarity.

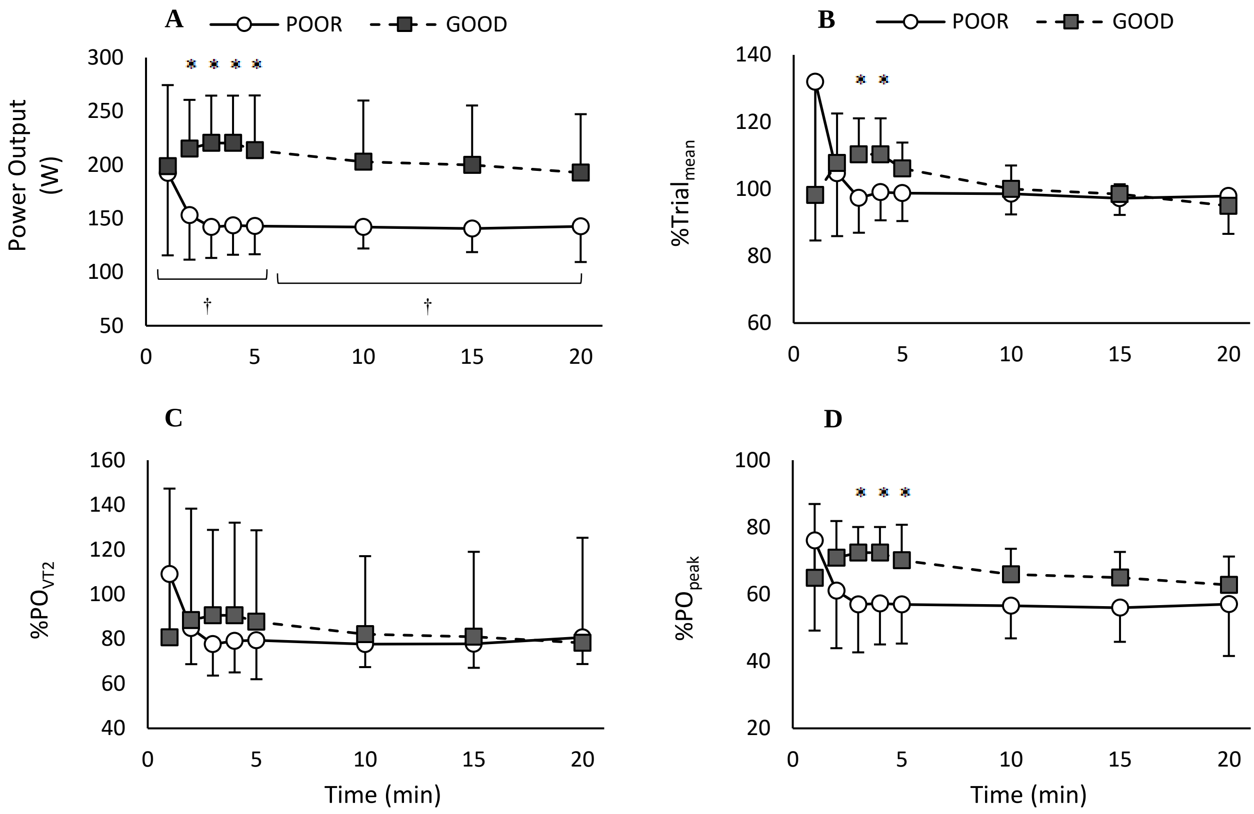


Figure 7.2. Power output (PO) responses during the 20-minute self-regulated exercise task at hard-to-very-hard rating of perceived exertion (RPE16) for both good (GOOD) and poor (POOR) heartbeat perceivers. PO represented in absolute terms (A), normalised to participants average PO over the duration of the trial (B), normalised to the participants peak PO obtained in the graded exercise test (C), and normalised to participants PO at the second ventilatory threshold (D).† denotes a significant GROUP effect. * denotes significant *post hoc* differences between groups for the GROUPxTIME interaction effect. Main effects for TIME and GROUPxTIME omitted for clarity.

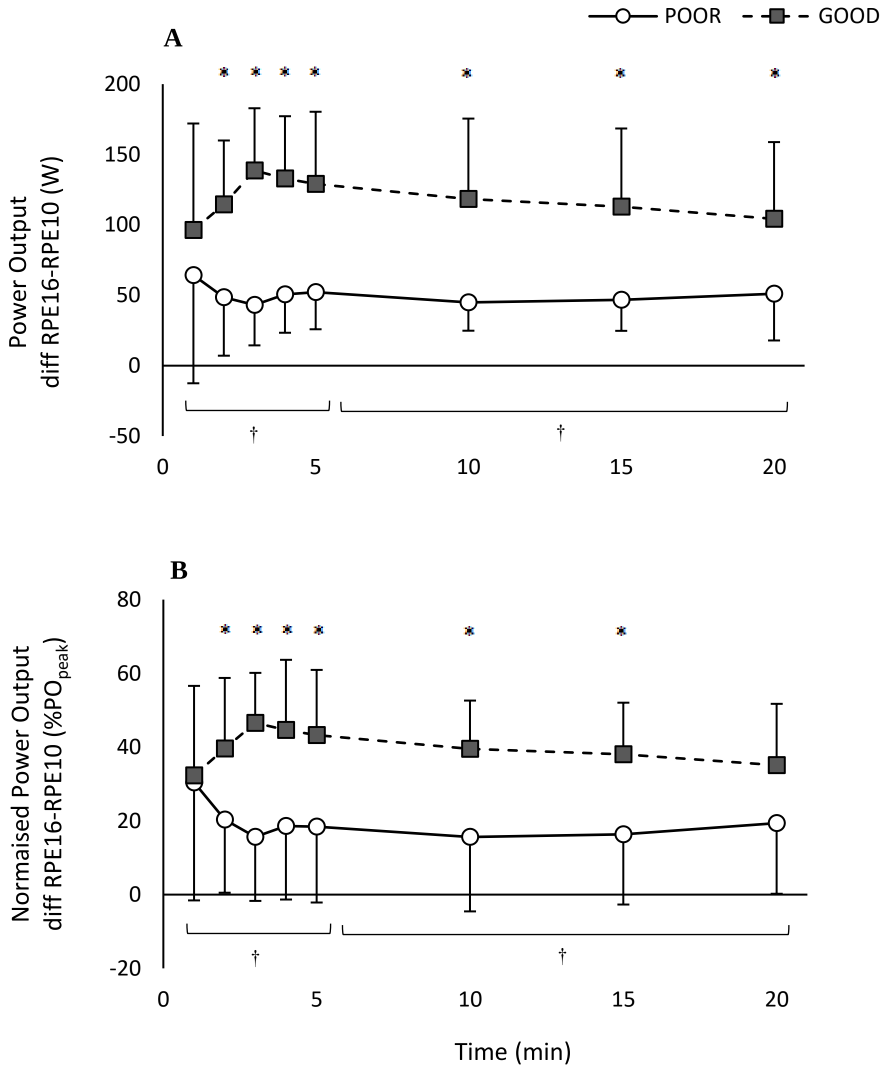


Figure 7.3. Change in power output (PO) between light intensity exercise (RPE10) and hard-to-very hard (RPE16) between good (GOOD) and poor (POOR) heartbeat perceivers. PO examined in terms of both absolute (A) and relative (B; normalised to the peak PO observed in the graded exercise test) intensities. † denotes a significant GROUP effect * denotes significant differences between the two groups. Main effects for TIME omitted for clarity.

Correlational analysis of the change in participant's average PO (normalised to $\%PO_{peak}$) from RPE10 to RPE16 with their interoceptive characteristics indicated a significant positive relationship with heartbeat discrimination accuracy (Figure 7.4a; $\tau_{(20)} = .335$, $p = .046$). Conversely, relationships between the other measures of cardiac interoception and changes in $\%PO_{peak}$ from RPE10 to RPE16 were found to be non-significant (Figure 7.4; $p > .05$).

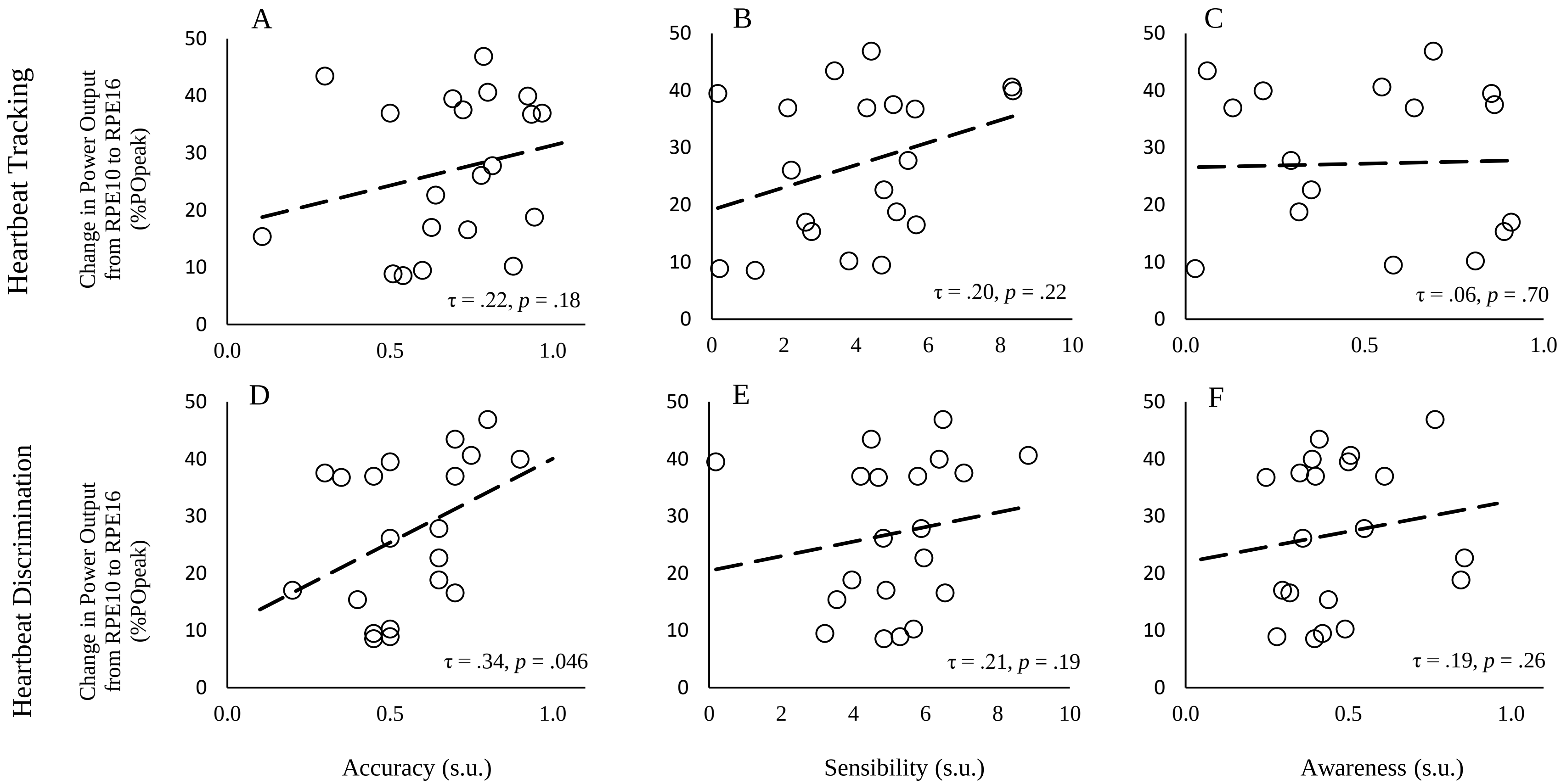


Figure 7.4. Relationship between changes in average power output (normalised to $\%PO_{peak}$) from RPE10 to RPE16 with interoceptive characteristics for: (A) tracking accuracy, (B) tracking sensibility, (C) tracking awareness, (D) discrimination accuracy, (E) discrimination sensibility, (F) discrimination awareness. τ = Kendal's rank correlation coefficient.

Physiological Responses

Summary of the ANOVAs for f_c, $\dot{V}O_2$, and RER are presented in Table 7.6.

Heart rate responses to the fixed-RPE tasks are shown in Figure 7.5. For RPE10, the ANOVA revealed a significant effect of GROUP over the first 5-minutes (GOOD: 58 ± 3 %Peak; POOR: 66 ± 2 %Peak) only. A significant effect of TIME was also evident over the first 5-minutes (p =.01) only. No significant interaction (GROUPxTIME) effects were found for either minutes 1-5 or minutes 10-20 (Table 7.6). For RPE16, a significant effect of TIME was found for the first 5-minutes ($p < .01$), no other significant effects were identified in the ANOVA (Table 7.6).

For the change in f_c between RPE10 and RPE16, the ANOVA revealed a significant effect of GROUP for the first 5-minutes (GOOD: 21 ± 3 Δ%, POOR 12 ± 3 Δ%) only. A significant effect of TIME was also observed for the first 5-minutes only (Table 7.6). No significant interaction effects were found for the change in f_c.

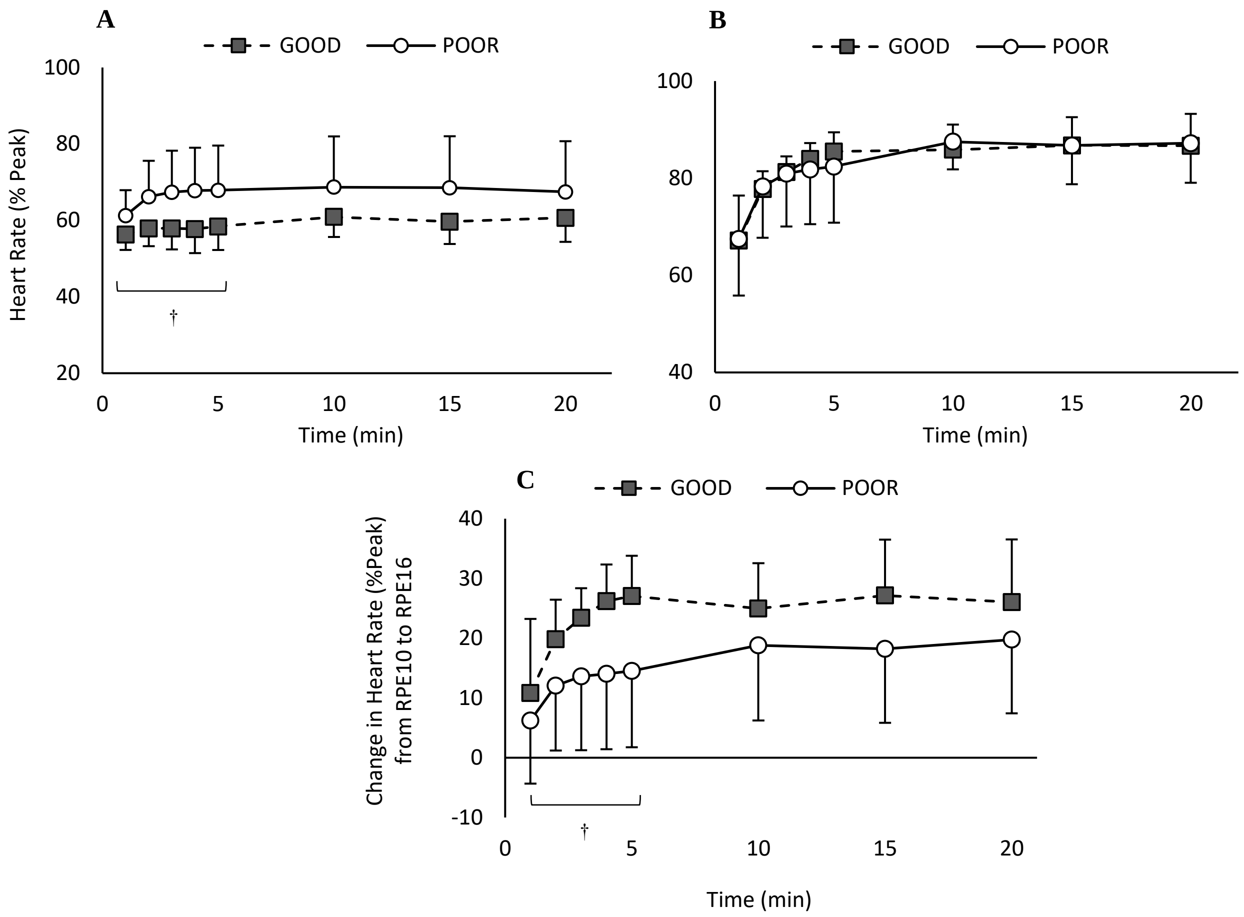


Figure 7.5. Heart rate (f_c) responses (relative to peak f_c observed in a graded exercise test: %Peak) during 20-minutes of cycling at both light (A: RPE10) and hard-to-very hard (B: RPE16) intensity exercise, as well as the change in f_c between RPE10 and RPE16 (C) for good (GOOD) and poor (POOR) heartbeat perceivers. † denotes a significant main effect of GROUP. TIME effects omitted for clarity.

Relative oxygen consumption responses to the fixed-RPE tasks are shown in Figure 7.6. For RPE10, the ANOVA revealed a significant TIME effect for the first 5-minutes for RPE10, RPE16, and the difference between RPE10 and RPE16 (Table 7.6). No other significant effects were found.

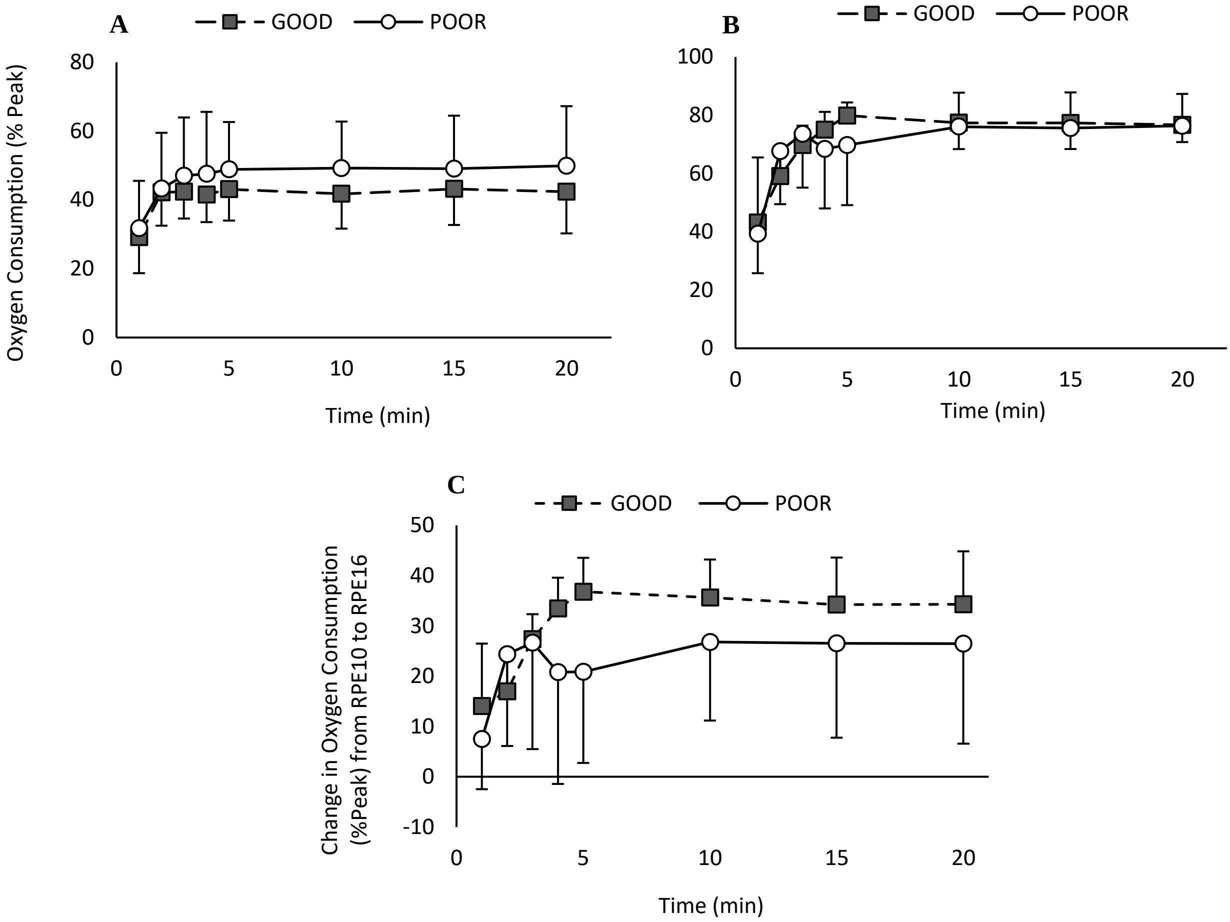


Figure 7.6. Oxygen consumption ($\dot{V}O_2$) (relative to peak $\dot{V}O_2$ observed in a graded exercise test: %Peak) during 20-minutes of cycling at both light (A: RPE10) and hard-to-very hard (B: RPE16) intensity exercise, as well as the change in $\dot{V}O_2$ between RPE10 and RPE16 (C).

For RER, the ANOVA revealed significant GROUP effects for RPE10 for both the first 5-minutes (GOOD: 0.86 ± 0.07 a.u.; POOR: 0.96 ± 0.06 a.u.) and also minutes 10-20 (GOOD: 0.87 ± 0.07 a.u.; POOR: 0.97 ± 0.04 a.u.) (p's < .01). A significant TIME effect was also evident in RPE10 for the first 5-minutes only (Table 7.6). However, no significant interaction effect was found for RPE10. For RPE16, the ANOVA indicated a significant effect of TIME for both the first 5-minutes ($p < .01$) and minutes 10-20 ($p = .01$) (Table 7.6). However, the effect of GROUP was not significant for RPE16. Nevertheless, a significant interaction effect was observed for the first 5-minutes in the RPE16 condition (Table 7.6, $p < .01$). *Post hoc* analysis of this effect revealed that GOOD and POOR were significantly different at minutes 2, 3, and 4 (Figure 7.7B).

The change in RER values from RPE10 to RPE16 also revealed significant GROUP effects for both the first 5-minutes (GOOD: 0.15 ± 0.11 Δ a.u.; POOR: 0.13 ± 0.10 Δ a.u.) and also minutes 10-20 (GOOD: 0.12 ± 0.10 Δ a.u.; POOR: 0.04 ± 0.05 Δ a.u.) (p's < .01). TIME effects were also found for the first 5-minutes only (Table 7.6). Finally, a significant interaction (GROUPxTIME) effect was found for the first 5-minutes only ($p < .01$). *Post hoc* analysis of this effect revealed differences between the two groups at minutes 10 and 20 (Figure 7.7C).

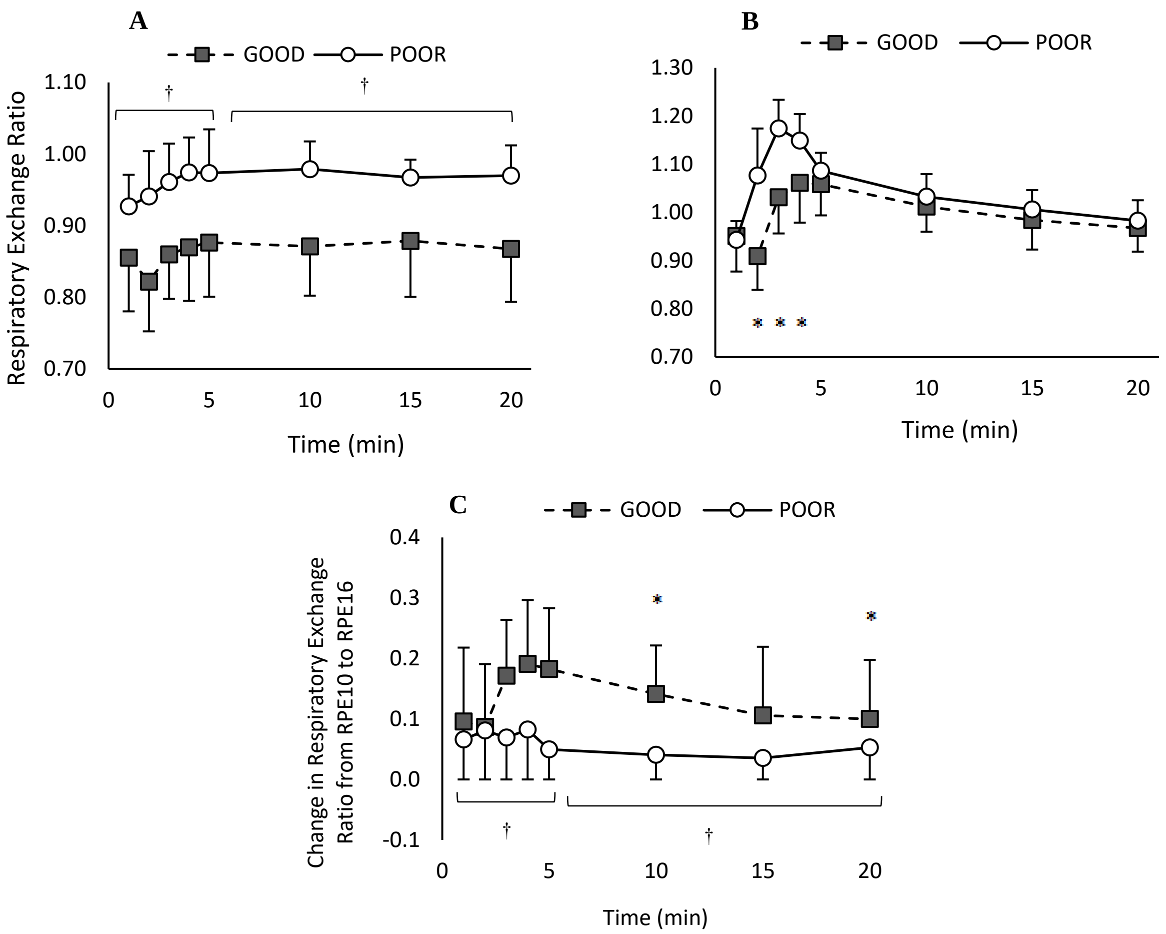


Figure 7.7. Respiratory exchange ratio (RER) responses during 20-minutes of cycling at both light (A: RPE10) and hard-to-very hard (B: RPE16) intensity exercise, as well as the change in RER between RPE10 and RPE16 (C). † denotes a significant main effect of GROUP. * denotes significant *post hoc* differences between groups for the GROUPxTIME interaction effect.

Table 7.6. Summary of the main effects within the ANOVA for heart rate (f_c), oxygen consumption ($\dot{V}O_2$), and respiratory exchange ratio (RER). ANOVAs are presented separately by analysis of the first 5-minutes (minutes 1-5, 1-min averages) and the final 15-minutes (minutes 10-20, 5-min averages).

minutes 1-5		GROUP			TIME			GROUPxTIME		
		F	*p*	η_p^2	*F*	*p*	η_p^2	*F*	*p*	η_p^2
f_c	RPE10	5.6	.03*	.24	6.9	.01*	.28	2.3	.13	.12
	RPE16	2.2	.15	.11	364.6	<.01*	.95	2.0	.16	.10
	RPE10-RPE16	4.6	.045*	.21	33.9	<.01*	.65	3.7	.05	.17
$\dot{V}O_2$	RPE10	0.6	.45	.03	16.5	<.01*	.48	0.4	.59	.02
	RPE16	1.8	.20	.09	213.4	<.01*	.92	1.1	.34	.06
	RPE10-RPE16	0.9	.37	.05	8.6	<.01*	.32	3.4	.06	.16
RER	RPE10	16.7	<.01*	.48	0.5	<.01*	.24	1.1	.35	.06
	RPE16	1.4	.25	.07	186.6	<.01*	.91	1.7	.19	.09
	RPE10-RPE16	0.2	.64	.01	17.2	< .01*	.49	5.0	<.01*	.22

minutes 10-20		GROUP			TIME			GROUPxTIME		
		F	*p*	η_p^2	*F*	*p*	η_p^2	*F*	*p*	η_p^2
f_c	RPE10	2.8	.11	.14	0.4	.70	.02	2.8	.11	.14
	RPE16	0.1	.81	.00	0.1	.80	.00	0.7	.44	.04
	RPE10-RPE16	2.2	.16	.11	0.4	.69	.02	0.9	.44	.05
$\dot{V}O_2$	RPE10	1.4	.26	.07	0.6	.50	.03	1.4	.26	.07
	RPE16	0.1	.76	.01	0.0	.91	.00	0.3	.61	.02
	RPE10-RPE16	1.3	.27	.07	0.2	.72	.01	0.1	.84	.01
RER	RPE10	16.8	<.01*	.48	0.2	.75	.01	16.8	<.01*	.48
	RPE16	1.1	.30	.06	10.1	<.01*	.36	0.1	.92	.00
	RPE10-RPE16	7.3	.01*	.29	5.7	.01*	.24	0.5	.62	.03

*$p < .05$

7.5. Discussion

The present study was the first to examine the effect of cardiac interoception on self-regulatory exercise behaviour at fixed ratings of perceived exertion. Heartbeat perception accuracy was found to influence the change in exercise work rates between *light* (RPE10) and *hard-to-very hard* (RPE16) intensity exercise, with good heartbeat perceivers (GOOD) demonstrating a greater difference in their PO between the two RPE conditions compared with poor heartbeat perceivers (POOR; Figure 7.3). Furthermore, the two groups were found to adopt significantly different pacing strategies over the first 5 minutes of RPE16, with POOR demonstrating decreases in their PO from minute 1 to 5 whereas GOOD demonstrated small increases in PO from minute 1 to 5. The differences in these behavioural effects resulted in significantly greater changes between conditions for both f_c and RER for GOOD compared with POOR.

7.5.1. The Use of Fixed-RPE Protocols to Examine Exercise Behaviour

Comparing the fixed-RPE data from the present study to those previously reported in trained cyclists (Swart et al., 2009; Tucker et al., 2006), comparable findings are noted with respect to PO at RPE16 in terms of initial PO at the start of the exercise (63% relative to PO_{peak} (first 3 minutes averaged across both groups in the present study) compared with 66-70 $\%PO_{peak}$ (averaged over first 3 minutes)), and also the reduction in PO over time (11% in the present study compared with 9-13% from the start of exercise to minute-20). The agreement in these findings occurred despite differences in the training status of populations between the studies, suggesting that individuals regulate their exercise work rates in a similar manner under fixed-RPE conditions regardless of training status. Similarly, $\%\dot{V}O_{2peak}$ also demonstrated reasonable agreement with previously published data for cycling exercise (Eston & Williams, 1988; Eston, Lamb, Parfitt, & King, 2005). Specifically, the $\%\dot{V}O_{2\ peak}$ reported by Swart and colleagues (~76 $\%\dot{V}O_{2\ peak}$; Swart, Lamberts, Lambert, et al., 2009) at the end of a cycling task at RPE16 were identical to the $\%\dot{V}O_{2\ peak}$ was observed over the final 15 minutes of the RPE16 task in the present study (76%). Additionally, comparing against the data from Eston and colleagues (2005) for RPE and $\dot{V}O_2$ responses during a graded exercise test, a good agreement is observed for $\%\dot{V}O_{2\ peak}$ at both RPE10 and RPE16 compared with the present study, despite notable differences in the exercise task type (Figure 7.8).

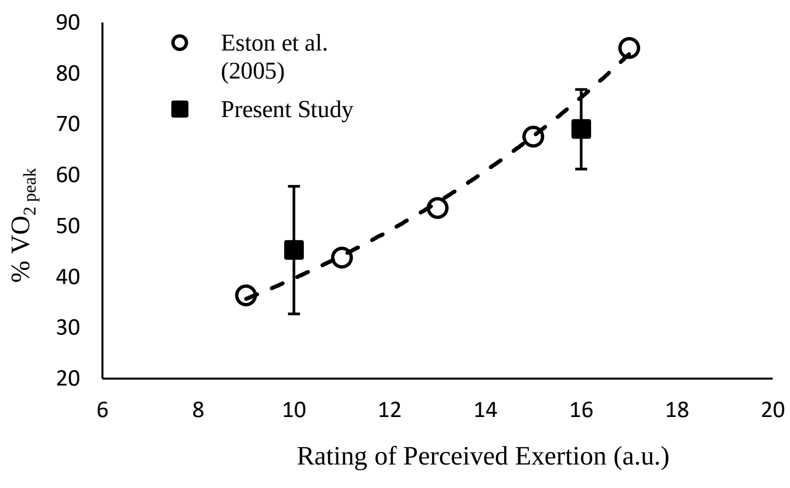


Figure 7.8. Comparison of the relationship between $\%\dot{V}O_{2\ peak}$ and rating of perceived exertion (RPE) for a graded exercise test (Eston et al., 2005) and 20-minute cycling task at fixed-RPE of 10 and 16 (Present Study). Error bars used to represent a ± 1 SD distribution of the $\%\dot{V}O_{2\ peak}$ obtained from the analysed sample of the present study (n = 20).

Importantly, fixed-RPE protocols have been used as a novel approach for examining exercise behaviour. The findings from studies using fixed-RPE protocols provide evidence to support the influence of peripheral (Browne & Renfree, 2013; Flood, Waldron, & Jeffries, 2017; Tucker, Marle, Lambert, & Noakes, 2006) and central (Swart, Lamberts, St Clair Gibson, et al., 2009) nervous system inputs on the regulation of muscular work. Consequently, these previous studies support the role of RPE as a primary regulator of muscular work rate during self-paced exercise (Tucker, 2009). The present study adds to this literature by (1) examining the effect of intrinsic factors on self-regulatory behaviour, notably the effect of individual differences in cardiac interoception, and (2) examining these effects at two distinctly different exercise intensities.

7.5.2. Cardiac Interoception and Exercise Behaviour

The findings of this study strongly suggest that interoceptive accuracy constitutes a major factor in the behavioural regulation of physical workloads during self-paced exercise. Specifically, the results showed that good heartbeat perceivers were able to discriminate between exercise intensities to a greater extent compared with poor heartbeat perceivers. This was reflected in the PO, f_c, and RER data which all indicated greater changes from RPE10 to RPE16 in the good perceiver group. At initial inspection, this finding may appear to support a tautologic position, whereby differences in exercise pacing are examined in the context of inter-individual differences in interoceptive sensitivity (i.e., cardiac interoceptive accuracy) using a perceptual construct that purportedly relies on sensitivity to interoceptive cues (i.e., RPE). However, performance in heartbeat perception tasks reflects only one interoceptive channel, which does not always correspond with performance across other interoceptive axes (Garfinkel et al., 2016; Herbert et al., 2012). This consideration is important as RPE is thought to emerge through the synthesis of information across various interoceptive axes (Borg & Kaijser, 2006; Jameson & Ring, 2000), is inclusive of signals processed from non-interoceptive channels (de Morree et al., 2012; Parry, Chinnasamy, & Micklewright, 2012; Zénon et al., 2015), and is likely to be moderated by both cognitive and teleoanticipatory factors (Albertus et al., 2005; Barwood et al., 2015; Castle, Maxwell, Allchorn, Mauger, & White, 2012). Consequently, the observation that perceptual sensitivity to heartbeats occurring at rest influences PE during self-paced exercise represents a novel finding, particularly as the salience of interoceptive inputs are likely to substantially different during physical exertion compared with rest (e.g., Khalsa, Rudrauf, Sandesara, et al., 2009; Machado et al., 2019; Williamson et al., 1999).

These findings also support previous research demonstrating that greater sensitivity (Herbert, Ulbrich, et al., 2007) or attention (Pennebaker & Lightner, 1980) to interoceptive feedback was associated with reductions in the physical work rates exerted by the participants in those studies. The inclusion of two separate exercise intensity domains provided a more comprehensive explanation of the role of interoceptive accuracy in this study compared with previous interpretations. Specifically, the generalised decrease in work rates at selected perceptual anchors (i.e., preferred exercise intensity) related to either greater interoceptive accuracy or increased interoceptive attention (Herbert, Ulbrich, et al., 2007; Pennebaker & Lightner, 1980) were not observed in the data for this study. Instead, the differences between the two groups indicated that poor perceivers exerted greater relative effort (f_c, RER, and $\%PO_{VT1}$) for the *light* intensity condition (RPE10) but were not different from good perceivers at the harder exercise intensity (RPE16) (Figures 7.1, 7.2, 7.5, 7.7).

The present study also provided the first evidence showing that a person's interoceptive characteristics may also influence their pacing profiles, particularly during the early stages of exercise of harder exercise intensity (Figure 7.2). Poor perceivers were found to adopt work rates in the first minute of RPE16 that were 34% greater compared with minute 5 and also 33% greater than the average PO for the trial. Conversely, the initial work rate (first minute) for good perceivers was found to be consistent with their POs at all other time points including at both minute 5 (7% difference) and also with their trial mean (2% difference). For poor perceivers, this more "aggressive" pacing strategy likely reflected either (1) a greater reliance on non-interoceptive information (i.e., proprioceptive and motor inputs) to estimate perception of exertion, or (2) a behavioural strategy designed to increase the certainty of PE through large and immediate changes in interoceptive signalling, which facilitated a greater precision (i.e., confidence) in the perception of changes in bodily states.

A person's interoceptive characteristics may influence their exercise behaviour differently depending on the perceptual cues used to regulate that behaviour. Discrepancies in the exercise behaviour data from this study compared to those previously reported (Herbert, Ulbrich, et al., 2007; Pennebaker & Lightner, 1980) may reflect the differing intentions of the respective exercise protocols, specifically the use of preferred exercise intensity compared with perceived exertion. Preferred exercise intensity, as used in previous studies, is likely to reflect the optimisation of a person's core affective experience during exercise (Oliveira, Deslandes, & Santos, 2015), a measure that describes the integration of hedonic and arousal components (Russell, 2009) whereas RPE more strongly reflects a generalised perception of somatic stress (Borg, 1982). Although affect and exertion are thought to emerge in part, from the processing of afferent inputs within shared cortical networks (Critchley & Nagai, 2012; Williamson et al., 2014), previous studies have demonstrated that these two perceptual constructs are dissociable during exercise (Eston, Stansfield, Westoby, & Parfitt, 2012; Hamlyn-Williams, Freeman, & Parfitt, 2014; Renfree, West, Corbett, Rhoden, & St Clair Gibson, 2012; Sheppard & Parfitt, 2008). Consequently, this study provides further understanding by demonstrating that interoceptive sensitivity is involved in the evaluation of somatic stress (i.e., RPE) experienced during exercise, adding to previous data supporting the role of interoception in the determination of emotional/affective states (i.e., 'preferred' exercise intensity) related to physiological changes.

In support of the observations in the present study, researchers have previously shown that occlusion of interoceptive feedback through spinal blockade of small-diameter afferent neurons significantly impairs athlete's ability to effectively regulate their exercise intensity during a self-paced exercise task (Amann, Proctor, Sebranek, Pegelow, & Dempsey, 2009; Blain et al., 2016). The loss of interoceptive feedback was found to result in greater power outputs at the start of exercise leading to substantially greater increases in peripheral muscular fatigue despite comparable RPE's reported in both conditions. Precise perceptions of bodily signals are therefore important in the self-control of physical work rates, with diminished sensitivity to these signals leading individuals to under-estimate their physical load. Consequently, the assessment of interoceptive accuracy may be an important tool in identifying individuals at risk of overexerting themselves during physical activities, particularly among clinical populations where high-intensity exercise may present a risk to health (Strzelczyk, Quigg, Pfeifer, Parker, & Greenland, 2001).

7.5.3. Limitations

Fixed-RPE protocols provide a novel approach to investigate the factors involved in self-regulated exercise behaviour; however, they are not without limitation. Specifically, constraining exercise intensity based on single-item measures of RPE, as determined using the Borg scale, may be limited in their application as these measures represent super-ordinate constructs that may not directly reflect changes in the underlying physiological responses (Venhorst et al., 2018b). Consequently, the single-item RPE measures may be deficient in their capacity to distinguish between qualitatively distinct variations of perceived exertion which might occur across different physiological systems, reducing certainty of perceptual cues driving exercise behaviour under different contexts. Application of more localised RPE measures, directed towards specific axes of an interoceptive process (i.e., focussing on specific sources of sensory information directed towards cardiovascular function), may represent a more effective and comprehensive multidimensional model for examining the potential implications of person-to-person differences in interoceptive processing on the sensitivity to physiological strain during exercise (Christian et al., 2014; Garfinkel, Manassei, et al., 2016; Venhorst et al., 2018c).

7.6. Conclusion

In summary, this study is the first to examine the effect of cardiac interoception on self-regulatory exercise behaviour at fixed ratings of perceived exertion. The results suggest that heartbeat discrimination accuracy strongly influences self-regulated exercise behaviours, resulting in differences in relative work rates at *light* exercise intensities as well as differing pacing strategies at *hard-to-very hard* exercise intensities. This demonstrates that individuals regulate their exercise intensity differently from one another, depending on their trait interoceptive sensitivity. Further research is required to understand whether trait differences across other interoceptive axes might influence exercise behaviour and the attentional salience given to sources of sensory information.

CHAPTER 8. GENERAL DISCUSSION

8.1. Introduction

This thesis aimed to investigate the interaction between physical activity and interoception to better understand the bidirectional influence of these two phenomena. Accordingly, two primary avenues of interest were explored. Firstly, the influence of aerobic fitness and adaptations to exercise training on markers of cardiac interoception; and secondly, the influence of individual differences in cardiac interoception on the regulation of exercise intensity and tolerance to exercise-induced physiological strain. Consequently, four separate studies were conducted to address this aim:

In Study 1 (Chapter 4), the relationship between aerobic fitness and cardiac interoception was investigated. Applying Garfinkel and colleague's (2015) multidimensional approach to examining cardiac interoception, both heartbeat tracking and heartbeat discrimination tests were compared and the influence of aerobic fitness on cardiac interoception was examined to include markers of interoceptive sensibility and awareness for the first time. Other notable physiological variables such as resting heart rate and body composition were also examined in this study to better understand their influence as mediating factors in the relationship between aerobic fitness and cardiac interoception.

Building on the findings from Study 1, Chapter 5 (Study 2) aimed to experimentally challenge the causal relationship between aerobic fitness and cardiac interoception using a 4-week exercise-training intervention. Additionally, interest was also given to the effect of fatigue, which typically develops during periods of intensified exercise training, on cardiac interoceptive parameters to further investigate the relationship between interoception and changes in an individual's physiological condition. Identification of best and worst performances (for participants in the training group) was used to control for potential divergences in the magnitude of experiential fatigue following the exercise training intervention. This was important as interoception and perceived fatigue are reported to interact with one another (Harrison et al., 2009; Sharp et al., 2021) and may influence the assessment of aerobic fitness through a moderation of exercise tolerance resulting from changes to perceived effort during exercise (Greenhouse-Tucknott, Butterworth, Wrightson, Harrison, et al., 2021). To our knowledge, this is the first study to investigate the experimental basis of this relationship between interoception and aerobic fitness.

In Study 3 (Chapter 6) the influence of cardiac interoception on exercise tolerance was investigated. Using a constant-load cycling exercise task, exercise-pacing behaviour was constrained to directly examine individual differences in the magnitude of physiological strain experienced at the point of volitional exhaustion and its relationship to markers of cardiac interoception.

Finally, the aim of Study 4 (Chapter 7) was to examine the effect of cardiac interoception on exercise behaviour when the intensity of exercise was self-regulated by the participant according to a fixed rating of perceived exertion. As part of this study, the effect of exercise intensity on exercise behaviour was also assessed, anchoring participants to either *light* (RPE10) or *hard-to-very hard* (RPE16) intensity exercise.

The present chapter will summarise and discuss the principal findings from the experimental chapters 4 - 7 (Section 8.2). This will be followed by a discussion of the progress within the research area from this thesis while focusing on a potential link between cardiac interoception, aerobic fitness, and the regulation of exercise behaviour relating to both exercise pacing and exercise tolerance (Section 8.3). Data across different studies within this thesis have been pooled together in the general discussion to strengthen some discussion points when appropriate. Additionally, estimation of the standardised effect sizes (using Hedge's *g*) are reported to facilitate comparisons between various studies. Finally, this chapter will conclude with some general consideration of the limitations and assumptions of the present findings (Section 8.4) to then propose directions for future research (Section 8.5).

8.2. Principal Findings

The first experimental chapter (Chapter 4) examined the relationship between aerobic fitness and cardiac interoception. Aerobic fitness was examined according to the established laboratory procedures which consider: 1) maximal aerobic capacity, 2) submaximal thresholds (as indicated by ventilatory thresholds), and 3) cycling efficiency (Coyle, 1999) as the principal markers of fitness. Cardiac interoception was investigated using both heartbeat tracking and heartbeat discrimination tests, describing interceptive characteristics for accuracy, sensibility, and awareness across both tests. Individuals more accurate in their heartbeat discrimination accuracy achieved $\dot{V}O_2$ values are 23% higher at peak and 27% higher at VT_2 than poor heartbeat perceivers. These differences between the two groups were also evident for PO produced at peak and VT_2. However, cycling efficiency was not significantly different between heartbeat perception groups. Partial correlation analysis further supported a positive relationship between cardiac interoception and aerobic fitness, with significant positive correlations evident despite controlling for differences in age, gender, and body composition. Significant relationships were most consistently observed for heartbeat discrimination accuracy, suggesting that this measure of cardiac interoception had the strongest relationship with an individual's aerobic fitness. Interestingly, no significant correlations were observed between measures of interoception and aerobic fitness when controlling for resting heart rate, indicating that cardiodynamic factors (which can be influenced by a person's fitness or training status) may exert the greatest influence on performance in tests of cardiac interoception.

Study 2 (Chapter 5) of the thesis examined the effect of a 4-week high-intensity aerobic exercise training intervention on cardiac interoception with participants allocated to either a training group (EX) or control group (CON). Aerobic fitness and cardiac interoception parameters were assessed pre-training intervention and on three occasions post-testing, identifying best (BEST) and worst (WORST) time-to-task failure performances in the multi-stage graded exercise test for EX for subsequent analysis. Both groups were similar at PRE for all measured variables. No significant changes were observed in CON for either aerobic fitness or cardiac interoception over the duration of the study. For EX, accuracy, sensibility, and awareness measures for heartbeat tracking and heartbeat discrimination tasks remained unchanged for both BEST and WORST. Similarly, with the exception of an 18% improvement PO_{peak} from PRE to BEST, no significant changes were observed for any other dependent variables during exercise for BEST or WORST were observed. Therefore, the results of this study suggested that the 4-week exercise intervention was not sufficient to induce significant changes in either cardiac interoception or the majority of measured aerobic fitness parameters.

The aim of Study 3 (Chapter 6) was to examine the influence of cardiac interoception on exercise tolerance in a constant-load cycling exercise task at a PO equivalent to 80% $\dot{V}O_{2\,peak}$ (GOOD: 97% PO_{VT2}; POOR: 103% PO_{VT2}). Time-to-task failure was not statistically different between the two groups (GOOD: 433 ± 112 s, POOR 414 ± 78 s; g = .19). Additionally, analysis of the physiological responses during the constant load task also revealed that the two groups were not different for $\dot{V}O_2$, minute ventilation, tidal volume, RER, or f_c across any of the measured time-points, including at the point of task failure (e.g., f_c at task failure, GOOD: 97 ± 3 %$f_{c\,max}$; POOR: 99 ± 3 %$f_{c\,max}$). Similarly, RPE was also not statistically different between the two groups, suggesting that the relationship between physiological and perceptual strain was comparable between GOOD and POOR. However, $f_{c\ recovery}$ was significantly greater over the first-minute post-exercise in GOOD (44 ± 16 b·min^{-1}) than POOR (29 ± 8 b·min^{-1}). Consequently, cardiac interoception does not appear to influence an individual's tolerance to exercise-induced strain during constant-load exercise but may influence cardiodynamic responses observed during recovery post-exercise.

Finally, the aim of Study 4 (Chapter 7) was to examine the effect of cardiac interoception on self-regulated exercise behaviour using a fixed-RPE based protocol at both *light* (RPE10) and *hard-to-very hard* (RPE16) perceived exertional intensities. The data demonstrated that GOOD exhibited greater changes in their exercise work rates between the two exercise intensities compared with POOR (GOOD: 41 ± 17 %PO_{peak}; POOR: 20 ± 19 %PO_{peak}; g = 1.11). Interestingly, this effect reflected lower relative magnitudes of physiological strain experienced by GOOD in the RPE10 condition (e.g., RER, GOOD: 0.87 ± 0.07 a.u.; POOR: 0.97 ± 0.03 a.u.). By comparison, no significant differences were observed for relative physiological parameters between the two groups in the RPE16 condition (e.g., RER, GOOD: 0.99 ± 0.04 a.u.; POOR: 1.03 ± 0.03 a.u.). These findings suggested that good heartbeat perceivers demonstrate a more 'finely-tuned' sensitivity to physical exertion, particularly at low exercise intensities where the input of physiological afferents remains vague and difficult to interpret.

8.3. Progression of Research

The present thesis aimed to investigate the interaction between physical activity and interoception to better understand the influence that these two phenomena have on one another. Accordingly, two primary avenues of interest were explored. Firstly, the influence of aerobic fitness and adaptations to exercise training on markers of cardiac interoception; and secondly, the influence of cardiac interoception on the regulation of exercise intensity and tolerance to exercise-induced physiological strain.

8.3.1. Physiological Factors Influencing Cardiac Interoception

Performance in objective tests of interoceptive accuracy is known to differ between persons, suggesting that intrinsic characteristics related to the individual may influence their sensitivity to interoceptive signals (Ainley, Apps, Fotopoulou, & Tsakiris, 2016; Ludwick-Rosenthal & Neufeld, 1985). Importantly, previous studies indicate that physiological (e.g., cardiac function and body composition) and demographic factors (e.g., age and gender) may influence these differences (Knapp-Kline & Kline, 2005; Rouse et al., 1988). Although some of these factors are considered to be trait characteristics, modifiable influences such as greater physical activity behaviour and aerobic fitness have been shown to correspond with better accuracy in tests of interoception (Georgiou et al., 2015; Jones & Hollandsworth, 1981; Perakakis, Luque-Casado, Ciria, Ivanov, & Sanabria, 2017). However, despite these positive effects, evidence for the influence of aerobic fitness was not strongly supported within a larger evidence base, with contrasting findings reported in other studies (Herbert, Ulbrich, & Schandry, 2007; Machado et al., 2019; Montgomery, Jones, & Hollandsworth, 1984). Consequently, one of the main aims of this thesis was to explore this relationship and provide greater clarity concerning this research topic.

The relationship between interoception and aerobic fitness was first investigated in Study 1 (Chapter 4) of this thesis which showed that good heartbeat perceivers were significantly more aerobically fit than poor heartbeat perceivers. Following-up with partial correlations revealed that the strongest effects existed for interoception as measured using the heartbeat discrimination task, specifically accuracy and awareness. Importantly, demographic factors such as age, gender, and body composition did not confound the presence of these relationships. The strength of effects observed in this chapter was typically larger than those previously reported in comparable studies using heartbeat detection approaches to assess interoception (*see* Table 1 and Table 2 for comparisons). Importantly, across the other studies of this thesis, moderate-to-large effect sizes were consistently observed, further supporting the relationship between aerobic fitness and discrimination accuracy (Table 2). Differences in these findings compared with those previously reported are likely to reflect varying methodological approaches used to explore this research question. Therefore, the following sections explore the influence of methodological considerations related to the assessment of aerobic fitness and interoception as well as the effects of sample selection on the effects observed within respective studies.

Table 8.1. Summary of studies related to the examination of cardiac interoception and aerobic fitness/ training status.

Author	Date	Sample	Assessment Methods		Findings	ES (g)
			Interoception	**Aerobic Fitness/ Training Status**		
Jones and Hollandsworth	1981	36 healthy adults (18M, 18F, age: 14-42 yrs)	HRD	Training status determined based on self-reported physical activity. Participants allocated to 'Distance runner', 'Tennis', or 'Sedentary' groups. Equal distribution of males and females in each group.	Male distance runners were significantly more accurate in their HRD at rest compared with all other sub-groups	-
Hollandsworth, Montgomery, and Jones	1984	24 healthy males (age: 18-25 yrs)	HRD	Training status determined based on self-reported physical activity. Twelve participants allocated to either 'High Fitness' or 'Average Fitness'	No difference in HRD between groups at rest	-
Herbert, Ulbrich, and Schandry	2007	34 healthy sedentary adults (15M, 19F, age: 20-40 yrs)	HBT Grouping based on accuracy threshold of 85% (GOOD: n = 14, POOR: n =20)	Fitness assessed based on GXT, PWC150 exercise task and reported relative to body mass ($W \cdot kg^{-1}$)	No difference in PWC150 between GOOD and POOR	0.07
Georgiou et al.	2015	49 healthy pre-adolescent children (29M, 20F, age: 9.7 + 0.6 yrs)	HBT	Fitness assessed based on distance covered in the Dordel-Koch test (a 6-minute running task)	Significant positive relationship between HBT accuracy and distance covered (T = 2.02, B = 0.29, p = .04)	0.38
Perakakis, Luque-casado, Ciria, Ivanov, and Sanabria	2017	37 adult males (age: 22 + 2 yrs), 20 'high-fit' (endurance athletes) and 17 'low-fit' (sedentary)	HEP	GXT, cycle ergometer, expired gases. Termination: achievement of RER > 1.0	Significant difference in $\dot{V}O_2$ and relative PO at termination ($p < .01$). HEP significantly greater in 'high-fit' group ($p = .02$)	4.22
Machado et al.	2019	32 healthy sedentary adults (age: 21-28)	HBT Grouping based on accuracy threshold of 85% (GOOD: n = 17, POOR: n =15)	GXT, cycle ergometer Termination: volitional exhaustion	No significant difference between groups for PO_{peak} or estimated $\dot{V}O_{2\,max}$ (p's > .48)	0.57

Abbreviations: yrs (years), M (males), F (females), HRD (heart rate discrimination), HBT (heartbeat tracking), GOOD (good heartbeat perceivers), POOR (poor heartbeat perceivers), HEP (heartbeat evoked potential), HBD (heartbeat discrimination), GXT (graded exercise task), PWC150 (power output at a heart rate of 150 $b \cdot min^{-1}$), $W \cdot kg^{-1}$ (watts per kilogram of body mass), RER (respiratory exchange ratio), PO (power output) $\dot{V}O_2$ (oxygen consumption), ES (effect size), *g* (Hedge's g).

8.3.2. Assessment of Aerobic Fitness

Various methods have been used to assess aerobic fitness in the context of its relationship with interoception. However, these different methods vary considerably in their reliability and validity when assessing aerobic fitness. Self-reported measures, similar to those used by Jones and Hollandsworth (1981), have been shown to provide good test-retest reliability (Craig et al., 2003; Mäder, Martin, Schutz, & Marti, 2006; Sallis & Saelens, 2000) with good concurrent validity across different self-reported instruments (Craig et al., 2003; Mäder et al., 2006). However, assessment of criterion validity against accelerometery data (Mäder et al., 2006) and construct validity related to markers of physical health and aerobic fitness (Hagströmer et al., 2006) are reported to be poor. Dyrstad and colleagues (2014) also reported that self-reported instruments maybe be subject to reporting bias with individuals overestimating the amount of vigorous activity completed and underestimating sedentary behaviour. This has been shown to result in misclassifying individuals according to activity levels (active vs. inactive) (Mäder et al., 2006), which is particularly confounded among inactive populations (Dyrstad et al., 2014) and also exaggerated in males compared with females (Kolkhorst & Dolaener, 1994).

Conversely, the use of field tests, such as the 6-minute run test used by Georgiou et al. (2015), appears to provide better criterion validity with a strong agreement to physiological markers obtained from direct assessment of aerobic fitness (e.g., Bandyopadhyay, 2015; von Haaren, Härtel, Seidel, Schlenker, & Bös, 2011) as well as good test-retest reliability (Penry & Wilcox, 2011). However, performance in field tests may be influenced by learning effects due to the self-paced design of these tasks, with studies showing improved performance when field tests are repeated across visits (Metaxas, Koutlianos, Kouidi, & Deligiannis, 2005, 13.6%; Lim, Lambrick, Mauger, Woolley, & Faulkner, 2016, $\eta^2_p = .31$). Laboratory-based protocols have also been used to assess aerobic fitness in the context of interoception (Herbert, Ulbrich, et al., 2007; Machado et al., 2019; Perakakis et al., 2017). These previous studies have utilised either submaximal performance tests (Herbert et al., 2007; Perakakis et al., 2017) or have estimated physiological parameters based on test performance (Machado et al., 2019). Submaximal performance tests have been shown to demonstrate good test-retest reliability (e.g., Cink & Thomas, 1981; Macsween, 2001; McArdle, Katch, Pechar, Jacobsen, & Ruck, 1972) but with conflicting findings towards criterion validity when related to physiological data obtained from exhaustive graded exercise tests (e.g., good validity: Vehrs, George, Fellingham, Plowman, & Dustman-Allen, 2007; poor validity: Peric & Nikolovski, 2017). Similarly, equations used to estimate physiological parameters based on test performance have been shown to both underestimate (Peric & Nikolovski, 2017) and overestimate (Macsween, 2001) $\dot{V}O_{2\ max}$ and demonstrate differential bias, overestimating $\dot{V}O_{2\ max}$ in aerobically fit individuals but not low fitness individuals (Penry & Wilcox, 2011).

Consequently, the four experimental studies within this thesis offer an important contribution to our understanding of the relationship between aerobic fitness and interoception by providing, for the first time, indirect calorimetry data obtained during graded exercise testing to volitional exhaustion. These protocols have previously been shown to have good test-retest reliability (e.g., Weltman et al., 1990), good construct validity when compared to exercise performance (McLaughlin, Howley, Bassett, Thompson, & Fitzhugh, 2010; Noakes, Myburgh, & Schall, 2008) and are considered to be the criterion measure of aerobic fitness. Data from Chapter 4 provided notable support for this relationship, demonstrating significant differences between good and poor heartbeat perceivers for PO and $\dot{V}O_2$ when measured at VT_2 and also peak. Partial correlations further revealed that the relationship between peak aerobic fitness (PO_{peak} and $\dot{V}O_{2\ peak}$) and heartbeat discrimination accuracy was independent of gender, age, BMI, and body composition but not independent of resting heart rate. This finding was important as it suggested that the relationship between aerobic fitness and interoception was strongly related to physiological adaptions associated with endurance performance and not a tertium quid of other demographic factors. Furthermore, replication of these assessment methods across the other three studies indicated good consistency in the effect sizes for the first three experimental chapters, but not the final study (Table 8.2). The difference in the effects for the second experimental chapter are discussed below (*see* Comparison of Homogenous versus Heterogeneous Fitness Samples). Interestingly, for Chapters 4, 6, and 7 (Studies 1, 3, and 4) effects for PO were consistently larger than those observed for $\dot{V}O_2$ (by $g \approx 0.2$). The difference in these effects reflects the fact that PO (at VT_1, VT_2, and peak) provides a composite measure that integrates both the capacity to utilise oxygen to meet metabolic demands and the efficiency to translate that energy production into external work (Jones & Carter, 2000). Previous studies have shown that these composite measures provide the strongest predictors of endurance exercise performance (e.g., Midgley, McNaughton, & Jones, 2007; Noakes et al., 2008). As such, these measures of exercise work capacity (PO at VT_1, VT_2, or peak) provide the best singular measures of aerobic fitness and support the overall tenant that aerobic fitness is strongly related to cardiac interoception.

Table 8.2. Effect sizes (Hedges *g*) across the four experimental studies of the thesis for power output (PO), oxygen consumption ($\dot{V}O_2$) at first and second ventilatory thresholds (VT_1 and VT_2) as well as peak. Analysis performed comparing good and poor heartbeat perceivers based on accuracy in the discrimination task and 95%CI criterion for group membership.

Study	VT_1		VT_2		Peak	
	PO (W)	$\dot{V}O_2$ ($L \cdot min^{-1}$)	PO (W)	$\dot{V}O_2$ ($L \cdot min^{-1}$)	PO (W)	$\dot{V}O_2$ ($L \cdot min^{-1}$)
1	1.06*	.80*	1.84*	1.66*	1.49*	1.21*
2	-	-	-	-	.02	.28
3	1.12*	.85	1.17*	.89	1.21*	0.89*
4	.91	.71	.87	.67	.85	.65

* $p < .05$

Comparison of Homogenous versus Heterogeneous Fitness Samples

Different sampling approaches across previous studies may have also confounded interpretation of the relationship between aerobic fitness and interoception, which has not previously been accounted for. The strongest effects (and those achieving statistical significance) have typically been observed in populations where a large range of aerobic fitness abilities are present (Georgiou et al., 2015; Perakakis et al., 2017), with smaller non-significant effects observed in more homogenous samples (Herbert et al., 2007; Machado et al., 2019). Interestingly, these differing effects were also observed in this thesis. Compared with the large effect sizes observed in Chapter 4 (Study 1), retrospective analysis of the data for Chapter 5 (Study 2) revealed a trivial effect for the relationship between aerobic fitness and interoception (Figure 8.1, based on discrimination accuracy and $\dot{V}O_{2\ max}$ at baseline). However, the range of aerobic fitness capacities between participants in Chapter 5 was smaller than that observed in Chapter 4, with a large cluster of participants with relative $\dot{V}O_{2\ peak}$ values in the range of 35-45 $mL \cdot kg^{-1} \cdot min^{-1}$ (Figure 8.4). This observation illustrates that representation of the true strength of the relationship between aerobic fitness and interoception may be best observed in heterogeneous samples, which reflects the wide range of aerobic fitness characteristics found within the general population.

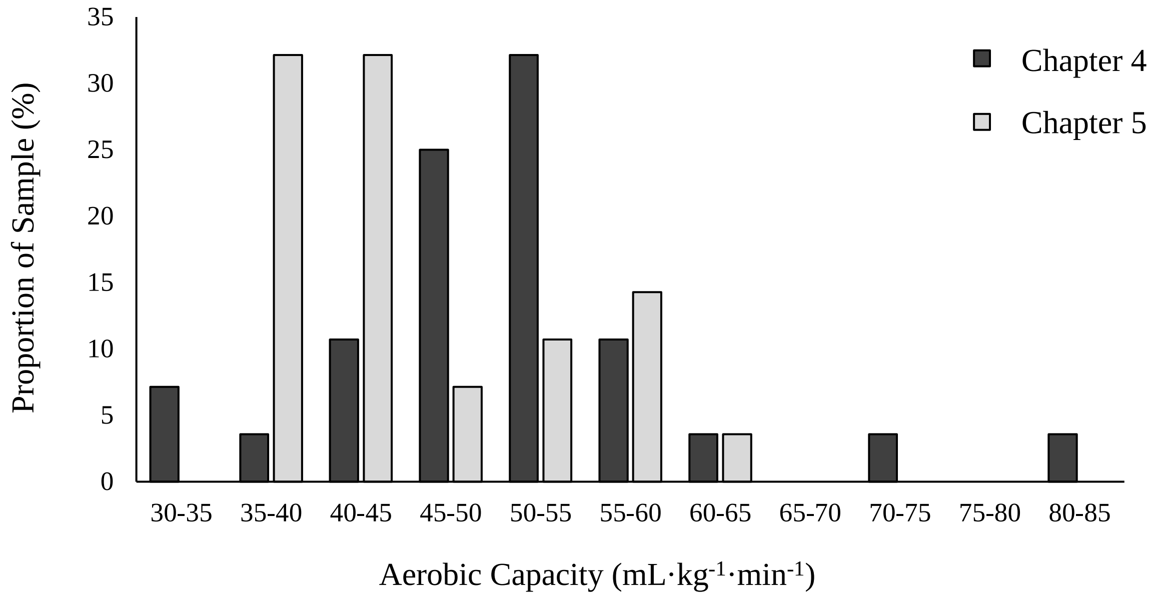


Figure 8.1. The distribution of aerobic capacities (mL·kg^{-1}·min^{-1}) obtained from participants in Chapter 4 (Study 1, n = 28) and Chapter 5 (Study 2, n = 28).

Effect of Different Approaches to Measuring Interoception

Previous work investigating the relationship between interoception and physical fitness has predominantly quantified interoception according to objective accuracy in heartbeat tracking tasks. Consequently, relatively little was known about the reproducibility of these effects in other tests of cardiac interoception. To overcome this limitation, the experimental studies of this thesis examined interoception according to the multidimensional interoceptive assessment approach developed by Garfinkel and colleagues (2015). This approach includes the use of both heartbeat tracking (Rainer Schandry, 1981) and heartbeat discrimination (Whitehead et al., 1977) tasks. Additionally, this approach also considers interoception beyond objective performance (interoceptive accuracy) to include a measure of subjective beliefs (interoceptive sensibility) and a metacognitive measure of the relationship between interoceptive accuracy and sensibility (interoceptive awareness).

Several novel findings emerged concerning the relationship between interoception and aerobic fitness as a result of consideration of these multidimensional constructs. Firstly, the data from Chapter 4 indicated that the heartbeat discrimination task revealed stronger and more consistent relationships with aerobic fitness compared to the tracking task, particularly for measures of discrimination accuracy and awareness. These findings are important as previous studies have largely employed variants of the heartbeat tracking task to assess interoceptive accuracy (Georgiou et al., 2015; Herbert, Ulbrich, et al., 2007; Machado et al., 2019). This raises important issues when considering the use of the heartbeat tracking methodology for examining the relationship between interoception and aerobic fitness (Zarza, Sanabria, & Perakakis, 2019). This is pertinent as previous studies have demonstrated that accuracy in the tracking task may be biased by temporal expectations of heart rates, suggesting that performance in the tracking task may be influenced by non-interoceptive factors (Phillips et al., 1999; Ring et al., 2015). This was an important consideration within the present thesis as the sample demographic were young, healthy, and physically active. As such, many participants were familiar with heart rate measuring devices and likely exhibited strong prior beliefs about their resting heart rates (which could influence group membership i.e., good vs poor) thereby confounding interpretation of the relationship between aerobic fitness and interoception. Overcoming these biases, Perakakis and colleagues (2017) previously reported very large effects (*see* Table 1) when comparing interoception between ‘high’ and ‘low’ aerobically fit participants. The authors attributed the strength of their effects on the use of HEP as a neurophysiological index of cardiac interoception, which negated the influence of participant's subjective beliefs. Similarly, the heartbeat discrimination task is considered to be more robust to subjective beliefs around resting heart rate compared with the tracking task (Phillips et al., 1999). Consequently, the data from Chapter 4 supports the relationship between aerobic fitness and interoception, suggesting that the strength of this relationship may be stronger than previously reported in the literature.

Secondly, the findings from Chapter 4 provided new knowledge regarding the relationship between aerobic fitness and the three facets of interoception: accuracy, sensibility, and awareness. Data from Chapter 4 indicated that the interoceptive accuracy and awareness elicited the strongest correlations with objective markers of aerobic fitness. However, state interoceptive sensibility was not significantly associated with measures of aerobic fitness for either the tracking or discrimination tasks. Researchers have previously demonstrated that these three facets are at least partially independent from one another (Forkmann et al., 2016; S. N. Garfinkel et al., 2015), suggesting that factors associated with aerobic fitness may selectively influence interoceptive accuracy and awareness but do not alter a person’s sensibility. Moreover, regression analysis on data reported in these previous studies supports a hierarchical organisation of these interoceptive facets and identifies interoceptive accuracy as the core (central) construct underpinning higher inferences such as metacognitive awareness.

Consequently, it can be concluded that parameters related to aerobic fitness predominantly influence lower-order processing of interoceptive afferents reflecting objective perceptions of physical sensations arising from the body.

Exercise Training as an Approach to Influence Interoception?

Building on the findings of Chapter 4, the second experimental study (Chapter 5) aimed to examine the causal basis of the relationship between interoception and aerobic fitness. This question presented particular interest as difficulty in manipulating interoception, compared to exteroception, has been considered a limitation within this research domain (Khalsa et al., 2018; Vaitl, 1996). Indeed, despite studies demonstrating transient improvements in interoceptive accuracy under contexts of increased arousal (Jones & Hollandsworth, 1981; Khalsa, Rudrauf, Sandesara, Olshansky, & Tranel, 2009) or attention to self (Ainley, Maister, Brokfeld, Farmer, & Tsakiris, 2013; Ainley, Tajadura-Jiménez, Fotopoulou, & Tsakiris, 2012), robust evidence demonstrating the effectiveness of interventions to elicit stable, enduring changes in interoceptive accuracy remains elusive. This was recently demonstrated by Khalsa and colleagues (2020) who showed that experienced meditators were not superior in the cardiac perception accuracy compared with matched non-meditator controls. Following up on this finding, the authors performed a meta-analysis on the available data comparing meditators and non-meditators, demonstrating no mean difference (MD = -.30, 95%CI [-9.12, 29.9]) in interoceptive accuracy between the two populations. Conversely, improvements in tracking accuracy have been demonstrated following biofeedback training where participant's knowledge of their heartbeats is improved (Peira et al., 2014; Phillips et al., 1999). However, this effect may be associated with improvements in knowledge of resting heart rates, akin to improvements in the precision of prior expectations regarding the temporal characteristics of their cardiac cycle. Similarly, measures of bodily awareness (analogous to trait interoceptive sensibility) are greater in experienced meditators (Cebolla et al., 2018), indicating greater self-efficacy beliefs in interoceptive experience in those regularly practicing bodily attention. Taken together these different findings represented conflicting evidence for experimental manipulation of trait aspects of interoception.

The relationship established between aerobic fitness and interoception in Chapter 4 indicated a potentially effective approach for modulating trait interoceptive characteristics. However, despite the implications of these observations research had previously only determined this relationship through observational studies, and explanation of the underlying cause of these effects differs between factors related to physiological adaptations (Machado et al., 2019; Perakakis et al., 2017) and interoceptive exposure (Georgiou et al., 2015; Jones & Hollandsworth, 1981). In contrast to the hypotheses, the findings from Chapter 5 demonstrated that the 4-week exercise intervention was not sufficient to induce significant changes in either aerobic fitness (except for PO_{peak} for best performance) or cardiac interoception, indicating that recurrent exposure to vigorous physical activity alone was not sufficient to alter cardiac interoceptive parameters when markers of aerobic fitness remained statistically unchanged. Importantly, these null effects were observed despite the optimisation of the data analysis procedure towards identifying the best performance in the post-training period. Interpreting this finding with appropriate caution, the data potentially suggests that the relationships identified between markers of aerobic fitness and cardiac perception were likely related to physiological adaptations rather than interoceptive exposure alone.

This finding is supported by observations that interoceptive accuracy is strongly tied to the condition of the physiological construct that is being perceived. With respect to cardiac perception and cardiac function, researchers have demonstrated that interoceptive accuracy is positively associated with lower $f_{c\ rest}$ (e.g., Chapter 4), lower heart rate variability (Knapp-Kline & Kline, 2005), stroke volume, and momentum (a composite measure describing the product of stroke volume and the velocity of ejected blood volume; Schandry, Bestler, & Montoya, 1993), greater cardiac reactivity to an isometric handgrip task (Pollatos, Herbert, et al., 2007), and increased cardiovascular arousal (Khalsa et al., 2009). Interestingly, the application of retrospective bivariate correlations revealed inconsistent evidence across the four studies for a relationship between $f_{c\ rest}$ and measures of cardiac interoception (Table 8.2). Findings reported by Ring and colleagues (1994) may help to explain these mixed findings, with the authors reporting that changes in stroke volume and resting heart rate did not influence heartbeat tracking accuracy using postural manipulation (tilt-table). Consequently, the authors postulated that cardiac contractility may be the most likely cardio-physiological candidate for explaining cardioceptive accuracy. Contractility is influenced by certain morphological characteristics of the heart, which are modifiable following persistent exercise training (Baggish et al., 2008; Fagard, 2003; Kemi, Haram, Wisløff, & Ellingsen, 2004). These effects demonstrate that precise perception of cardiodynamic processes emerges (at least in part) from the presence of 'stronger' (i.e., more precise) sensory inputs (Ainley, Apps, Fotopoulou, & Tsakiris, 2016). Moreover, regression analysis of the three different facets of interoception (accuracy, sensibility, and awareness) performed in previous studies positions interoceptive accuracy and $f_{\text{c rest}}$ as the core constructs within this model, influencing a person's experience of both sensibility and awareness (Forkmann et al., 2016; Garfinkel et al., 2015). Furthermore, the lack of change in the physiological construct ($f_{\text{c rest}}$) may adequately explain the observed conservancy in the interoception data reported in Chapter 5 of this thesis following the exercise training intervention.

Table 8.2. Relationship between resting heart rate and measures of cardiac interoception across the four experimental studies of this thesis.

		Heartbeat Tracking			Heartbeat Discrimination		
		Accuracy	Sensibility	Awareness	Accuracy	Sensibility	Awareness
Chapter 4	Correlation	-.40*	-.40*	.12	-.64*	-.48*	-.57*
	p-value	.04	.04	.57	.00	.01	.00
	95% CI	[-.66, -.04]	[-.65, -.04]	[-.19, .44]	[-.81, -.43]	[-.70, .19]	[-.76, -.27]
Chapter 5	Correlation	.05	-.15	.03	-.24	-.21	-.26
	p-value	.81	.46	.90	.23	.29	.20
	95% CI	[-.38, .37]	[-.49, .17]	[-.33, .41]	[-.46, .03]	[-.53, .14]	[-.52, .07]
Chapter 6	Correlation	-.37	-.50*	.01	-.28	-.33	-.21
	p-value	.08	.02	.96	.19	.12	.33
	95% CI	[-.66, .02]	[-.74, -.04]	[-.28, .32]	[-.76, .20]	[-.63, -.04]	[-.51, .09]
Chapter 7	Correlation	-.30	-.39	-.01	-.43*	-.42*	-.28
	p-value	.17	.06	.97	.04	.049	.20
	95% CI	[-.61, .16]	[-.74, .05]	[-.36, .37]	[-.78, .03]	[-.64, .14]	[-.59, .11]

*$p < .05$

Influence of Cardiac Interoception on Exercise Regulation

Exercise imposes acute pressures on the physiological resources supporting homeostasis, which are partially managed through observable behavioural adjustments in work rates (Renfree et al., 2012). Importantly, perception of bodily states and appraisal of the expected consequences of these perceptions are purported to influence these regulatory behaviours (Micklewright et al., 2015; Rauch et al., 2005). However, despite the importance of interoception within this process, relatively few studies have previously examined whether individual differences in the sensitivity to somatic afferents influence our perceptual and behavioural responses to exercise. Of the limited data available, Herbert and colleagues (2007) demonstrated that good heartbeat perceivers exerted less physical effort, and elicited less cardiovascular strain (i.e., lower exercising f_c), in a 15-minute cycling task compared with poor heartbeat perceivers. Importantly, the two heartbeat perception groups were comparable in their post-exercise fatigue ratings and were also found to be similar in their aerobic fitness. Taken together, these findings indicated that the disparity in the physical exertion and cardiovascular strain resulted from differences in the perceptual sensitivity to interoceptive cues between the two groups, with good heartbeat perceivers being more sensitive to changes in their physiological *milieu* than poor heartbeat perceivers. Whereas, Machado and colleagues (2019) did not observe differences in cycling performance between good and poor perceivers in a graded exercise task to volitional exhaustion. Importantly, both studies examined performance in sedentary populations and as such performance may have been confounded by a lack of familiarisation with the exercise tasks. Moreover, differences in the task designs between these two studies preclude a definitive explanation of the difference in the reported effects. Finally, to the author's knowledge, no published findings existed within the literature to explain the possible influence of interoceptive sensitivity on pacing profiles (i.e., the distribution of exercise work rate over the duration of a given exercise task), despite the proposal that interoceptive afferents are likely to significantly contribute to this processes (e.g., St Clair Gibson, Swart, & Tucker, 2017)

Chapters 6 and 7 provide specific contributions within this thesis, affording greater clarity on the influence of resting cardiac interoceptive accuracy on exercise regulation. Firstly, Chapter 6 (Study 3) demonstrated that individual differences in cardiac interoceptive accuracy at rest did not influence exercise tolerance, as indicated by the duration of task engagement to task failure. Furthermore, the physiological data demonstrated that the magnitude of physiological strain (e.g., f_c and RER) experienced during the constant-load task was comparable between good and poor perceivers. RPE was also similar between the two groups throughout the exercise task, suggesting that interoceptive accuracy did not influence the relationship between perceived exertion and physiological strain. Extending on these findings, Chapter 7 demonstrated more nuanced effects when comparing the pacing behaviours of good and poor perceivers at *light* (RPE 10) and *hard-to-very hard* (RPE 16) perceived intensities in a self-regulated exercise task. In this study, good perceivers showed greater differences in PO between the two exercise intensities compared with poor perceivers. This effect was reflected in a lower magnitude of physiological strain (f_c and RER) for good perceivers in the RPE10 condition, with no differences at the higher exercise intensity between the two groups. Interestingly, concerning the findings in Chapter 7, Köteles and colleagues (2020) demonstrated comparable effects with moderate positive correlations between heartbeat perception accuracy at rest and the reproduction of heart rates at low exercise intensity (r_s = .32) with no correlation at moderate and higher exercise intensities (r_s's < .10). Taken together with the findings from Study 3, this suggests that interoceptive accuracy is likely to exert the greatest influence on exercise behaviour at lower exercise work rates where physiological strain is minimal.

The differences in these findings can be consolidated when we consider the effect of arousal and attention on interoceptive accuracy. Transient improvements in cardiac interoceptive accuracy have been demonstrated when physiological arousal is augmented immediately following exercise, with subsequent decays in accuracy with declining arousal during recovery (Jones & Hollandsworth, 1981). In agreement with this finding, pharmacological studies using isoproterenol have demonstrated similar improvements in heartbeat perception accuracy in response to increased heart rate (Khalsa, Rudrauf, Sandesara, Olshansky, & Tranel, 2009; Khalsa, Rudrauf, Hassanpour, Davidson, & Tranel, 2020). However, this positive effect of physiological arousal on cardiac interoceptive accuracy appears greater in those individuals demonstrating low interoceptive accuracy at rest with negligible changes evident in good perceivers (Jones & Hollandsworth, 1981). Further evidence, drawn from studies using biofeedback training, shows comparable findings with poor perceivers demonstrating greater improvements in interoceptive accuracy (Meyerholz et al., 2019). These effects suggest that interoceptive accuracy may transiently improve under contexts of increased arousal or attention to physiological states, but only in those people for whom baseline accuracy is low. Consequently, it may be stipulated that good and poor perceivers experience exercise differently depending on the intensity at which exercise is performed.

8.4. Assumptions and Limitations

The present thesis was conducted under several assumptions and limitations. In considering the generalisability of the findings reported in this thesis it should be noted that the data was collected using physically active, healthy young adults and therefore may not reflect effects within other populations. Furthermore, several assumptions within this thesis can be related to the application of heartbeat detection tasks as a measure of individual differences in interoception. The use of heartbeat detection tasks was potentially limited on the following accounts:

1. *Performance in tests of heartbeat perception reflect interoceptive perceptions*

   Performance in heartbeat detection tasks may not solely reflect sensitivity to interoceptive signals and may be confounded by sensory inputs transmitted along other neural pathways. For instance, signals generated along mechanosensitive afferent pathways transmitting from cutaneous tissues that are distinct from interoceptive pathways, projecting to different regions of the brainstem and cerebral cortex (e.g., somatosensory cortex vs. insula cortex; Khalsa, Rudrauf, Feinstein, Tranel, & Author, 2009), may influence performance in a test of heartbeat perception. This has implications on whether heartbeat perception should be considered as visceral sensation, cutaneous sensation, or both. Nevertheless, despite these potential confounds, objective performance in heartbeat detection tasks has been shown to correspond with structural and functional differences in the insula cortex, specifically positive correlations are reported for right anterior grey matter volume and activity (Critchley et al., 2004). Moreover, observations of positive relationships between heartbeat perception accuracy and emotional experience (e.g., Herbert, Pollatos, Flor, Enck, & Schandry, 2010; Pfeifer et al., 2017) lends support to the construct validity of these tools when considering theoretical frameworks describing embodied emotional experience.

2. *Heartbeat perception as a generalised interoceptive measure.*

   Measures obtained from heartbeat perception tasks are often interpreted as a generalised indicator of a person’s sensitivity to interoceptive stimuli. However, interoception encompasses a broad range of sensory inputs arising from the many different tissues of the body, contributing to perceptions such as temperature, pain, hunger and thirst, dyspnoea, sensual touch, and others (Craig, 2003). Given the breadth of inputs involved, perceptual acuity across these different interoceptive pathways are not always equivalent (Ferentzi et al., 2018). For instance, Garfinkel et al. (2016) demonstrated that despite a dissociation between cardiac and respiratory measures of interoceptive accuracy a positive relationship between cardiac and respiratory measures of interoceptive awareness was observed. Extending to other interoceptive axes, stronger relationships have been reported between cardiac and gastric interoceptive accuracy (Herbert, Muth, Pollatos, & Herbert, 2012; Whitehead & Drescher, 1980), partially owing to the shared overlap in cortical processing of these two visceral inputs (Avery et al., 2015). However, data regarding associations between other measures of interoceptive perception remain scant. Consequently, the effects observed in the present thesis are limited to the influence of cardiac interoception and may not accurately reflect the effects observed in relation to other interoceptive axes.

3. *Misclassification of good heartbeat perceivers*

   The basic threshold used to distinguish good heartbeat perceivers (i.e., median demarcation) was notably less conservative than the threshold previously applied within signal detection approaches. Specifically, an established *d'* threshold for good heartbeat perceived is reported as ≥ 0.75 (Whitehead et al., 1977). This would require an accuracy of 75%, which reflects a performance of 15 correct answers for every 20 trials in the context of the present thesis. For Chapters 4, 6, and 7 (where between-groups analyses were performed based on interoceptive accuracy) mean group scores for HBD accuracy ranged from 0.72 to 0.76, indicating that a meaningful number of individuals in these good perceiver groups would likely be reclassified using this erstwhile signal detection approach.

4. *Relationship between resting heart rate and cardiac interoceptive accuracy*

   Although a key finding of the present thesis, the relationship between resting heart rate and cardiac interoceptive accuracy has been highlighted as an area of concern (Zamariola et al., 2018). Arithmetically, the equation to derive heartbeat tracking accuracy can be simplified as the ratio of report heartbeats to the product of f_c and time (Ainley et al., 2020). Lower $f_{c\ rest}$, therefore, enables a higher quotient values (i.e. accuracy score) for a given dividend (reported heartbeats) through a relative diminution in the divisor (number of recorded heartbeats), particularly as the vast majority of people are biased towards under-reporting their heartbeats (Zamariola et al., 2018). For the heartbeat discrimination task, lower $f_{c\ rest}$ are not always correlated with better accuracy scores (Ring et al., 2015). However, perception of 'in-sync' and 'out-of-sync' conditions may be plausibly easier to identify in those with slower resting heart rates, as the presentation of audible tones are more distant to subsequent heartbeats and therefore less likely to be erroneously perceived as congruent to these subsequent heartbeats. To explain this point, consider the issue of the heartbeat discrimination task as a tool to assess interoceptive accuracy during exercise. As heart rate increases, particularly during exercise (e.g., $f_c > 120$ b·min^{-1}), the presentation of audible tones in ‘out-of-sync’ conditions may be perceived as being ‘in-sync’ as a result of the fixed delay periods used in the two conditions. Although this example is extreme compared with typical resting heart rates observed in the general population, small differences in the temporal synchronisation between the presentation of the pulse and its subsequent perception may influence performance in the heartbeat discrimination task as function of higher or lower f_c. Nevertheless bivariate correlations revealed that $f_{c\ rest}$ was only likely to be mediating factor in the results of Chapters 4 and 7, where accuracy in the HBD task was inversely related to $f_{c\ rest}$ (Table 8.2).

5. *Cardiac interoceptive cues influence perceptions of exertion during exercise (including discussion of the role of other sources of sensory feedback)*

The experiments reported in this thesis specifically studies 3 and 4 (Chapters 6 and 7), examined the influence of cardiac interoception on RPE. Acknowledging the assumptions outlined immediately above, it must be considered that the sensitivity of cardiac afferents may not solely influence the perception of bodily states during physical work. For instance, studies have long shown that heart rate and RPE may be differentiated experimentally following administration of atropine and practolol (da Vies & Sargeant, 1979) or caffeine (Doherty & Smith, 2005). Furthermore, the contribution of other afferent inputs is also known to influence RPE. These include the influence of breathing sensation (Faull, Dearlove, Clarke, & Cox, 2019) as well as afferents that signal changes within the musculoskeletal *milieu* (e.g., Zinoubi, Zbidi, Vandewalle, Chamari, & Driss, 2018). This suggests that RPE is driven by a multisensory integration of physiological afferents. It also remains unclear whether individuals differ in their attentional preferences underlying the appraisal of perceived exertion during exercise (i.e., do individuals prioritise different sources of sensory information when evaluating perceived exertion compared to others). This is an important question as it may influence a person’s perceptual experience (defined in terms of quality, intensity, and hedonicity) of exercise, which may ultimately influence adherence to exercise regimes.

8.5. Future Directions

The findings of the present thesis led to the following recommendations for future research:

Firstly, there appears to be a necessity to extend beyond cardiac interoception alone to examine the potential influence of interoception emerging across other axes (i.e., respiratory interoception) with aerobic fitness and exercise behaviour. Exploration of this question may contribute to an understanding of whether individuals differ in their use of sensory inputs when evaluating the costs associated with ongoing exercise engagement (i.e., do individuals more sensitive to respiratory sensations selectively prioritise these inputs over other sources of sensory information such as cardiac sensations).

Secondly, and in relation to the recommendation made above, there is a need to explore the influence of interoception on broader perceptual experiences emerging during exercise, extending beyond RPE-based measures. Perceptions can be defined in their experience according to quality, intensity, duration, and hedonicity. Studies have already demonstrated that affective (hedonic) experiences strongly influence exercise behaviours, whether defined in terms of acute tolerance to an ongoing bout (e.g., Greenhouse-Tucknott, Wrightson, Raynsford, Harrison, & Dekerle, 2020) or long-term adherence to exercise behaviours (e.g., Hargreaves & Stych, 2013). However, the question of whether cognitive-emotional appraisal of exercise is influenced by a person's basal interoceptive characteristics remains unclear, despite a robust body of evidence indicating a role for interoception on cognitive-emotional experience in other contexts (Critchley & Nagai, 2012; Eggart, Lange, Binser, Queri, & Müller-Oerlinghausen, 2019; Khalsa et al., 2015). Consequently, exploration of this question is necessary to better understand one of the key barriers preventing some individuals from consistently engaging in sufficient physical activity to maintain or promote physical and psychological well-being.

Thirdly, those findings emerging from Study 3 and Study 4, which indicated an intensity-dependent effect related to the influence of resting interoceptive sensitivity and the relationship between physiological strain and perceived exertion, warrant further investigation. To achieve this aim, a more systematic investigation of this effect is needed to both validate this initial observation and also provide a clearer explanation of the mechanisms involved.

Fourthly, there is a need to generate a greater understanding of the influence of interoceptive sensitivity on more discrete aspects of pacing behaviour. This may be elucidated through non-linear analytical techniques, which can identify the presence of non-random fluctuations in work rates occurring over multiple timescales (Hoos, Boeselt, Steiner, Hottenrott, & Beneke, 2014). These fluctuations are purportedly tied to ongoing evaluations of current versus desired physiological states (Tucker et al., 2006) and have been shown to reduce physiological strain when compared with fixed-paced exercise (Billat, Wesfreid, Kapfer, Koralsztein, & Meyer, 2006). It is therefore plausible that the structure of these fluctuations may be influenced by a person's sensitivity to the signals referencing homeostatic-relative information.

Finally, there is a need to examine the influence of aerobic fitness on interoception in populations that are characterised by atypical interoceptive processing. This proposal serves two purposes. The first is to demonstrate the generalisability of the findings more broadly than is currently reported. Secondly, the findings of the current thesis have implications on the understanding of the role of exercise as a non-clinical treatment for persons with depression or anxiety. Both of these conditions are associated with atypical interoceptive processing (Domschke et al., 2010; Eggart et al., 2019; Wiebking et al., 2015), and exercise is known to improve symptoms (Carek, Laibstain, & Carek, 2011). It seems plausible, therefore, that one possible mechanism for this effect of exercise may be linked to manipulation of the appraisal of interoceptive afferents (Sabourin et al., 2008).

CHAPTER 9. CONCLUSION

This present thesis investigated two principal lines of enquiry. Firstly, the question regarding the relationship between cardiac interoception and aerobic fitness was explored. The second focus of this thesis examined the influence of cardiac interoception on exercising pacing and tolerance.

The findings of this thesis support the notion that accuracy and awareness of heartbeat perception are improved among persons of greater aerobic fitness. Importantly, this thesis was the first to demonstrate that this effect was independent of age, gender, and body composition and appears to be predominantly influenced by resting cardiac function. However, the applicability of exercise training as a tool to influence interoception could not be reliably established in this thesis, as neither aerobic fitness nor interoception was altered following a 4-week exercise intervention.

Additionally, findings from this thesis provide an important and novel contribution to our understanding of the influence of interoception on a person's perceived physical experience of exercise, with cardiac interoceptive accuracy selectively influencing perceptions of physical exertion at low exercise intensities but not high exercise intensities. Importantly, this suggests that greater sensitivity to cardiac afferents does not reduce tolerance to exercise-induced physiological strain but instead appears to support a person's ability to discern between different exercise intensities, particularly in contexts where physical symptoms are difficult to distinguish.

Future research should extend on these findings to include additional population groups and analytical techniques, and exercise domains. A greater exploration of these factors may contribute to further understanding of the effects observed within this thesis.

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