The role of caregiver mental health and interoception in dyadic interactions and interoceptive processing development

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Acknowledgements

Doing a part-time PhD at the same time as working has been one of the toughest things I've done. Spanning over 6 years, I am convinced I chose the busiest 6 year period of my life to date, so the experience has been punctuated by many big life events, including a pandemic. I couldn't have got to this point without considerable support.

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Writing this thesis concerned with developmental origins, I am ever more grateful for my own developmental origins. Thanks Mum, Dad and Michelle for the unwavering support and encouragement. *#You'll never walk alone.*

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Summary of Work

Interoception, the processing of internal bodily signals, is associated with mental health in adulthood. However, very little is known about the early development of interoceptive processing. In the UK, prevalence of childhood anxiety disorders has been increasing steadily, both pre- and post- the COVID-19 pandemic. Given the relationship between interoception and anxiety in adulthood, understanding the early development of interoceptive processing is both important and urgent. This thesis seeks to explore the factors influencing the early development of interoceptive processing and its relationship with anxiety risk. In recent years, several theories on the development of interoceptive processing have emerged. These theories consistently suggest that an infant's early social experience, specifically interactions with their primary caregiver, facilitate the development of interoceptive processing. If so, caregivers' skills in these early interactions could be influencing the development of interoceptive processing in their infants. For example, which of the caregivers' specific behaviours are important? What factors influence caregivers' ability in these behaviours? Do these early influences endure throughout childhood and are they associated with susceptibility to anxiety? Despite the importance of this topic, studies providing empirical evidence of interoceptive processing in infants remain sparse, with mixed findings. To add to what is known about the early development of interoceptive processing, I conducted five studies of caregivers and their infant or child, revealing several relationships between caregiver interoception, caregiver mental health and caregiver and infant behaviour. In addition, I demonstrated a strong association between caregiver and child interoception and an association between caregiver interoception and child threat sensitivity, a risk factor for anxiety. Together, these findings provide empirical support for theories on the development of interoceptive processing, adding to what little is known of its early development. In addition, these findings potentially shed some light on the underlying mechanisms behind familial relationships in anxiety disorders.

Impact of COVID-19

My original plan for this thesis was to conduct a longitudinal study, based on face-to-face studies in the University of Essex Babylab. As part of that process, I planned to evaluate different measures of interoceptive processing in infants, using physiological and neuroimaging methods.

Having invested the first year of my PhD in researching and setting up my first pilot test using physiological measures, the first COVID lockdown forced an abrupt halt to this testing. I then had to investigate alternative ways to address my research questions that could be conducted during the period in which the Babylab remained closed. I decided to conduct online behavioural studies, making use of caregivers' ability to record themselves interacting with their infants at home. This change of methodology forced a change in the overall direction of the thesis towards dyadic interactions between caregivers and infants, rather than focusing on evidence of interoceptive processing in the infant, as per the original plan. Empirical evidence of interoceptive processing in infants was, and remains, sparse.

Moving studies online required new skills, such as the programming of tasks on the Lookit platform, incorporated within the ChildrenHelpingScience.com website. In addition, recruitment relied on participants enrolling with the ChildrenHelpingScience.com website, which added a further step in to the already difficult process of recruiting families to take part in studies.

As a part-time student conducting this PhD over 6 years, I was able plan and run my final study in the Babylab once the lockdown was lifted. However, by this stage, the new direction for my research was established and it was too late to return to the original plan. However, I have been able to incorporate some physiological evidence into my thesis, both from the initial pilot study and the final study, alongside my behavioural observations. I believe my thesis is richer for this combination, even if I did not get to master the techniques I had hoped to use during my research.

In summary, COVID-19 had a significant impact on my planned research and cost valuable time in planning new, online studies. However, I did learn additional skills during this difficult period and I am pleased that I was able to continue to investigate the early development of interoceptive processing, albeit in a different way from planned.

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Chapter 1

Introduction

1.1 Introduction

Research on adults suggests that anxiety is related to interoception, i.e. the processing of internal bodily signals (Brewer et al., 2021; Khalsa et al., 2018; Nord and Garfinkel, 2022). Despite this important relationship, little is known about the development of interoceptive processing early in life. However, better understanding of the early development of interoceptive processing could offer clues about the relationship between interoception and anxiety and whether differences in the development of interoceptive processing are associated with risk of anxiety difficulties as the child grows. The increasing prevalence of mental health problems, particularly anxiety disorders, among children in the UK (Newlove-Delgado, 2023), coupled with increases in waiting lists for treatment in recent years (England and Mughal, 2019; National Audit Office, 2018), places greater importance than ever before on understanding the underlying mechanisms behind anxiety and its risk factors. Improved understanding of the underlying mechanisms of anxiety could facilitate earlier diagnosis and intervention, as well as therapeutic development. This thesis seeks to explore the factors that influence the early development of interoceptive processing and its relationship with anxiety risk. In this chapter, I provide an overall introduction to the topics under investigation. In Section 1.2, I begin by reviewing the current literature on interoception, considering what is known about interoception in adulthood, the theoretical models that have been put forward in the past decade, and the definitions of interoception and its dimensions. In Section 1.3, I review the literature concerning the development of interoceptive processing early in life, and the role of caregiver-infant interactions as a prerequisite for this development. Section 1.4 covers the importance of understanding the development of interoceptive processing as a potential risk factor for child mental health. Finally, in 1.5 I summarise the research underlying this PhD thesis, and introduce the key research questions resulting from gaps in the current literature.

1.2 Interoception in adulthood

Throughout history, the relationship between body and mind has been widely documented, even if not thoroughly understood (Hannesdóttir, 2022). In literature and the arts, the heart has received particular attention, often depicted as the centre of our emotional being, for example, in expressions of love, happiness, distress, or trauma (Hannesdóttir, 2022). These descriptions and depictions, even in ancient cultures, make perfect sense since emotions are typically accompanied by physical sensations, many of which originate inside the body - a pounding heart, butterflies in the stomach, etc. In modern times, the relationship between physiological sensation and emotional states was depicted in one of the earliest theories of emotion, produced simultaneously yet independently by American philosopher William James and Danish physician Carl Lange in 1884 and 1885 respectively (Lange and James, 1967). The James-Lange theory of emotion suggested that the experience of emotion is triggered by physiological arousal. Early study of the nervous system shed further light on this connection between mind and body, and, in 1906, the concept of interoception was first introduced. Then, the term interoception was used to describe the flow of information between the visceral organs and the brain, and is credited to Sherrington in a series of lectures on the nervous system (Ceunen et al., 2016; Sherrington, 1906). Regular use of the term "interoception" began to appear in journal articles during the 1940s and 1950s (Airapetyantz and Bykov, 1956; Ceunen et al., 2016). In tandem with the development of new experimental approaches, research on interoception has been the subject of renewed and sustained interest over the last twenty years (e.g. Craig, 2002; Critchley, 2002; Garfinkel et al., 2015; Khalsa et al., 2018; Murphy, 2023; Desmedt, Luminet, Maurage, and Corneille, 2023). This focus of research is understandable when considering the wide-ranging role that interoception is believed to play. Our bodies form the foundation for all our perceptual and cognitive experiences. We perceive our external environment through our exteroceptive senses such as vision, touch, and hearing. In addition, we sense our relationship with our immediate environment via proprioception (Sherrington, 1952). However, our bodies are also a source of constant internal sensations which provide information about our physiological condition (Pace-Schott et al., 2019).

Our ability to perceive and identify our physical state is fundamental in enabling us to respond to these signals appropriately, for example, to sleep when tired, drink when thirsty, etc. This ability is thought to be the cornerstone of self-regulation as it allows us to perform the behaviours necessary to return to homeostasis, a state of optimal physiological balance. While we rely on these signals to carry out many actions consciously (through activities such as eating, going to sleep, seeking help for pain), this is only part of the story. Most interoceptive signalling and the resulting alterations in bodily state occur subconsciously, through covert reflexes (Tsakiris and Critchley, 2016; Khalsa et al., 2018). One example of this is the baroreflex, which continuously alters blood pressure and heart rate without the need for any conscious perception (Schulz and Vögele, 2015). Homeostatic maintenance therefore relies on both conscious and subconscious interoceptive information, as well as requiring appropriate behavioural responses. Homeostatic regulation is essential for physical health, highlighting the importance of interoceptive processing for wellbeing, as will be discussed next.

A large and growing body of research confirms this link between interoception and health (Khalsa et al., 2018). For example, atypical interoception has been associated to obesity (Herbert and Pollatos, 2014) and diabetes (Pauli et al., 1991). As well as physical health, interoception has been suggested to relate to higher-order cognition, such as learning and decision making (Critchley and Garfinkel, 2018; Garfinkel et al., 2015; Herbert and Pollatos, 2014; Pauli et al., 1991) and emotion and mental health, a topic which continues to attract considerable research attention (e.g. Brewer et al., 2021; Critchley and Harrison, 2013; Garfinkel and Critchley, 2016; Khalsa et al., 2018; Murphy, Brewer, Catmur, and Bird, 2017b; Murphy, 2023; Nord and Garfinkel, 2022; Paulus, 2013; Quadt et al., 2018). In recent years, for example, dysfunction of interoception has been linked to mental health conditions such as anxiety disorders, major depressive disorder, and eating disorders (Khalsa et al., 2018; Murphy, Brewer, Catmur, and Bird, 2017b; Eggart et al., 2019; Crucianelli et al., 2016). Alterations in interoception have also been observed in neurodevelopmental disorders such as autism (Garfinkel and Critchley, 2016; Quattrocki and Friston, 2014). The research mentioned here demonstrates the breadth of the role attributed to interoception in day-to-day physical and emotional functioning, as well as in a variety of physical and mental health conditions.

Despite the extensive role attributed to interoception, this research field is marked by ongoing debate. For example, there is no universally accepted definition of interoception; instead, researchers have employed several differing definitions (see Desmedt, Luminet, Maurage, and Corneille, 2023 for a review). In addition, debates persist regarding the sources of bodily information classified as interoceptive, the relevant neural pathways involved, and the functional significance of interoceptive information. These discussions have shaped varying conceptualizations and models of interoception, each employing distinct terminology (Brewer et al., 2021; Murphy, Bird, and Catmur, 2019; Garfinkel and Critchley, 2013; Garfinkel et al., 2015). Additionally, updated definitions of interoception have been proposed (Desmedt, Luminet, Maurage, and Corneille, 2023; Murphy, 2023). In the sections that follow, I will summarise the definitions and classifications of interoception that have evolved during the last two decades, highlighting the ongoing debates that characterise the field.

1.2.1 What is interoception?

In broad terms, interoception refers to the processing of internal bodily signals (Brewer et al., 2021), allowing us to perceive internal changes in sensations, such as hunger, thirst, sleepiness, and our emotions. In other words, interoception enables us to know how we feel (Tsakiris and Critchley, 2016). fMRI studies have highlighted several brain regions involved in the processing of interoceptive information. Quadt et al. (2018) provide an overview of the neurobiology of interoception, highlighting the involvement of brainstem, subcortical and cortical regions in interoceptive processing (Quadt et al., 2018). Interoception has been originally defined as the sense of the physiological condition of the body (Craig, 2002). This definition was based on the neurobiology underpinning the processing of afferent information received by the central nervous system (Craig, 2002). Through a considerable body of work defining the lamina I spinothalamocortical system (e.g. Craig, 1996; Craig et al., 2000), Craig demonstrated that this information came from all tissues in the body, rather than just the viscera - as previously suggested in Sherrington's earlier conceptualisation of interoception (Sherrington, 1906). According to Craig (2002, 2003), afferent viscerosensory information converges in the brain stem, in the nucleus of the solitary tract (NTS). This is where spinal laminar 1 and vagus nerve inputs converge, critical for management of physiological state and triggering changes, for example, to blood pressure. The NTS contains the visceral receptors from distinct organs and it has been implicated in the processing of interoceptive signals across different domains of interoception, e.g. cardiac, respiratory and gastric interoception. The NTS projects to the hypothalamus, ventrolateral medulla and parabrachial nucleus, providing initial control of hormonal, immune and autonomic outputs. Prethalamic midbrain pathways project further to the hypothalamus and amygdala, in tandem with thalamocortical projections to the insular cortex and anterior cingulate cortex (Craig, 2002; Craig, 2003). In addition to providing a neurobiological depiction of interoception, Craig (2002) also linked interoceptive information with the subjective awareness of feelings, by highlighting the involvement of the right anterior insula in both the processing of interoceptive information and in the experience of emotion (Craig et al., 2000). This important work provided a cornerstone for research on this field over the last two decades, upon which further debates and refinements to the definition of interoception have been built. For example, the insular cortex, IC, was initially identified as the core of interoceptive processing activity (Craig, 2002; Critchley et al., 2004; Critchley, 2004; (Quadt et al., 2018). Since then, more specifically, the anterior insular cortex has been found to predict performance on interoceptive tasks, with the right anterior insular cortex reactivity predicting accuracy in heartbeat detection tasks and its volume predicting sensibility (Critchley et al., 2004 Quadt et al., 2018). Interoceptive information is projected in the posterior insula and to the anterior insular cortex, where interoceptive signals integrate with exteroceptive and motivational information (Critchley, 2002). The role of the anterior cingulate cortex, ACC, is also highlighted, with the ACC understood to work alongside the IC as a unit (Critchley, 2002; Quadt et al., 2018). Khalsa et al. (2009) questioned the role of the IC and ACC in interoceptive awareness, however, since patients in studies of lesions in the IC and ACC appear able to demonstrate interoceptive awareness comparable to healthy individuals. Within this study, it is suggested that afferent somatosensory information from the skin could play a mediating role in the sensation and perception of cardiac activity (Khalsa, Rudrauf, Feinstein, et al., 2009). Studies of the neural underpinnings of interoception have led to more recent acceptance that interoceptive processes rely on the bidirectional flow of information through neural channels, with the insula appearing to act as a hub where information is received and projected, in order to trigger the changes required for homeostatic maintenance (L. F. Barrett and Simmons, 2015; Desmedt, Luminet, Maurage, and Corneille, 2023). This contradicts early definitions of interoceptive information as afferent (Craig, 2002).

Berntson and Khalsa (2021) reinforced the view that interoceptive information is bi-directional. They suggested that interoception relies on both afferent and efferent information , arguing that the interaction between these two signals is necessary for both homeostatic regulation and influencing cognitive, emotional and behavioural processes (Berntson and Khalsa, 2021), widely considered to be important functions of interoception (e.g. Tsakiris and Critchley, 2016). In addition, Berntson and Khalsa (2021) added to our understanding of afferent interoceptive information, by providing a detailed overview of the wide variety of the sensors (e.g. chemoreceptors, humoral receptors, mechanoreceptors and free nerve endings), pathways (e.g. vagal, cranial and somatosensory), systems (e.g. central and peripheral nervous system, cardiovascular, gastrointestinal, limbic systems) and circuits (e.g. cognitive, affective, threat) involved. The authors also highlighted that most interoceptive signalling and the resulting alterations in bodily state occur subconsciously, through covert reflexes (Tsakiris and Critchley, 2016; Khalsa et al., 2018). One example of this is the baroreflex, which continuously alters blood pressure and heart rate without the need for any conscious perception (Schulz and Vögele, 2015). Berntson and Khalsa (2021) further describe how conscious awareness is triggered when homeostasis, a state of optimal physiological balance, is perturbed, such as by pain, tiredness, a full bladder, etc. Importantly, the triggering of our awareness and how we then respond to these signals once our awareness is fundamental for homeostatic maintenance.

In a seminal paper that brought together all the major interoception researchers, Khalsa et al. (2018) conceptualized interoception as the process by which the nervous system senses, interprets and integrates signals arising from within the body (Khalsa et al., 2018). This important paper provided a summary of the consensus between participants at the first Interoception Summit organised by the Laureate Institute for Brain Research in 2016. The collective authors focused on summarising the state of the art at that point, in four key topics: interoceptive assessment, interoceptive integration, interoceptive psychopathology and a roadmap for further research. Priorities emerging from this summit included the need to work towards a consistent, agreed taxonomy for interoception, as well as further refinement and testing of models of interoception.

More recently, interoception has been referred to more broadly, as the processing of internal bodily signals (Brewer et al., 2021; Murphy, 2023). This recent definition has the added convenience of enabling researchers to focus on the *function* of the signal, i.e. signals which provide information on internal body states, rather than the *source* of the information being communicated. More importantly, this definition also encompasses further sources of bodily information, such as that of touch via the skin, or skeletal muscle fibres. Touch, particularly, raises an important point in the debate over definitions of interoception, since sensations originating from the skin would classically be considered exteroceptive. However, certain types of touch have been found to activate the same neural pathways as interoception (see Section 1.3.2). In other words, while the stimulus is external, the sensations are processed in a similar way to interoceptive information. For this reason, Crucianelli and Erhsson (2023) more recently argued for the inclusion of skin in the definition of interoception, suggesting that the contribution of this organ to the field of interoception has been, to some extent, neglected (Crucianelli and Ehrsson, 2023).

As the definition of interoception has become more broad, representing a shift in focus from the source of interoception to the function of interoceptive information, there remains a lack of distinction between conscious and subconscious interoceptive processing. This was discussed recently by Desmedt (2023), who reviewed the state of the art of interoception research. Desmedt highlights that, while previous definitions of interoception were concerned with the origins, functions and pathways of interoceptive information, leading to a more broad definition, a limitation of this wider definition is that it does not distinguish between conscious and subconscious interoceptive activity, even though this distinction is widely acknowledged (Desmedt, Luminet, Maurage, and Corneille, 2023). This is an important distinction for researchers. Interoceptive activity that reaches consciousness, for example, the perception of one's heartbeat (Garfinkel et al., 2015), and subconscious interoceptive activity, such as the regulation of heart rate by the nervous system (Porges, 1995b), rely on different mechanisms within the body. However, both are referred to within the broad field of interoception. The consideration of higher versus lower levels of the processing of interoceptive signals within the brain has also led to recent calls for the development of more comprehensive, hierarchical models of interoception which consider the level of consciousness involved in the processing of interoceptive information (Desmedt, Luminet, Maurage, and Corneille, 2023). Classifications of interoception, including this distinction between conscious and subconscious interoceptive processing, are discussed next.

1.2.2 Classifications of interoception

In the last decade, the development of theoretical models has attempted to clearly conceptualise interoception (Garfinkel et al., 2015 Murphy, Bird, and Catmur, 2019). However, interoception is a broad term comprising of different dimensions, which all rely on a number of cognitive processes (Murphy, Bird, and Catmur, 2019; Garfinkel and Critchley, 2013; Garfinkel et al., 2015). These include our ability to sense and perceive interoceptive signals, how accurately we interpret their meaning, how much attention we pay to them, and how confidently we trust our own abilities to do so. The multidimensionality of interoception has led to the identification of dissociable components and the construction of different theoretical models (Garfinkel and Critchley, 2013; Garfinkel et al., 2015; Murphy, Bird, and Catmur, 2019; Murphy et al., 2020).

Garfinkel et al. (2015) first proposed a formal classification of interoception, the *three-dimensional model*. In this model, *interoceptive accuracy* is considered an objective measure, which refers to the performance on tasks where participants are asked to detect internal sensations such as their heartbeat (e.g. Schandry, 1981; Wiens and Palmer, 2001). Interoceptive accuracy therefore relies on some degree of sensation and perception of heartbeat, to be able to provide such information. *Interoceptive sensibility* refers to how able to detect internal signals individuals believe themselves to be, as reported by self-report confidence ratings or questionnaires, such as the Multidimensional Assessment of Interoceptive Awareness, or MAIA (e.g. Mehling et al., 2012; Mehling et al., 2018). Finally, *interoceptive awareness* measures the relationship between *sensibility* and *accuracy* and hence taps into the meta-cognitive level of interoception. In the development of this model, *sensibility* and *accuracy* were observed to be dissociable (Garfinkel et al., 2015).

Building on this initial classification, Khalsa et al. (2018) presented an inclusive, consensus-based outline of interoception, defined as the processing of information from all over the body by the central nervous system. The agreed model of interoception here was based on eight features of interoception: attention (the observing of internal sensations), detection (presence or absence of conscious report), magnitude (perceived intensity), discrimination (ability to differentiate/localise the sensation from others), accuracy (correct and precise monitoring), insight (meta-cognitive confidence-accuracy correspondence), sensibility (self-perceived trait-based tendency to focus on sensation), self-report scales (questionnaires). In addition, it was noted that the sensing of interoceptive information could be both painful and non-painful, both positive and negative relating to both high and low levels of arousal and occurs primarily outside of conscious awareness unless during homeostatic perturbation. This collaborative paper also presented a unified call for consistent nomenclature and further investigation of the relationships between different dimensions of interoception and different mental health symptoms and diagnoses.

A difficulty arising from these classifications is that different methodologies are included within the same dimension. This can sometimes tap into different components of interoception or require different domain-general cognitive abilities. Recognition of this difficulty has led to further development of the classification of interoception along with methodological development. For example, Murphy et al. (2019) questioned the dissociation between interoceptive sensibility and interoceptive accuracy proposed by Garfinkel et al. (2015), since while questionnaire scores relating to body awareness rarely correlate with objective measures of interoceptive accuracy, confidence ratings sometimes do (Murphy, Bird, and Catmur, 2019). Highlighting this methodological distinction, Murphy et al. (2019) argued instead for a 2 x 2 factorial model, in which, *what* is being measured (factor 1 - accuracy or attention) is considered alongside *how* it is being measured (factor 2 - beliefs or performance) Murphy, Bird, and Catmur, 2019). According to Murphy and colleagues (2019), *interoceptive accuracy* refers to how accurate an individual believes themselves to be when interpreting their bodily signals, while *interoceptive attention* refers to how much attention an individual pays to their bodily sensations. *Performance* is measured by an objective task, while *beliefs* are measure by self-report questionnaires. Building on this model, beliefs about *interoceptive accuracy* and *interoceptive attention* measured by self-report have been found to be dissociable (Murphy, Bird, and Catmur, 2019) leading to the development of two new self-report scales, the Interoceptive Accuracy Scale, IAS, and the Interoceptive Attention Scale, IATS (Gabriele et al., 2022; Murphy, Bird, and Catmur, 2019; Murphy et al., 2020). In a further development of this model, Murphy proposed to also include the dimension of one's propensity to use conscious interoceptive information, i.e. *interoceptive propensity*, which considers an integration of interoceptive sensibility and awareness to inform beliefs and action (Murphy, 2022). This important consideration takes adaptability into account, i.e. whether one can choose to act on or ignore interoceptive signals depending on one's current circumstances. These scales developed alongside Murphy's factorial model of interoception offer important tools to researchers examining the roles of different dimensions of interoception, allowing us to separately measure accuracy and attention, and are discussed in detail in Chapter 2.

The models of interoception presented so far rely on explicit measures of interoception, i.e. an individual's ability to perceive and report on their sensations and, as such, while useful in the conceptualisation of conscious interoceptive processing, they take no account of implicit interoceptive activity. In light of this, Suksasilp and Garfinkel (2022) have built on the original three-dimensional model to include five further dimensions (neural representation, strength of afferent signals, preconscious impact of afferent signals, interoceptive insight and interoceptive attention), taking account of both higher and lower order processing of interoceptive information. As a result, they present a model of interoception that reflects the distinct levels of interoceptive processing, from the visceral strength of the afferent signals arising from the body, through the preconscious and conscious awareness of internal signals, right up to the meta-cognitive awareness of attention to interoceptive signals and their explicit attribution and interpretation (Suksasilp and Garfinkel, 2022).

The development of various theoretical models highlighting different dimensions of interoception represents attempts to bring about consistency among researchers and work towards a consensus on how interoception is classified (e.g. Khalsa et al., 2018). However, despite these attempts, the significant increase in research papers on the topic published over the past two decades, combined with previous work using outdated terminology, means inconsistencies remain throughout the literature. One example of inconsistent terminology is the use of *interoceptive sensitivity*, which is often used to describe the ability to perceive one's internal bodily state. Since many of the studies using this terminology are based on heartbeat detection tasks (e.g. L. Barrett et al., 2012; Domschke et al., 2010;Tsakiris et al., 2011), *interoceptive sensitivity* appears interchangeable with *interoceptive accuracy* as used in the three-dimensional model (Garfinkel and Critchley, 2013; Garfinkel et al., 2015) in these specific cases. However, since the development of the IAS (Murphy, Bird, and Catmur, 2019), there is further potential for confusion over the use of *interoceptive accuracy*, which now refers to either performance on a heartbeat detection task, as in the three-dimensional model (Garfinkel et al., 2015), or a score on the IAS, a self-report measure aligning with the 2 x 2 factorial model (Murphy, Bird, and Catmur, 2019). Similarly, Khalsa et al. (2018) refer to *interoceptive sensibility* as a trait-based tendency to focus on sensations, which could appear similar to Murphy's definition of *interoceptive attention*, whereas in the three-dimensional model it refers to a confidence rating of one's ability. While these additional classifications and new measures of dimensions of interoception enable researchers to be more specific in the future, it remains important to remain cautious when comparing findings between studies and over time.

The evolution of the theoretical models of interoception described above has focused primarily on cardiac interoception. However, interoceptive processing can be observed through several bodily systems, e.g. cardiac, respiratory, gastric and endocrine. Existence of common neural pathways for interoceptive information perhaps encourages a convenient assumption that interoception is a unitary system, in other words, that high sensitivity to heart rate represents high sensitivity to other interoceptive signals. However, research examining correlations between interoceptive abilities in different domains is inconclusive, casting doubt over this assumption (Brewer et al., 2021; Garfinkel et al., 2015; Murphy, Brewer, Catmur, and Bird, 2017b). Studies have found correlations between heartbeat perception abilities and gastric distension (Herbert et al., 2012; Whitehead and Drescher, 1980), but no correlation was found with high blood pressure, or self-reported symptoms of sweaty hands or shortness of breath (Steptoe and Vögele, 1992). Similarly, meditation has been observed to improve respiratory interoceptive sensitivity (Daubenmier et al., 2013), but not cardiac sensitivity (Khalsa et al., 2020). Together, this evidence suggests that interoceptive abilities across different channels may be, at least partially, independent. However, despite these different channels of interoception now attracting research attention, much of the existing literature considering interoceptive abilities relies on measures relating to cardiac interoception. This research focus is for largely practical reasons.

Cardiac activity is straightforward to measure with ECG or a pulse oximeter (see Chapter 2 for a description of these methods) and requires only minimal instructions for study participants. Measurement of interoceptive accuracy has typically utilised tasks such as the heartbeat detection task (Schandry, 1981), which involves participants counting the number of heartbeats in a specified time window, or heartbeat discrimination, involving reporting the timing of individual heartbeats (Brener and Kluvitse, 2018). Other tasks have involved reporting synchrony or asynchrony of external stimuli, such as audible tones, with the heartbeat (Garfinkel et al., 2015; Wiens et al., 2000; Wiens and Palmer, 2001). As will be discussed in detail in Chapter 2, these tasks rely on several different cognitive skills and relate to the different dimensions of interoception described above. However, these tasks may not be appropriate for all individuals. For example, a pre-verbal infant would not be able to report on their sensations. Similarly, approximately one third of typical, healthy adults have no conscious perception of their resting heartbeat (Khalsa, Rudrauf, Sandesara, et al., 2009). Within this thesis, I focus on the relationship between anxiety and interoception, both in the caregiver and in the infant and child. Since how we attribute changes to our sensation of heartbeats often characterises anxiety and anxiety disorders (Hoehn-Saric et al., n.d.), the focus on cardiac interoception is justified here. The relative merits of tasks used in the measurement of explicit cardiac interoception are discussed at length in Chapter 2.

Within this thesis, I focus on the relationship between interoception and anxiety in caregivers and the role of these factors in the development of interoceptive processing in infants and older children. To do this, I adopt the broad definition of interoception as the processing of internal bodily signals (e.g. Brewer et al., 2021). In the studies presented in Chapters 3, 4 and 5, I refer to *interoceptive accuracy*, specifying in each case whether this relates to objective performance on heartbeat detection tasks (Garfinkel et al., 2015) or self-reported levels of accuracy assessed by questionnaires (Murphy, Bird, and Catmur, 2019). I also use measures of interoceptive sensibility (Garfinkel et al., 2015) and interoceptive attention (Gabriele et al., 2022). Even though consensus is yet to be reached on precise theoretical and biological models of interoception, many studies have highlighted the importance of interoception in mental health, generally, and anxiety, specifically (Khalsa et al., 2018). A key component in mental health and anxiety is the processing and regulation of emotional state (Gross and Muñoz, 1995;

Gross, 2015; Pandey and Choubey, 2010). The relationship between interoception, emotion and anxiety is discussed in detail next.

1.2.3 Interoception, emotion and anxiety

Anxiety is described as an emotional state characterised by the integration of sympathetic arousal response (Hoehn-Saric and McLeod, 2000). To understand anxiety and its relationship with interoception, it is therefore imperative to first understand what emotions are. Damasio (2004) defined an emotion as a collection of changes in body and brain states triggered by a dedicated brain system that responds to specific perceptions, actual or recalled, relative to a particular object or event (Damasio, 2003). More recently, emotion has been defined as a multifaceted, whole-body process involving coordinated changes in the domains of subjective experience, behaviour and peripheral physiology (Gross and Thompson, 2007; Mauss et al., 2007). However, like the field of interoception itself, the field of research in emotion is also characterised by a lack of clarity, inconsistent terminology, and debate over precise definition (Gross, 2007). In this section, I will review theoretical descriptions of emotion, how we regulate our emotions, the role of the nervous system and the relationship between interoception and emotion.

Theories of emotion

Historically, philosophers depicted emotions as centred in the body with cognition based in the brain. As mentioned in Section 1.1, the work of American philosopher William James and Danish physician Carl Lange in 1884 and 1885 respectively (Lange and James, 1967) first depicted, in academic terms, a relationship between bodily sensation and emotion. The James-Lange theory suggests that physical sensations of arousal, such as a racing heart, drive a change in our emotional state, such as becoming afraid. Since then, several subsequent theories have reconceptualised emotion. For example, the Cannon-Bard theory (Cannon, 1927), proposes that emotions and arousal occur at the same time and independently, raising an important criticism of the James-Lange theory in that it is possible to experience physiological arousal that is not linked to a specific emotion. More recently, Schachter and Singer's two-factor model (Schachter, 1962), more widely adopted in psychology and clinical practice, proposed that arousal sensations and cognition combine to create emotion, with both elements being essential in the recognition of specific emotions (Strongman, 2014). However, this theory overlooks the possibility of experiencing physiological aspects of emotion before cognitive recognition of that emotion. Despite continued debate and ongoing research into the precise definition and neurobiology of emotion (see Moors, 2009 for an overview of theories of emotion), it can be seen that internal physiological sensation is a fundamental component of our experience of emotion, suggesting an important role for interoception, as accounted for in more recent models of emotion. Along with somatic experience, several other characteristics contribute to the experience of emotion (Moors, 2009): a motivational component driving action such as fight or flight, a cognitive component such as awareness of a trigger and recognition of the change in mood and a motor response, such as movements and vocalisations.

A more recent model of emotion is the theory of constructed emotion, TCE, (L. F. Barrett, 2017), which hypothesises that emotions are whole-body phenomena, with interoception and allostasis being at the core. Allostasis is the process by which the brain integrates dynamic, multi-sensory information to predict future physiological needs based on previous experience, e.g. change in blood pressure when standing up from a chair (L. F. Barrett, 2017; Sterling, 2012). As unanticipated information arrives in the brain, it creates a prediction error, so the brain must calculate the difference between those predicted requirements and the current status, then activate appropriate physiological change. The TCE is based on the biological and functional aspects of brain structure to describe a biological basis for emotion. The TCE proposes this biological basis is driven by the process of allostasis and highlights the need for metabolic efficiency in brain activity. The formation of representations of the entire body and its experiences in relation to the world contributes to the development of concepts of emotion. The TCE hypothesises that the brain categorises incoming sensory information according to these concepts, with the resulting affect being labelled as emotion. The afferent information informing this process is interoception, which, according to this theory, is directly involved in the creation of emotional response (L. F. Barrett, 2006; L. F. Barrett, 2017). The neurobiology of emotion is highly complex, with the creation of emotion depending on multiple sources of information from the body mapping simultaneously onto multiple brain regions, both cortical and subcortical, including, but not limited to, the insula, amygdala and hypothalamus (L. F.

Barrett, 2017; C. Shaffer et al., 2024). In addition, this activity is adaptive, relying on the ongoing supply of information in order to bring about changes in emotional state. (L. F. Barrett, 2017). While the detailed neurobiology of emotion is beyond the scope of this thesis, it is important to note here that interoception, beyond specific models of emotion, is widely understood to play a crucial role in contributing to the experience of emotion (Critchley and Garfinkel, 2017; Seth, 2013).

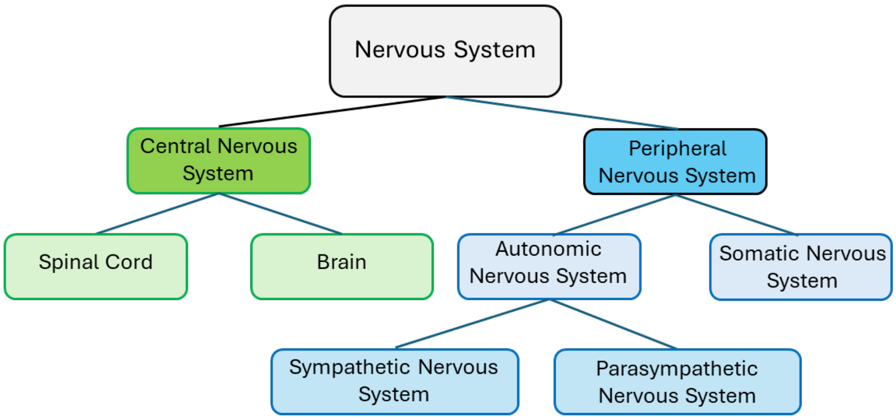
Our emotions must rely on a constant state of adjustment if we are not to end up stuck in a permanent state of misery, elation, or terror, thus suggesting that the ability to regulate emotions is also critical for maintaining balance. It has been proposed that emotion regulation takes place in two ways; automatically and deliberately (Mauss et al., 2007). While deliberate emotion regulation is considered effortful, relying on conscious processes, such as inhibition of an urge to laugh or cry, automatic emotion regulation is regarded as fast and efficient, such as the action of quickly turning away from an upsetting image (Mauss et al., 2007). Emotion regulation therefore relates to individuals' deliberate or automatic attempts to manipulate which emotions are experienced and when, as well as how they are experienced and expressed (Mauss et al., 2007). More succinctly, emotion regulation has been described as the activation of a goal to influence the emotion trajectory (Gross et al., 2011). The *Extended Process Model of Emotion Regulation* (Gross, 2015) defines several stages in the process of regulating emotions, namely *identification*, concerned with whether to manipulate emotion, *selection*, concerned with which strategy to adopt and *implementation*, concerned with specific actions. Gross' conceptualises emotion regulation as an iterative process, with each stage cycling through a valuation process influenced by conscious thought, behavioural habits and previous experience. This process of valuation relies, initially, on an understanding of whether the emotional state is positive versus negative, leading to goals orientated towards emotional state becoming more positive. According to Gross (2011), valuation depends on an integration of spinal cord reflexes, subcortical and cortical activity in a combination of automatic and consciously considered appraisal of emotional state and whether it needs to be altered. The conscious strategies then employed in emotion regulation can either be responsive (including behavioural choices, such as to enter a discussion, cognitive reappraisal, such as reminding oneself of one's ability in a challenging situation), or proactive (including situation selection, referring to a choice to avoid a certain unpleasant situation). Gross' model of emotion regulation highlights the integration of many complex sub-conscious and conscious processes, leading to individual differences in the ability to regulate emotions, and these differences have been related to emotional difficulties. For example, in cases of poor emotion regulation, or emotion dysregulation, problems with maintaining goal-directed behaviour and accepting, identifying, and managing emotions have been observed (Beauchaine, 2015; Gratz and Roemer, 2004). But can emotion regulation be improved? Interestingly, it has been shown that regular practice can improve the automatic response to negative emotions, evidenced by both self-reported changes to emotional state and measurement of changes to physiological state (heart rate) (Christou-Champi et al., 2015).

The nervous system, emotional arousal and anxiety

The models of emotion and emotion regulation described so far highlight the importance of interoceptive information in the construction and regulation of emotions. Yet, as described in Section 1.1, interoception in turn relies on the integration of information from a variety of sources within the body, such as the nervous system, endocrine, cardiac and respiratory systems. Therefore, in considering the relationship between interoception and anxiety, the nervous system deserves special attention. This is because it not only plays an important role in conveying interoceptive information, but it also modulates interoceptive information in order to carry out regulatory activities (Carlson and Birkett, 2017; Porges, 1995b). The nervous system also triggers perhaps one of the most important physiological responses in the experience of anxiety, namely the *fight or flight* response. First described by Cannon (Cannon, 1929), the fight or flight response is a stress response of enhanced alertness and physical abilities in response to perceived threat, triggered by concurrent hormone and neurotransmitter release (McCarty, 2016). To understand the mechanism of the fight or flight response, as well as the body's regulation of this response, it is necessary to provide an overview of the structure of the nervous system, the complex network of nerve tissue sending and receiving information between the body and the brain (see Figure 1.1).

The nervous system consists of the central nervous system, the CNS, and peripheral nervous system, PNS. While the CNS consists of the brain and spinal cord, the PNS consists of the network of nerve tissue connecting the CNS to the rest of the body. One component of the

Figure 1.1
Divisions of the Nervous System



PNS is the autonomic nervous system, ANS, responsible for control and regulation of the major organs, operating largely subconsciously. The ANS is further subdivided into the sympathetic and parasympathetic divisions and it is here that activation and regulation of anxious arousal, such as the fight or flight response takes place. While the sympathetic nervous system encompasses adrenal gland activity, where the secretion of hormones triggers physiological changes in preparation for vigorous activity, the parasympathetic nervous system provides the opposite function, working to restore a state of calm once the threat is no longer present, but also providing a regulatory effect on sympathetic activity to prevent the heart rate from getting too high, for example. When fight or flight arousal is triggered by a perceived threat, the heart rate is increased, pupils become dilated and blood flow to the major muscles is increased in preparation for physical action. Other functions are suppressed, for example, blood flow to the digestive system is reduced. Once the threat has passed, the parasympathetic nervous system works to reverse the sympathetic response, for example, by slowing the heart rate, increasing salivation and reactivating digestion (Carlson and Birkett, 2017).

An evolutionary perspective on the fight or flight response is often argued, since the physiological changes resulting from heightened arousal can be seen to be useful in primitive survival, such as thinking and acting quickly in order to escape a predator or outwit a rival (Porges, 1995b). However, in the modern world, it can be argued that the physical benefits of the fight or flight response are rarely required for survival. Nevertheless, this emotional response to threat still exists, even though the threats we face today are often very different and more varied. For example, the fight or flight response in the modern world might be activated in situations relating to social or professional threat, such as public speaking. At a sub-clinical level, the sensations relating to threat are correctly identified and tolerated, with arousal levels returning to normal levels once the threat has passed. However, poor abilities to tolerate the sensations of fight or flight arousal, or misinterpretation of the physical sensations, are commonplace in anxiety, panic and phobia disorders (Hoehn-Saric et al., n.d.). Porges' Polyvagal Theory, PVT, provides a useful theoretical background to understanding anxious arousal and the fight or flight response (Porges, 1995b; Porges, 2007).

PVT accounts for the development of the autonomic nervous system from an evolutionary perspective, with early social interaction proposed to provide a facilitating framework in its development (Porges, 1995b; Porges, 2007). PVT describes the role of the autonomic nervous system in terms of three distinct functions: social engagement in a safe environment, fight or flight mobilisation in threatening situations and, finally, the shutting down of the nervous system as a second level of defence when a threat cannot be avoided, referred to as *freeze*. According to this theory, the ventral vagal, dorsal vagal, and sympathetic subdivisions of the ANS contribute to the subconscious collection of information from the environment, which is then communicated via interoceptive signalling, in order to bring about involuntary changes in state. PVT focuses particularly on the role of the vagus nerve in this communication, referring to the quality of functioning of the vagus nerve in this role as 'vagal tone.' Porges (1992) described the role of vagal function as analogous to that of a brake that remains activated in safe situations, inhibiting the reflexes of the sympathetic nervous system. Once a threat is detected, this break is released. This facilitates activation of the sympathetic nervous system through a series of subconscious reflexes resulting in the physiological arousal required to deal with the threat, such as increased heart and respiratory rates (Porges, 1992). This suggests that vagal tone is fundamental to one's regulatory abilities. More specifically, vagal tone is here related with interoception, endocrine and somatosensory information, the integration of which enables the interpretation of danger and the regulation of emotion (Porges et al., 1994). According to PVT, higher vagal tone would reflect better adaptability in the regulation of emotion.

In contrast with PVT, the biological behavioural model (Grossman and Taylor, 2007), describes the role of vagal tone as an adaptive characteristic which responds to behavioural changes. In this case, vagal tone is considered to act as an energy reserve, ready for when action is required. , but highlights difficulties in using respiratory sinus arrhythmia, RSA, as a direct index of cardiac vagal tone. In this model, the vagus is responsible for performing the role of energy exchange, whereby respiration is synchronized with cardiovascular activity during behavioural changes. Whereas PVT encourages the use of RSA, as an index of vagal tone, Grossman urges caution in the interpretation of vagal tone based on RSA. This is due to the confounding effect of activity and even mental tasks on the relationship between RSA and cardiac vagal tone. Grossman proposes a series of controls, such as controlling the breathing rate, to increase the degree to which RSA reflects parasympathetic activity. Despite the different approaches to vagal tone in these two models, Porges and Grossman agree that higher resting cardiac vagal tone is considered preferable for emotion regulation. This suggests that, if better vagal tone relates to better response to threat and emotion regulation, finding ways to improve vagal tone would appear important. Indeed, studies have related breathing exercises, including those used for decades, such as in Yoga, to improvements in vagal tone in adults (Goldstein et al., 2016; Hepburn et al., 2005; Magnon et al., 2021). When vagal tone is used in studies of infants, the controls suggested by Grossman, such as instructions to control breathing, cannot be followed. Instead, researchers must be mindful of the factors influencing RSA, such as activity, in experimental design. Nevertheless, developmental studies of vagal tone early in life have revealed several associations between infant vagal tone and characteristics in both the infant and their caregiver (Rattaz et al., 2022) and these are discussed in 1.3.1 below.

Anxious arousal and the fight or flight response provide examples of a clear function for emotion, related to a need for survival. Another theory describes a further practical purpose for emotional response; Damasio's *Somatic Marker Hypothesis* explains how emotion guides our decision making, describing what is commonly referred to as 'gut-feeling' (Damasio et al., 1991). The somatic marker hypothesis posits that somatic markers, or signals arising from within the body contribute to an emotional indicator that guides choice and decision. Damasio's research was initially based on historical studies of patients with lesions to the orbitofrontal cortex. Despite intact intellect, Damasio observed that these patients often made decisions that were disadvantageous to themselves, a change to the behaviour they exhibited before their illness or injury (Bechara et al., 2005). This observation led to the suggestion that additional factors, in addition to knowledge, contributed to decision making, and that emotion likely played a part. Development of this idea led to the proposal that physiological changes in the body were associated with memories of previous experiences and that, in decision-making situations, the relevant experiences are accessed and the associated sensations once again arise, guiding our decision. The experiencing of associated physical sensations, or markers, without the conscious recalling of the memory, led to use of the term 'gut feel'. Research exploring the somatic marker hypothesis has described practical implications of this proposition for decision making and risk-taking, along with effects as far reaching as business and the economy (Bechara et al., 2005; Critchley, 2005; Dunn et al., 2006). However, Damasio recognised that the influence of emotion on decision-making could be both beneficial and detrimental, depending on the level of uncertainty of the situation and whether the emotion was relevant to the task in question (Bechara et al., 2005). This relationship between bodily sensations and decision-making tasks is supported by empirical evidence confirming activity in brain regions associated with heightened emotional arousal in participants taking part in decision-making tasks (Critchley, 2005). This suggests a much wider role for the emotional interpretation of bodily sensations, beyond that of survival.

Research evidence of associations between dimensions of interoception and anxiety

The theories presented so far describe the important function of physiological arousal for emotion and its regulation, and the role of interoceptive information in contributing to these processes. One could therefore expect interoception, emotional regulation, and mental health difficulties to all be related to each other. Empirical studies appear to support these associations. Here I will discuss evidence of the relationships between 1) interoception and emotion regulation, 2) emotion regulation and anxiety and 3) the direct relationship between dimensions of interoception and anxiety.

Firstly, studies of the relationship between interoception and emotion regulation have highlighted a link between the two (L. F. Barrett, 2006; Critchley and Garfinkel, 2017; Füstös et al., 2013Pinna and Edwards, 2020; Porges, n.d.; Schuette et al., 2021). For example, higher interoceptive accuracy has been associated with better emotion regulation (Critchley and Garfinkel, 2017; Füstös et al., 2013). Additionally, a recent systematic review suggested that higher interoceptive accuracy and interoceptive awareness both predict more efficient emotion regulation

(Pinna and Edwards, 2020). This could be because those better at noticing their bodily sensations have also been found to be more efficient at using adaptive, rather than maladaptive, strategies to regulate their emotions (Schuette et al., 2021), suggesting that interoception not only relates to the somatic experience, but also the cognitive response to somatic sensations. Nevertheless, findings have also demonstrated opposite associations, i.e. that interoceptive accuracy negatively correlates with emotion regulation (L. F. Barrett, 2006; Critchley and Garfinkel, 2017). This could suggest that the relationship between interoception and emotion regulation is potentially more complex than suggested by correlation studies, likely involving a combination of factors. In addition to correlation studies, neuroscientific evidence also relates emotion with interoceptive processing. For example, heartbeat-evoked potential amplitudes correlate with self-reported measures of empathy, independently of cardiac activity (Fukushima et al., 2011). In addition, increases in HEP amplitude in response to increased induced emotional arousal appear to be modulated by alpha oscillatory power (Luft and Bhattacharya, 2015). Heartbeat-evoked responses also appear greater in response to negative versus positive emotions (Kim et al., 2019). Together these studies provide neuroscientific evidence of interoceptive processing during emotional arousal. However, the direction of the relationship between emotion processing and dimensions of interoception remains unclear, since correlational studies have related interoceptive accuracy with emotion regulation both positively (Critchley and Garfinkel, 2017; Füstös et al., 2013; Pinna and Edwards, 2020;Schuette et al., 2021) and negatively (L. F. Barrett, 2006; Critchley and Garfinkel, 2017). This raises questions regarding whether different aspects of emotion regulation relate to increased or decreased interoceptive accuracy and whether other variables are influencing this relationship. At its extreme, the inability to identify emotional feelings, alexithymia, has also been associated with impaired interoceptive ability (Brewer et al., 2016; Murphy, Catmur, and Bird, 2017; Murphy et al., 2018). Alexithymia is a characteristic of autism spectrum disorder and, while studies of ASD are beyond the scope of this thesis, it is important to note that studies of alexithymia and ASD have contributed to the study of interoception and emotion (e.g. Palser, Palmer, et al., 2018).

Secondly, studies have related emotion regulation difficulties directly with mental health and, more specifically anxiety. For example, with those who struggle with identifying, acknowledging and tolerating their emotions having been found to be at greater risk of anxiety and depression (Conradt et al., 2020; Gross and Muñoz, 1995). At sub-clinical levels, it can be seen that anxiety is an appropriate, temporary state in response to a real threat. For most, once the threat has passed, parasympathetic activity returns the body to a state of calm. However, in cases of clinical anxiety and anxiety disorder, this regulatory process is not straightforward. In some cases, poor regulatory abilities can lead to a chronic state of stress, such as in post-traumatic stress disorder, PTSD (McLean and Foa, 2017), or relate to frequently repeated stress responses in inappropriate situations, such as in panic disorder, generalised anxiety disorder, and phobias (Hoehn-Saric et al., n.d.). As well as reduced emotion regulation capabilities, anxiety disorders are also characterised by increased attentional focus toward the threatening stimulus combined with overestimation of threat (Mogg and Bradley, 1998), which is usually accompanied by behaviours aimed at avoiding the perceived threat, thus perpetuating the fears triggering the anxiety (Aupperle and Paulus, 2010). Together, this demonstrates that clinical anxiety involves a combination of somatic, cognitive, emotional and behavioural aspects. As mentioned previously, studies of alexithymia and ASD have contributed to our understanding of interoception and its relationship with mental health and, specifically, anxiety.

Finally, as discussed, interoception contributes to somatic, cognitive and emotional experience, relating interoception directly with mental health. Previously, altered interoception has been modelled, in broad terms, in both anxiety and depression (Paulus and Stein, 2010). More specifically, a growing body of literature relates dimensions of interoception directly with several specific mental health difficulties (see Khalsa et al., 2018 and Nord and Garfinkel, 2022 for an overview). In clinical practise, patient-reported symptoms of anxiety vary greatly across somatic, cognitive, and emotional dimensions of anxiety, leading to highly heterogeneous experiences of anxiety and anxiety disorder (Rose and Devine, 2014). Some of this variation could be due to variations in ability in different dimensions of interoception. Several studies have associated different dimensions of interoception with anxiety, as follows:

Interoceptive accuracy

Many studies have examined the relationship between interoceptive accuracy in heartbeat detection tasks and anxiety (see Domschke et al., 2010 for a review). Several associations have been published. For example, panic disorder patients demonstrate higher interoceptive accuracy than controls (Ehlers et al., 1995; Zoellner and Craske, 1999). Interoceptive accuracy has been found to positively relate to trait anxiety (Pollatos et al., 2007; Pollatos et al., 2009) and anxious arousal (Dunn et al., 2010), but also to mediate the relationship between trait anxiety and unpleasant feelings, with more anxious participants with higher interoceptive accuracy reporting higher sensations of unpleasantness (Pollatos et al., 2007). This suggests that the relationship between how we experience anxiety, in this case unpleasant feelings, and interoceptive accuracy is not straightforward. Despite such studies reporting a positive relationship between interoceptive accuracy and anxiety, findings are mixed. A systematic review and meta-analysis found no such association between interoceptive accuracy and anxiety (Adams et al., 2022), while other studies have suggested a negative relationship between interoceptive accuracy and anxiety symptoms, such as in social anxiety (Werner et al., 2009; Werner et al., 2013). These mixed findings could indicate a disorder-specific nature to the relationship between interoceptive accuracy and anxiety, requiring replication within studies of specific disorders to confirm. Interoceptive accuracy has been related to cognitive function when processing emotionally salient words in an emotional Stroop task, with higher accuracy relating to higher attention interference and poorer performance on the task, even though in this case there was no association between cardiac interoceptive accuracy and trait anxiety (Werner et al., 2014). This highlights the potential subconscious nature of the relationship between interoception and anxiety, since self-reported trait anxiety did not relate to interoceptive accuracy, even though performance on the emotional task was impaired in participants with higher accuracy. In health anxiety, patients demonstrated no association between cardiac interoceptive accuracy and self-reported health anxiety symptoms, but higher anxiety was related to an over-estimation of skin conductance fluctuations, in an alternative approach to measuring interoceptive accuracy (Krautwurst et al., 2014). This study provides a reminder of the gap in the research examining the relationship between anxiety disorders and different channels, as well as dimensions, of interoception. As models of interoception have evolved to classify interoception according to an increasing number of dimensions, studies have begun to consider the relationships between these dimensions. For example, one study comparing self-reported interoceptive sensibility with interoceptive accuracy on a heartbeat detection task and emotional susceptibility supported the idea that interoceptive accuracy and awareness are independent constructs, but also revealed a complex relationship between aspects of interoceptive sensibility, such as not worrying, and emotional susceptibility (Calì et al., 2015). In a study examining a behavioural component of anxiety and depression, brooding, with interoceptive accuracy, those demonstrating high brooding combined with low accuracy were more likely to report higher anxiety symptoms, while those demonstrating low broodiness but higher interoceptive accuracy reported lower anxiety symptoms (Lackner and Fresco, 2016). This reinforces the importance of examining interoception in relation to cognitive and behavioural measures, rather than placing emphasis purely on interoceptive accuracy.

Interoceptive attention

Interoceptive attention refers to the extent to which we attend to interoceptive sensations (Gabriele et al., 2022; Nord and Garfinkel, 2022). Enhanced focus on internal sensations characterises several anxiety difficulties, such as social anxiety (Mansell et al., 2003) and panic disorder (Ehlers et al., 1995). Interoceptive attention is distinct from interoceptive accuracy (Gabriele et al., 2022), although several studies have associated enhanced attention on bodily sensations with increased interoceptive accuracy (Critchley, 2005; Critchley, 2002; Garfinkel and Critchley, 2016; Mulcahy et al., 2019). However, a recent study relating interoceptive attention and health anxiety highlighted an important distinction in the kind of attention paid to bodily sensations (Trevisan et al., 2023). Trevisan et al. (2023) categorised attention as either *adaptive* or *maladaptive*. Adaptive attention related to a positive act of tuning in to the needs of one's body to support homeostatic regulation and deliberately foster good physical and mental health. Conversely, maladaptive attention related to a hyper-vigilant tendency to fixate on certain sensations, relating to heightened health anxiety symptoms. This distinction would appear important when interpreting interoceptive attention as a characteristic of anxiety.

Interoceptive sensibility

Interoceptive sensibility, one's confidence in one's interoceptive accuracy (Garfinkel et al., 2015), has also been related to anxiety and anxiety disorder. For example, Cali et al. (2015) found an association between interoceptive sensibility, but not interoceptive accuracy, and emotion susceptibility. This finding has been replicated in a similar study of interoceptive accuracy and sensibility, in which, specifically, one's trust in bodily signals appeared to drive the relationship between interoceptive sensibility and trait anxiety (Slotta et al., 2021).

Interoceptive attribution

Interoceptive attribution refers to a process of associating internal sensation with a cause and misattribution of such sensations occurs commonly in some mental health disorders (Nord and Garfinkel, 2022). One example is catastrophic misinterpretation, a feature of panic disorder, relating to a combination of cognitive and interoceptive processes leading to the misattribution of bodily sensations, e.g. noticing a change to heartbeat and attributing the change to an impending heart attack, which themselves become a source of anxiety (De Cort et al., 2013; Ohst and Tuschen-Caffier, 2018). Poor interoceptive attribution can occur independently of ability on other dimensions of interoception. While individuals with anxiety and panic disorders tend to report greater interoceptive awareness and higher interoceptive sensitivity (for a review see (Domschke et al., 2010), these abilities do not necessarily translate into more accurate attribution of internal states. Palser et al. (2018) propose that difficulty attributing sensations to emotions, alexithymia, when combined with heightened interoceptive sensibility, results in susceptibility to anxiety. This is based on self-reported alexithymia, trait anxiety and body perception. Together, these findings highlight the important role of individual attitudes and beliefs in the attribution of interoceptive sensations when considering the relationship between such sensations and anxiety tendencies.

Interoceptive insight

Interoceptive insight refers to the meta-cognitive aspect of interoception, i.e. the relationship between one's interoceptive accuracy and one's confidence in interoceptive ability (Nord and Garfinkel, 2022) and has previously been referred to as interoceptive awareness (Garfinkel et al., 2015). Studies of interoceptive insight in relation to anxiety are sparse, with this dimension of interoception relatively under-researched as yet (Suksasilp and Garfinkel, 2022). Methodological work to facilitate the study of the meta-cognitive aspects of interoception (Rominger and Schwerdtfeger, 2023; Rominger and Schwerdtfeger, 2024) will hopefully encourage further exploration of the relationship between interoceptive insight and anxiety. This would appear important, given the findings relating interoceptive attribution and interoceptive sensibility directly with anxiety, described above. Those dimensions suggest the importance of confidence in correctly attributing sensations, being able to trust in one's bodily sensations, when considering susceptibility to anxiety, so the meta-cognitive aspect which incorporates an understanding of how accurately we interpret our own bodily sensations appears to have the potential to alter the likelihood of anxiety susceptibility. Indeed, Garfinkel et al. (2016) suggested a negative relationship between interoceptive awareness and anxiety, meaning that low awareness of one's own ability relates to higher likelihood of anxiety. This could mean that someone with a high degree of confidence in their ability to detect and interpret their bodily sensations, despite poor accuracy, could be more susceptible to anxiety. Similarly, someone with a high degree of accuracy, but low confidence in their ability, could also be susceptible, perhaps due to mistrust in their ability or mis-attribution of their sensations.

The studies discussed in this section provide considerable evidence of the relationships between interoception, emotion regulation and anxiety. However, they also highlight the complexity of these relationships, since they demonstrate variation in direction of associations within as well as between dimensions of interoception and specific disorders, as well as demonstrating some interactions between different dimensions of interoception. The overall picture is, therefore, complex and remains incomplete. As can be seen above, interoceptive accuracy has been examined in numerous studies, whereas interoceptive insight is relatively unresearched. This inconsistency across dimensions of interoception was recently highlighted, along with the need for an up-to-date systematic review of all dimensions of interoception in relation to mental health (Jenkinson et al., 2024). The body of research relating interoception with anxiety, specifically, is characterized by inconsistent findings which raise further questions regarding heterogeneity in psychopathological presentations. Further, the relationships that are highlighted are predominantly correlational in nature. Therefore, questions regarding to what extent interoception influences the likelihood of anxiety disorder, or, conversely, the experience of anxiety disorder could alter one's interoceptive ability remain largely unanswered. Perhaps greater knowledge of the developmental trajectory of interoceptive processing could help to inform this understanding. It is yet to emerge whether interoception itself can be considered a trans-diagnostic component for all psychopathology, in other words, whether there are universal optimum levels of the different dimensions of interoception, deviation from which could be an indicator of risk for mental health difficulties. Indeed, it has recently been argued that disrupted interoceptive processing underpins psychopathology across disorders, thus suggesting interoception offers a trans-diagnostic criterion for anxiety risk (Saltafossi et al., 2025). More positively, the implication that interoception contributes to mental health difficulties also suggests it could be a useful target for therapeutic intervention. Clinical applications of interoception are discussed next, in 1.2.4.

1.2.4 Clinical applications of interoception in mental health

So far, it has been demonstrated that interoception is fundamental in the experience of emotion and, hence, in the experience of anxiety, since it both underpins our perception of physical state and influences our ability to perceive and regulate our emotions (Critchley and Garfinkel, 2017; Porges, 2007). Further, converging evidence comes from studies showing that heightened sensitivity to interoceptive signals is associated with anxiety and anxiety disorder (Domschke et al., 2010; Hoehn-Saric and McLeod, 2000; Porges, 1995a), although this is not consistently related to interoceptive accuracy as measured in commonly used heartbeat detection and tracking tasks (Adams et al., 2022). From a clinical perspective, understanding individual differences in the presentation of anxiety and corresponding interoceptive abilities is crucial. While terms like 'accuracy', 'sensitivity', and 'awareness' often imply that higher interoceptive abilities lead to positive outcomes, it is not clear whether being more sensitive to or accurate in interpreting interoceptive signals is always beneficial. For example, an individual suffering from health anxiety may display a preoccupation with bodily sensation, i.e. high interoceptive attention, combined with a frequent cognitive misinterpretation of those signals, despite high accuracy in sensation and perception (Hoehn-Saric and McLeod, 2000). Similarly, a panic disorder patient may demonstrate a finely tuned ability to notice internal sensations, combined with 'catastrophic misinterpretation' of these bodily signals, triggering a panic attack (Ohst and Tuschen-Caffier, 2018). While interoception is clearly related to anxiety, it is important to consider interoceptive abilities alongside cognitive interpretation of those interoceptive signals reaching our conscious awareness. The development of therapeutic tools based on interoception depends on whether interceptive abilities can be manipulated in the first place. Previous literature suggests interoceptive accuracy is stable across the lifespan once established (Critchley and Harrison, 2013), while interoceptive awareness is thought to decline with age (Khalsa, Rudrauf, and Tranel, 2009). However, this evidence raises questions relating to whether, to what extent and, importantly, when interoceptive abilities can be altered and whether any effects of such interventions are enduring. If the relevant dimension of interoception can be manipulated in each case, this opens up the possibility of the use of interoception in the development of novel mental health interventions.

Existing evidence-based clinical interventions for anxiety difficulties are typically talking based, using cognitive behavioural therapy (CBT), or pharmacology-based, through prescription of anti-depressants such as selective serotonin reuptake inhibitors, SSRIs (see Carl et al., 2020 for a meta-analysis of randomised controlled trials (RCTs)). These treatments are long-established, offering the best therapeutic outcomes from the options currently available. This is reflected by their promotion in clinical guidelines, such as those provided by the National Institute for Health and Care Excellence (NICE) in the UK (e.g. National Institute for Health and Care Excellence, 2011). CBT is focused on establishing long-term changes to cognition and behaviour to elicit improvements in mood, based on a highly personalised treatment plan. However, the time-consuming and, at times, distressing nature of talking therapies, often leads to high drop-out rates (McMain et al., 2015). Additionally, the skill of the therapist in accessing underlying cognitions and relating these to the behaviours of the patient is fundamental in establishing a highly targeted treatment plan. Therapeutic outcomes of CBT are, therefore, variable. Pharmacological treatments are widely available and have been found to be as effective as CBT in the short term, but side-effects of long-term use of anti-depressant medicines can be off-putting, while high rates of relapse result from short-term use (e.g. Walkup et al., 2008; Roshanaei-Moghaddam et al., 2011). In addition, evidence comparing long-term efficacy of these treatments is sparse (Carl et al., 2020). These drawbacks to current treatments encourage ongoing research and development to improve treatment options and interoception could play a role in new therapeutic approaches. In fact, interoception is already a familiar concept in the clinical environment. Interoceptive exposure exercises are an established component of CBT, featuring in the treatment of a variety of anxiety and panic disorders (K. Lee et al., 2006). These exercises are designed to elicit internal sensations consistent with anxiety symptoms, such as increased heart and respiration rates, light-headedness, nausea, etc. The patient then practises focusing on these sensations to facilitate habituation, improved tolerance and greater confidence. Such exercises have been in use since the early 1990s (e.g. Schmidt and Trakowski, 2004).

More recently, clinical developments based on interoception have focused on training and improving interoception skills, rather than simply habituation to the internal sensations as is used in existing CBT. However, early findings relating to interoceptive training are inconsistent. For example, in one trial focused on interoceptive training, participants undergoing an eight-week body scanning programme demonstrated increased interoceptive accuracy, but no change to interoceptive sensibility (Fischer et al., 2017). Conversely, a short mindfulness intervention resulted in increased interoceptive sensibility, but no change to interoceptive accuracy (de Lima-Araujo et al., 2022). Importantly, neither of these studies examined the longer-term effects of the intervention following participation in the study, so whether there is an enduring effect from the interventions remains unknown. Consistent with de Lima et al (2022), a study of meditators versus non-meditators found no difference in interoceptive accuracy between the two groups, although higher interoceptive sensibility was reported in the group of meditators who displayed greater confidence and found the task easier than the non-meditators (Khalsa et al., 2008). Meyerholz et al. (2019) reported a significant improvement in interoceptive accuracy following bio-feedback. In a comparison between participants receiving bio-feedback, undertaking breathing exercises and a control group, interoceptive accuracy significantly improved in those receiving bio-feedback (Meyerholz et al., 2019). In a direct replication, however, Rominger et al. (2021) observed no significant effect for bio-feedback relative to breathing exercises, despite increases in interoceptive accuracy in both interventions (Rominger et al., 2021). To what extent alterations to interoceptive accuracy were enduring, rather than temporary, is unknown. Similarly, Schillings et al. (2022) reported no significant change to interoceptive accuracy or interoceptive sensibility, relative to a control group, following a three week heartbeat detection training programme (Schillings et al., 2022).

While these studies have focused on testing the malleability of interoceptive abilities, some very recent trials have gone further, by measuring the outcome of interoceptive training in terms of direct symptom reduction (Fischer et al., 2016; Payne et al., 2015; Quadt et al., 2021; Suksasilp et al., 2024). For example, Aligning Dimensions of Interoceptive Experience (ADIE) is a therapeutic intervention which has recently undergone clinical trial. By helping autistic individuals understand bodily sensations through practise using computer-based exercises, it was found that anxiety levels could be reduced (Quadt et al., 2021). Following on from these encouraging results, Suksasilp et al. (2024) have reported increased cardiac interoceptive accuracy and reduced anxiety as a result of interoceptive training (Suksasilp et al., 2024). Promising trials based on training of interoceptive abilities have also been carried out in the treatment of anorexia nervosa (Fischer et al., 2016) and trauma (Payne et al., 2015), with both showing significant decreases in symptoms. While these studies suggest some potential for improvement of interoceptive abilities and symptom reduction through interoceptive training, it is unclear to what extent the apparent symptom reduction is attributable to the intervention, as opposed to the exposure to bodily sensations in the first place, as per the classic interoceptive exposure described above, since taking part in heartbeat detection tasks requires the participant to attend to their sensations, by definition. Indeed, the positive findings of Khalsa et al. (2008) and de Lima (2022) discussed above both relate to increased focus on bodily sensation through mindful meditation, consistent with exposure-based approaches. To test this, results from interoceptive training interventions would need to be compared with results from classical interoceptive exposure exercises. Together these studies may point to the importance of increasing interoceptive sensibility, rather than focusing on interoceptive accuracy. This is consistent with the results of a meta-analysis of studies of interoceptive accuracy and anxiety, which found no significant relationship between anxiety and performance on explicit measures of cardiac interoceptive accuracy (Adams et al., 2022).

The studies discussed here so far relate specifically to explicit measures of cardiac interoception. However, a different approach to altering interoception was proposed by both Paciorek et al. (2020) and Villani et al. (2019), who suggested vagal nerve stimulation as a direct method for manipulating interoceptive accuracy. Paciorek et al. (2020) discuss the theoretical potential of vagal nerve stimulation to enhance interoceptive signal strength (Paciorek and Skora, 2020). Separately, Vilanni et al. (2019) provide empirical evidence to support this approach, by reporting observation of increased interoceptive accuracy (Villani et al., 2019). However, the effect of increased accuracy was only observed during active vagal nerve stimulation and related to heartbeat detection, but not heartbeat counting, performance, raising questions relating to long-term efficacy. Nonetheless, the ability to manipulate interoceptive accuracy, even temporarily, supports the pursuit of further clinical interventions based on interoception. Importantly, however, as pointed out by Schoeller et al. (2024), much work is necessary to provide standardized, validate measures of interoception across domains before direct manipulation of interoceptive processing can be applied safely within clinical settings (Schoeller et al., 2024).

While the literature presented thus far demonstrates a long-established acknowledgement of a relationship between interoception and anxiety in both research and clinical settings, this work refers to research and clinical trials carried out with adults. Little is known about the development of interoception early in life, let alone its significance for mental health through childhood and beyond. Although empirical research on interoception in infants remains limited, several studies in recent years have begun to address this gap. In addition, theoretical accounts on the early development of interoception have also begun to emerge. To better understand whether, and how, early development of interoception influences future mental health risk, we must explore the world of the growing infant. Section 1.2 considers the current state of research on the development of interoception, the factors influencing its development, and the potential for interoceptive development to influence a child's susceptibility to anxiety.

1.3 The infant world: developmental perspectives on interoception

The previous sections have provided an overview of the relationship between interoception, emotion, and anxiety. However, both the developmental trajectory of interoceptive processing and its connection to mental health remain largely unexplored. Research specifically examining interoception in infants is particularly scarce. To date, only a handful of studies have examined infant samples, a gap that has been previously recognised in the literature (Murphy, Brewer, Catmur, and Bird, 2017b). This is surprising when considering the long-term nature and increasing lifetime prevalence of mood disorders (Newlove-Delgado, 2023). Given the known associations between dimensions of interoception and psychopathologies (Khalsa, Rudrauf, and Tranel, 2009) and, more specifically, the role of individual differences in interoception as a potential contributor to the development of anxiety (Murphy, Brewer, Catmur, and Bird, 2017b), research examining early development of interoceptive processing is deemed essential (e.g. Khalsa and Lapidus, 2016). Not only does the development of interoception early in life remain relatively under-researched, no research to date has investigated whether individual differences in interoceptive sensitivity during infancy predicts the later emergence of mental health conditions. Similarly, it is unclear whether difficulties in learning to interpret changes in interoceptive states during infancy might serve as early precursors to anxiety tendencies. Understanding and recognising precursors of anxiety tendencies is important for identifying risk of significant anxiety later in development, since by the time anxiety and anxiety disorders present in a visible way during childhood and adolescence, they could actually have been developing unseen from much earlier on in life. Indeed, this is a common clinical view of many manifestations of childhood anxiety disorders (e.g. Blakey et al., 2017; Costello et al., 2003; Murphy, Brewer, Catmur, and Bird, 2017b). In the next section, I will review research and theory on interoceptive processing development. Following this, I will explore the special role of touch, since this is an essential feature of an infant's early life that could offer clues to the development of interoceptive processing. Finally, I will consider the crucial role of the primary caregiver during an infant's early life. Drawing on key theories, I will explore specific caregiver-related factors that may influence the development of interoceptive processing and the potential risk of anxiety in the infant.

1.3.1 The development of interoceptive processing in infancy

As discussed in Section 1.1, our ability to interpret and respond to internal physiological sensations is essential for self-regulation, and it plays a key role in how we experience and regulate emotions (Khalsa et al., 2018). The development of interoceptive processing is, therefore, of fundamental importance. Understanding this developmental process could provide valuable insights into the role of interoception in fostering appropriate emotional and regulatory abilities essential for both physical and emotional health. Further, since impaired interoceptive abilities are linked with the onset of psychopathology later in life, a clear understanding of the developmental trajectory of interoceptive processing could represent the key to understanding the development of disorders characterised by poor self-regulation, such as anxiety and depression, or even offer a potential biomarker of risk (Murphy, Brewer, Catmur, and Bird, 2017b).

Several emerging theories of the development of interoceptive processing suggest the infant's early environment, specifically the social interactions they experience in the early months of life, play a facilitatory role (Atzil et al., 2018; Filippetti, 2021; Fotopoulou and Tsakiris, 2017b). Twin studies highlight the importance of early environmental influence on interoceptive abilities in later childhood, since monozygotic twins have been observed to differ in their interoceptive abilities by eight years old (Eley et al., 2007), but there is a gap in the research earlier in life, with very little empirical evidence to support these theoretical accounts. Only a few studies directly examining infants' sensitivity to their interoceptive signals have been published to date. Here, I will discuss both the theoretical approaches to the development of interoceptive processing, as well as the empirical evidence that has been published to date.

Theoretical accounts of interoceptive processing development

One influential theory emphasised the significance of caregiver-infant interactions. Fotopoulou and Taskiris (2017) proposed that a primary purpose of caregiver-infant dyadic interaction is maintenance of the infant's homeostasis and that the iterative process of matching internal experience, such as visceral sensations, with external information, such as appropriate caregiving care, lead to simultaneous development of the infant's interoceptive processing along with their understanding of themselves relative to others in close proximity, such as their caregivers, i.e. the development of a minimal sense of self (Fotopoulou and Tsakiris, 2017b). This process relies on the appropriate responses of the caregiver to the infant's cues, with the caregiver's ability to infer the infant's need in turn influenced by the caregivers' own interoceptive processing. The caregiver's behaviour in turn reinforces the perception of interoceptive information in the infant. This developmental mechanism proposed by the authors is based on three primary observations. Firstly, that the integration of sensory and motor signals provides a foundation for a sense of self, referred to as *embodied mentalization*. Secondly, that interactions with others are based on similar principles and hence, mentalization of one's body can include signals from the bodies of others in close proximity, such as a caregiver. Finally, in infancy, the dependence on the primary caregiver for homeostatic maintenance provides considerable proximal interactions, facilitating the development of interoceptive processing in the infant.

Another prominent theory that highlighted the social dependence of human infants in the development of interoceptive processing was put forward by Atzil et al. (2018). The authors proposed that infants associate interoceptive information with exteroceptive information from their caregivers, resulting in conditioned associative learning that prompts the infant brain to regulate their internal milieu in the development of allostatic regulation by responding to social information (Atzil et al., 2018). According to this theory, it is these early social interactions that provide the necessary connectivity for the infant brain to begin to make sense of themselves and the world around them.

Building on these propositions, theoretical accounts have been advanced in recent years to further contextualise the development of interoceptive processing. For example, Filippetti (2021) focused on the intimate environment of feeding interactions to explain how both infant and caregiver factors play a role in the interplay of infant cues and caregiver responses, determining the distinction and blurring of the infant's interoception (Filippetti, 2021). Montirosso and McGlone (2020) propose that close proximity and nurturing touch in the caregiver-infant dyad lead to interoceptive stability and a sense of bodily-self in the infant. The authors account for this through the regaining of physiological synchrony after frequent misattunement in the dyad, referring to this process as *embodied reparation*. The important role of touch is discussed in detail in 1.3.2 and synchrony in the caregiver-infant dyad is discussed in 1.3.3, below.

Empirical evidence of interoceptive processing in infants

While the theoretical accounts discussed above provide a useful framework for the study of early interoceptive processing, empirical evidence to support them remains sparse. This is predominantly due to the fact that infant research in the field of interoception is subject to several methodological issues. Most measures of the dimensions of interoception already discussed in relation to research with adults rely on explicit responses to stimuli, such as reporting on one's own sensation of cardiac activity. Clearly, in infant research, we must rely on implicit measures of interoception, since the infant is unable to give a verbal response, demonstrate understanding of verbal instructions or carry out behavioural tasks prior to appropriate motor and cognitive development. Despite these difficulties, several studies examining evidence of interoceptive processing in infants have begun to appear in recent years, albeit with mixed results (Imafuku et al., 2023; Maister et al., 2017; Tünte et al., 2024; Weijs et al., 2023). Maister and colleagues (2017) published the first evidence of early sensitivity to interoceptive signals in 5-month-old infants (Maister et al., 2017). In this study, infants displayed significant looking-time differences when observing images pulsing either synchronously or asynchronously with their own heartbeat, referred to as the *iBeats* task, with infants preferring to watch the images presented asynchronously. In turn, amplitude of infants' HEP correlated positively with the strength of their looking preference and increased more when looking at negative emotions than positive, suggesting closer subconscious monitoring of infants' cardiac activity when observing negative emotions (Maister et al., 2017). Maister and colleagues' findings were replicated by Imafuku et al. (2023), who reported a preference for cardiac-asynchronous images in infants of 6-months of age (Imafuku et al., 2023). Weijs et al. (2023) also examined infant HEP, along with preferential looking towards heartbeat-synchronous versus asynchronous images in 5- to 7-month-old infants (Weijs et al., 2023). This study incorporated variation of asynchronous speed in the task design, to eliminate the possibility of a preference for speed. However, the researchers did not replicate a looking preference for either synchronous or asynchronous images, nor were infant HEP amplitudes related to emotional context. A similar method to examine interoceptive sensitivity in infancy was used in a study of both cardiac and respiratory interoception in 3-, 9- and 18-month-olds (Tünte et al., 2024). However, this study indicated that at 3 and 9 months, infants demonstrated preferential looking for images presented synchronously with their heartbeat, rather than asynchronously, as reported by Maister et al. (2017). In a similarly structured respiratory task, *the iBreath*, 9-month-old infants displayed a looking time preference for images presented synchronously, but no significant preference was observed at 3-months. No preferences were observed at 18-months in either the cardiac or respiratory tasks. The authors did not observe a strong relationship between cardiac and respiratory interoception at 3 or 9 months, but did observe a correlation at 18 months. Methodological variation could explain the mixed results between these studies, and also highlights the importance for future research to focus on standardising methodologies to improve comparability and replicability.

Importantly, while these studies examine HEP as an implicit measure of interoceptive processing with looking preference offering a potential behavioural measure of the perception of interoceptive signals, several other physiological measures may offer insights into the processing of interoceptive information by examining evidence of emotion processing in infants. As discussed in Section 1.2.3, the nervous system plays an important role in the implicit processing and regulation of emotion for adults. The development of the nervous system begins in the first weeks of embryonic development and by the third trimester of pregnancy, the developing fetus is believed to demonstrate signs of pain (Bellieni, 2019; Derbyshire and Bockmann, 2020) and reflex responses to touch along with growing touch sensitivity (Marx and Nagy, 2015; Reissland et al., 2014). Just as for adults, the activity of the sympathetic and parasympathetic branches of the nervous system can be observed in infants by examination of both cardiac data (heart rate and heart rate variability, HRV) and electrodermal activity, EDA, providing evidence of arousal and regulation (e.g. Ham and Tronick, 2008; Huffman et al., 1998; Porter et al., 2022; Wass, 2021). A measure of the beat-to-beat variation in heart rate can be used to represent vagal tone, and infant vagal tone has been used as a measure of infant physiology in many studies (see Rattaz et al., 2022 for a systematic review of 45 studies). For example, infant vagal tone has been associated with happiness and soothability (Huffman et al., 1998) and co-regulation in the caregiver-infant dyad (Porter et al., 2022). Studies have found associations between caregiver mental health and infant vagal tone (e.g. Somers et al., 2021). In addition, in their systematic review, Rattaz et al. related quality of interaction in the caregiver-infant dyad with infant's physiological measures (Rattaz et al., 2022). Caregiver influences on infant vagal tone are discussed in more detail in Section 1.3.3.

In addition to HRV and vagal tone, EDA, is also believed to provide evidence of implicit interoceptive processing via activation of the sympathetic nervous system. In 5-month-old infants, a clap-startle paradigm has been seen to elicit a measurable EDA response (Ham and Tronick, 2008). Additionally, EDA responses to angry faces have been observed to be greater than to happy faces (Nava et al., 2016). In the same study, infants also displayed an EDA response when faces were displayed subliminally, highlighting the subconscious element of emotion processing. While these studies did not directly assess interoceptive signals, they do add indirectly tap into the development of emotional and physiological processing, which are linked to interoception. In addition, and as also evidence by their use in infant research, the rapid, non-invasive and straightforward nature of the physiological measures discussed here render them suitable for use with infants (e.g. Ham and Tronick, 2008; Huffman et al., 1998; Nava et al., 2016;Porter et al., 2022; Rattaz et al., 2022; Wass et al., 2018). Methodological considerations in the collection of vagal tone and EDA data are discussed at length in Chapter 2.

Emotion processing and emotion regulation

When processing positive and negative emotional events, the infant must correctly detect their emotional states and also learn to sense and appropriately respond to changes in their physiological states. This will allow them to perform behaviours to maintain homeostatic balance, for example, by seeking physical contact with the caregiver or by turning their attention away from an aversive stimulus. Altered sensitivity to internal signals has been related to either heightened or dampened estimation of the intensity of physiological change, potentially leading to inappropriate responses to these signals (Khalsa et al., 2018; Khalsa and Lapidus, 2016; Quadt et al., 2018). In addition, the homeostatic mechanisms involved in emotion regulation are complex, in that positive and negative emotions appear to be processed differently (Camacho et al., 2019; Wass et al., 2018). When the ability to self-regulate to a state of homeostasis is compromised, it has been observed to lead to exacerbation of undesired emotions (Pine et al., 2005; Ray et al., 2008; Salkovskis, 1991), leading to a self-sustaining effect over time (Gross and Thompson, 2007). This state is referred to as metastasis (Wass et al., 2018) in work highlighting the longer lasting effects of increased arousal associated with negative emotions, relative to decreased arousal. The relationship between the processing of negative emotions and the manifestation of anxiety is long-established, but early responses to different emotions and understanding the differences in how they are processed is important in understanding how poor emotion regulation and anxiety behaviours begin to develop.

The distinction between processing of positive and negative emotions appears to differ between children and adults. As previously discussed, a hierarchical view of interactions between brainstem, limbic and cortical systems has been used in the study of adult emotional regulation (L. F. Barrett, 2017). Infant emotion research can provide further insight into this hierarchical relationship, since brainstem and limbic systems develop before frontal cortical systems (Carlson and Birkett, 2017). While the early environment appears crucial for directing the trajectory of healthy interoceptive processing and emotion development, emotion regulation abilities are understood to gradually mature throughout childhood and adolescence with evidence of the role of interoception in this process (Camacho et al., 2019; Opdensteinen et al., 2021; Silvers, 2022). In preschoolers, interceptive accuracy has been observed to relate to both emotion regulation behaviours and cortisol levels, with lower interoceptive accuracy predicting higher cortisol levels under stress (Opdensteinen et al., 2021). Camacho et al. (2019) observed differences in brain activity in emotion processing and emotion regulation between 8-year-old children and adults, demonstrating that maturation of emotion regulation is ongoing at this stage, also observing that regulation of negative emotions appears more protracted than positive emotions (Camacho et al., 2019). These studies suggest emotion regulation abilities continue to develop during childhood. Since emotion regulation relies on interoceptive processing and that early social interaction is proposed to provide a developmental framework for interoceptive processing, it follows that the infant's early interactive experiences in the caregiver-infant dyad may potentially alter the developmental trajectory of emotion regulation development.

In summary, the studies presented here provide empirical evidence of infants perceiving interoceptive signals and responding behaviourally to those signals from as early as three months old, albeit with inconsistent findings. However, studies of fetal development indicating responses to pain and touch within the womb suggest interoceptive processing begins to develop prenatally. This raises the possibility that some level of interoceptive processing is either innate or begins to develop in relation to the nervous system before birth (Bellieni, 2019; Derbyshire and Bockmann, 2020; Marx and Nagy, 2015; Reissland et al., 2014. Following birth, however, the number and variety of proximal interactions with the caregiver provide a rich environment in which interoceptive processing can further develop. During infancy, while examination of HEPs could offer a direct measure of implicit interoceptive processing, HRV, vagal tone, and EDA may provide not only physiological evidence related to emotional processing(Critchley, 2002; Storm, 2008), but could also be employed for the study of interoception without relying on perceptual awareness. The ongoing development of emotion regulation abilities throughout childhood raises questions regarding the role of early dyadic interaction. More specifically, do any specific characteristics of early dyadic interaction influence this development and does their influence endure throughout childhood? One crucial common denominator of regulation within the early environment and dyadic interactions for all infants is touch. Examination of the body's response to touch could provide an important source of evidence of interoceptive processing early in life, as well as shedding light on the developmental trajectory of interoceptive processing. Touch deserves special attention since *affective* touch, a precise type of touch, has been found to activate the same neural pathways as interoceptive information. The role of touch in the development of interoceptive processing is discussed next.

1.3.2 The importance of touch

Tactile interactions are an essential component of early dyadic interaction for all dyads, since touch is essential in the provision of basic instrumental care, such as feeding, bathing and soothing. In addition, playful and affectionate touch form an important part of an infant's early socio-emotional experience, with much of this touch coming from their primary caregiver (Crucianelli and Filippetti, 2018). The effect of touch on infants has been the subject of considerable research, resulting in behavioural and neuroscientific observations in response to actions such as a kiss better from a parent, a playful tickle or a soothing cuddle. The values of neonatal Kangaroo care (Cong et al., 2009), skin-to-skin contact at birth (Feldman et al., 2002), and baby massage (Kamiya et al., 2021; S. L. Smith et al., 2013) have attracted much attention over the past decades (Ferber et al., 2008; T. Field, 2019). Mercuri et al. (2023) describe the different kinds of touch infants experience change in the first months of life (Mercuri, Stack, De France, et al., 2023). In the first month, most touch is either soothing or static, whereas by 9 months, both the infant and the caregiver typically utilise a much broader range of touching behaviours, including playful touch, pulling, poking, etc. indicative of more complex social interactions. Cascio et al. (2019) suggest social touch taps into reward-based learning and that the experience of touch depends both on the neurobiological effects of touch, as well as 'top down' interpretation of touch based on contextual information, such as from whom touch is administered and the nature of that relationship (Cascio et al., 2019). The kinds of touch used have also been found to relate to caregiver mental health (Donaghy et al., 2024; Mercuri, Stack, Mantis, et al., 2023; Stepakoff and Beebe, 2024), as well as levels of coordination and synchrony in dyadic interactions (Carozza and Leong, 2021; Nguyen, Abney, et al., 2021). The early experiences of touch are also important for our long-term relationship with touch, since touch forms an important part of our social existence, taking different forms in different relationships across the lifespan (see Gallace and Spence, 2010 for an overview of social touch across the lifespan). A recent study has highlighted that caregivers' own experience of touch can influence the way they use touch with their infants and that their interoceptive sensibility mediates this relationship (Wigley et al., 2024). The authors of this study used self-report data to examine caregivers' frequency of use of stroking in relation to their own attitudes towards touch. They found that caregivers who had enjoyed a more positive experience of touch in their own childhood were more likely to use stroking caresses with their infant. In addition, those who had experienced more stroking reported higher interoceptive sensibility, which, in turn, was associated with greater use of stroking behaviours.

In this thesis, touch is considered as a particularly important aspect of an infant's early interactive experience. Touch is distinct from other forms of interaction, since it involves two parties synchronously, in this case the caregiver and the infant, and requires close proximity (Ciaunica and Fotopoulou, 2017). However, touch is also of particular interest in the development of interoceptive processing from a neurobiological perspective, as I will explore in this section.

The sense of touch begins to develop very early in the life of a growing fetus, with response to touch clearly observable in the womb (Marx and Nagy, 2015; Reissland et al., 2014). Following birth, the role of tactile interactions in the caregiver-infant dyad, and the resulting effects of touch on the infant, appear to have far-reaching consequences. Indeed, touch makes a significant contribution to an infant's early experience of their environment and the soothing effects of touch have received much research attention (e.g. Della Longa et al., 2019; T. Field, 2019; Fairhurst et al., 2014; Fotopoulou et al., 2022; McGlone et al., 2014). The importance of touch has been highlighted specifically in the development of homeostatic regulation, with the suggestion that the role of the skin has been under-researched in interoceptive processing development (Crucianelli et al., 2019; Crucianelli and Ehrsson, 2023; Fotopoulou and Tsakiris, 2017b). This is surprising when considering the large body of evidence demonstrating the positive benefits of touch early in life. For example, among hospital-based neonatal care, improved neurodevelopment was observed by EEG in those environments providing greater sensory exposure for the infant (Pineda et al., 2014). Specifically, early maternal touch has been observed to relate to greater connectivity in the developing infant brain (Brauer et al., 2016). Evidence of the positive effects of touch have also been observed on socio-cognitive development through improved face recognition when 4-month-old infants receive deliberate stroking from their caregiver (Della Longa et al., 2019) as well as on improved acquisition of speech (Abu-Zhaya et al., 2017). Touch has also been related with other domains of infant development, such as autonomic regulation and immune function (see Carozza and Leong, 2021 for an overview) and is thought to play an important role in improving the ongoing development of self-regulation, from early infancy (Feldman et al., 2002) and into childhood (Feldman, 2009).

Since early experience of touch has been associated with cognitive and socio-emotional development, it is reasonable to conclude that touch relates to both physical and mental health (Maitre et al., 2017; Sharp et al., 2012). This highlights the important role of early tactile interactions, bringing into question whether touch is related to infants' interoceptive processing development, both in terms of structural connectivity and sensory perception. Considering the models of interoception described in Section 1.2.2, it would appear reasonable to speculate that early touch could influence interoceptive signal strength and transmission, as well as interoceptive sensitivity. This is because a specific kind of touch, affective touch, has been demonstrated to be particularly relevant in the study of interoception. Light touch delivered on hairy skin, at a rate of 1-10 cm/s, optimally applied at body temperature, activates the unmyelinated C-tactile fibres, CT-afferents, in the skin. In other words, the afferent firing rate increases in response specifically to this pleasant touch. Crucially, this activation utilises a direct pathway to the anterior insula (Björnsdotter et al., 2010), a region playing a central role in the processing of interoceptive information (Löken et al., 2009). This so-called *affective touch* triggers pleasant feelings (McGlone et al., 2014; Olausson et al., 2010) and is associated with the instinctive, soothing touch administered by caregivers (e.g. Croy et al., 2016; Fairhurst et al., 2014; Löken et al., 2009; McGlone et al., 2014). Research has suggested that affective touch fulfils several functions in infant development. McGlone et al. (2014) refer to affective touch as a secondary touch system. While less obviously advantageous for survival than the more rapid primary touch system which activates a different nerve pathway, the authors suggest this second system plays a crucial role in development of the social brain (McGlone et al., 2014). The use of CT touch in dyadic interaction, along with close physical proximity, is proposed to facilitate the developing sense of bodily-self in the infant, as well as aiding the development of interoceptive processing through *embodied reparation*, the re-attunement of the caregiver-infant dyad based on physiological synchrony, following a period of misattunement (Montirosso and McGlone, 2020). Consistent with this view, Fotopoulou et al. (2023) suggest that affective touch fulfils three distinct roles in infancy. Firstly, it fulfils embodied predictions about proximity and attachment. Secondly, affective touch provides social enactment of homeostatic control and physiological regulation and, finally, that it regulates affect by allostatic regulation (Fotopoulou et al., 2022). Similarly, it is also suggested that touch enhances an infant's development of a sense of self, with 5-month-old infants demonstrating a preference for visuo-tactile synchrony versus asynchrony when receiving affective touch (Della Longa et al., 2021). In addition, 4-month-old infants receiving affective touch (vs non-affective touch) display longer looking at images of faces, suggesting that affective touch fulfils a socio-emotional function and facilitates greater social engagement (Della Longa et al., 2019). Together, the instinctive use of affective touch by caregivers, the socio-emotional functions of affective touch proposed in the research to date and the activation by touch of shared pathways with interoceptive information, support the idea that early affective touch within the caregiver-infant dyad is involved in the development of interoceptive processing.

Evidence for the early role of CT afferents comes from the study of fetal movements in response to touch, since they occur before development of other low-threshold mechanoreceptors (McGlone et al., 2014). This evidence from within the womb again encourages investigation of the role of touch in the very early development of emotion-regulation skills and, hence, interoception. Indeed, it has been observed that touch experienced through the mother's abdomen during pregnancy predicted mood at three months of age (Wang et al., 2015). One plausible explanation for the mechanism behind this association could be the calming effect on the mother leading to associated reduction in maternal blood cortisol, experienced by the fetus via the placenta. From birth, infants exhibit different physiological responses to various types of touch. Newborns receiving non-affective touch show reduced heart rate variability (HRV), whereas affective touch is associated with maintained HRV, indicative of a calmer state (Longa et al., 2021). Specifically, infants already respond differently to affective touch than other kinds of touch at 2 months of age, demonstrating different brain responses to affective and non-affective touch (Jönsson et al., 2018). The importance of touch for infants is further highlighted by neuroimaging studies, which have indicated that affective touch relates to neural synchrony, but not physiological synchrony, in caregiver infant dyads (Nguyen, Schleihauf, et al., 2021).

The soothing role of affective touch is of particular interest when considering interoceptive processing development in relation to mental health. For example, CT-optimal affective touch has been found to reduce arousal, leading to reduced heart rate and increased engagement in 9-month-old infants (Fairhurst et al., 2014). This study highlights a potential early interoceptive connection between affective touch and anxiety, encouraging further consideration of affective touch when examining potential mechanisms in the susceptibility to anxiety. In fact, a growing number of studies are now examining affective touch from a clinical perspective (Beebe and Lachmann, 2002;Crucianelli et al., 2016), as significantly reduced responses to affective touch could indicate impairment in the CT-afferent pathway, perhaps revealing more widely impaired interoceptive signalling. For example, patients suffering from anorexia nervosa demonstrate significantly lower response to affective touch than healthy controls, corresponding with impaired interoceptive sensitivity and distorted body representation (Crucianelli et al., 2016). Not only does this evidence highlight research avenues for understanding the mechanisms of interoception and anxiety and their impact in infant development, but it also hints at potential therapeutic potential for affective touch.

The studies reviewed here not only highlight the fundamental importance of touch in the world of the infant, but also suggest the special function of touch in the development of interoceptive processing. As discussed in Section 1.3.1, like adults, infants' experience of the world is influenced by their physiological and emotional responses to internal sensation, with consequences for the way they learn about their environment. It is, therefore, important to consider to what extent early experiences of touch can also shape the developmental trajectories of interoception (Burleson and Quigley, 2021; Fotopoulou and Tsakiris, 2017b). The role of administering touch to the infant falls largely with the primary caregiver. Since infants depend on their caregiver to provide the essential care for physiological balance as well as social and emotional experience, the caregiver's ability to promptly respond to and correctly interpret the infant's cues is likely to rely on frequent use of touch and may significantly impact the development of self-regulatory abilities (Diener et al., 2003; Sroufe, 1996). In the studies within this thesis, I examine several types of touch. In study 1 (Chapter 3), I observe instrumental and social touch (playful and affectionate), based on the definitions and method suggested by Crucianelli et al. (Crucianelli et al., 2019). In study 2 (Chapter 4), I refer to affectionate touch as gentle, stroking, soothing touch administered by the caregiver (McGlone et al., 2014). Before delving into these studies, I next discuss the caregiver's role in the development of infants' interoceptive processing through dyadic interaction, and the factors that may affect this development.

1.3.3 The role of caregivers

For an infant in the early months of life, their caregiver is their world. Infants depend on their caregivers' responses to meet their physiological needs, for example, to change them when they are wet, to feed them when they are hungry or to soothe them when they are tired. At the same time, the infant is highly dependent on their primary caregiver for the majority of social interaction in the first months of life. The caregiver's role in these early interactions is clearly important, but which specific features of their behaviour in this interaction relate to interoceptive processing development? Do differences between caregivers' behaviours alter the trajectories of interoceptive processing development for the infant? Within the caregiver, interoception, emotion regulation, and mental health in adulthood are likely to be related, as was discussed in 1.2. These factors may also shape the infant's interoceptive development, an area that remains under-explored despite its clinical importance. For instance, anxious caregivers are more likely to raise anxious children, though the mechanisms behind this transmission are unclear (Beidel and Turner, 1997; Warren et al., 2003). In this section, I will discuss the caregivers' potential to influence their infant's interoceptive processing development, considering the prenatal environment, theories highlighting the caregiver's role in dyadic interactions, the skills required for effective caregiving, and how caregiver factors influence infant development. I will also examine what this means for the infant's interoceptive and emotional development.

The importance of the early dyadic environment

Interoceptive processing development is considered important in theories of development, such as in infant learning based on reward, motivation and arousal (Fogel, 2011; Fotopoulou and Tsakiris, 2017b; Mundy and Newell, 2007), with much of an infant's learning resulting from experience of the environment around them. This begins in the womb, and there is growing evidence of early bodily sensations experienced prenatally. In fact, prenatal experience has been shown to significantly influence infants' development, according to evidence from studies investigating stress during pregnancy, indicating how stress contributes to later personality and emotional difficulties for the offspring (Brannigan et al., 2019; Grigoriadis et al., 2018). Postnatally, infant and child development has been described as a dynamic, hierarchical process where early interactive behaviour plays a crucial role in laying foundations on which further development is built (Karmiloff-smith, 1998). These examples lend support to the idea that an infant's early environment provides the framework for the development of a sense of self, as distinguished from others, and, more specifically, the development of interoceptive processing necessary for the social and emotional boundaries required in this understanding. Given this theoretical perspective, it is possible that the quality of early interactive behaviour could contribute to lifelong behavioural patterns that either increase or decrease the likelihood of difficulties in emotional processing.

Caregiver's interactive behaviours

The infant is both physically and socio-emotionally dependent on their caregiver. In the early weeks, both the new parent and the infant must begin to learn from each other. The infant must communicate their needs, while the caregiver must learn to interpret the infant's cues. Thus, each caregiver-infant dyad develops a unique pattern of communication, often likened to a dance (Provenzi et al., 2018). Early interactive behaviour occupies a vast field of research and it has long been believed that early interactions shape cognitive and affective learning (Diener et al., 2003; Sroufe, 1996). In their systematic review of 82 studies of caregiver-infant dyadic interactions, Provenzi et al. (2018) grouped characteristics of interaction into two broad groups, namely *attunement*, which refers to the ability to infer meaning and share intentions, and *coordination*, which refers to the matching or non-matching of behaviours in the back and forth turn taking of communication. These characteristics provide the foundations upon which synchrony between the caregiver and infant develops in response to each learning of the other's meaning through iteration (Provenzi et al., 2018). Theories of developmental psychology as well as bodies of empirical research can be considered within the categories of attunement, coordination and synchrony. Here, I will explore the research to date that relates these aspects of early communication with interoceptive processing development and, specifically, the caregiver's influence over them.

Attunement refers to the caregiver's ability to respond appropriately to their inference of their infant's emotional needs (Provenzi et al., 2018). Attunement is important in dyadic interactions, since it leads to interpersonal co-ordination and co-regulation (Montirosso and McGlone, 2020), characteristics which depend on both the caregiver and the infant. The caregiver's role relies on their ability to notice subtle changes in infant behaviour, such as shifts in facial expression, different movements and vocalising and to match this information to their own mental representations of emotional state. This enables them to infer the emotional state of the infant, whilst recognising that state as distinct from themselves. This ability is referred to as mentalizing, and is suggested to be informed by one's own emotional experience (Fonagy et al., 2018). To avoid confusion, it is important to note that mentalizing in this context relies on higher-order processing of emotional inference compared to the mentalizing used by Fotopoulou and Tsakiris (2017), in which the term is used to refer to lower-level embodiment of emotional processes (Fotopoulou and Tsakiris, 2017a). Mentalizing, in its original definition, is understood to foster empathic behaviour (Majdandžić et al., 2016) and has been found to activate similar brain regions to empathy (Hooker et al., 2008). Fonagy's seminal work on mentalizing (e.g. Fonagy and Target, 1998; Fonagy et al., 2018) has since informed the development of therapeutic approaches for children and adults alike, but it can also apply to caregivers of younger infants. For example, caregivers' mentalizing abilities with their 6-month-old infants have been related to the development of secure attachment at 12 months of age (Meins et al., 2001). These studies highlight the importance of caregivers' mentalizing abilities in their attunement with their infant. This suggests that caregivers' mentalizing abilities not only relate to the care they provide in the moment, but also to the infants' ongoing development.

Related to metalizing abilities, mind-mindedness refers to caregivers' abilities to view their infant as a separate being with their own mind, and accurately attribute mental states to them (Meins et al., 1998; Meins et al., 2001). It has been suggested that mind-mindedness facilitates the sense of self in the infant. In other words, the infant is able to recognise themselves as distinct from others because their caregivers think of them and treat them in that way (Gergely, 1999). Caregiver mind-mindedness has been consistently related to caregiver sensitivity, as well as to their child's theory of mind (see McMahon and Bernier, 2017 for a review). Caregiver mind-mindedness is positively related with attachment security, with caregiver sensitivity playing a mediating role in this relationship (Laranjo et al., 2008). Mind-mindedness has also been related to specific behaviours within the dyad. For example, caregivers displaying non-attuned mind-related comments towards their child use fewer contingent touch behaviours when interacting with their 12-month-old infants compared to caregivers who use fewer non-attuned comments (Crucianelli et al., 2019). These studies highlight the importance, not only of how well caregivers are able to accurately attribute mental states to their infant, but also to behave consistently with this understanding.

In addition to accurately inferring their infant's emotional state and empathising with how they might feel, caregivers are also required to act in ways that demonstrate their understanding. The matching of caregivers' behaviours with the emotional state or need of their infant is referred to as *contingency* (Beebe et al., 2010). Contingency is considered an important concept in the theoretical accounts of interoceptive processing development discussed in Section 1.3.1 (Atzil et al., 2018; Filippetti, 2021; Fotopoulou and Tsakiris, 2017b). When an infant expresses a need via a behavioural cue, a process of interaction with their caregiver begins. The caregiver's response will either be contingent, i.e. matching the expressed need of the infant, or non-contingent, influencing what happens next. A contingent response would satisfy the need of the infant, enabling both parties to move on. However, a non-contingent response could either lead the infant to try to make themselves understood once again, or to give up, depending on the infant. If these exchanges facilitate the development of interoceptive processing for the infant, it follows that how 'in tune' the infant will become with their own bodily sensations might depend on the delicate balance of these early exchanges (Fotopoulou and Tsakiris, 2017b). While it might appear that contingent first responses from the caregiver are ideal, this overlooks the inevitability of non-attuned responses from the caregiver and breakages in the chain of communication. Montirosso and McGlone (2020) proposed that the reparation process, which occurs after states of no co-regulation in the dyad (bodily misattunement) in order to reinstate co-regulation (attunement), is critical for infants' development of self-regulation abilities. They suggest that this reparation process, which uses physical proximity and synchrony between the caregiver and infant, leads to interoceptive stability in the infant and supports the experience of their bodily-self (DiCorcia and Tronick, 2011). As discussed in 1.3.3 above, the authors propose that touch plays a crucial role in the reparation of embodied attunement in the caregiver-infant dyad.

Before recent discussions of contingency in relation to interoceptive processing development, maternal contingency was already recognised as influential in an infant's development. Contingency is related to the concept of maternal sensitivity, which was considered a determinant of attachment by Mary Ainsworth in her seminal work (Ainsworth, 1972). Although contingency and sensitivity may appear similar, they are distinct concepts that are sometimes conflated in the literature. Ainsworth originally described sensitivity as a mother's ability to perceive and interpret her infant's signals and respond appropriately. In this definition, the focus is two-fold: 1) accurate interpretation, which relates to mentalizing and mind-mindedness, and 2) appropriate caring response. While this definition does not explicitly specify the timing of the caregiver's response to the infant's cue, the use of "appropriate" may imply it. That is, an appropriate response could refer to both temporal and qualitative aspects of the caregiver's behaviour. In more recent studies, such as Crucianelli et al. (2019), the term *contingency* is used to refer to the mentalization of the infant's need by the caregiver and the resulting matching of the behaviour to the infant's need (Crucianelli et al., 2019). This definition is also in line with the work of Gergely and Watson (1999), who discuss the abilities of the infant to detect and understand whether the caregiver's response that they receive matches their need (Gergely, 1999). This approach puts the infant in charge of the communication, since it is up to the infant to first communicate their need and then to assess whether that need was met. In this respect, contingency implies an adaptive quality in the caregiver, since Gergely and Watson (1999) propose that the infant learns to better recognise the contingency of the response as their sense of self develops. Since Ainsworth's original work on sensitivity and attachment, several studies have reported findings relating sensitivity, attachment and caregiver behaviour, highlighting the long-term effects of these processes on attachment type (see De Wolff and Van Ijzendoorn, 1997; Fox et al., n.d.; Koehn and Kerns, 2018 for meta-analyses). For example, sensitivity to infant distress is considered relevant in the emergence of secure attachment (Goldberg et al., 1999), with greater maternal sensitivity at six months of age predicting increased likelihood of secure attachment at 15 months (McElwain and Booth-Laforce, 2006). Meins et al. (2001) related caregiver mind-mindedness to secure attachment, demonstrating sensitivity and mind-mindedness as independent predictors of attachment, further suggesting mind-mindedness is actually a more accurate predictor of attachment than sensitivity (Meins et al., 2001). The early development of attachment is potentially important when considering the development of interoceptive abilities. Oldroyd et al. (2019) demonstrated differences in interoceptive abilities relating to different attachment styles among adults across the lifespan (Oldroyd et al., 2019), arguing that attachment is fundamental in the development of interoceptive ability. The authors highlight the importance of sensitive, attuned caregiving to reflect both the body and the mind of the child in the development of interoception and secure attachment. While this appears to support the theoretical approaches discussed in 1.3.1, it does not explain how interoceptive abilities develop early in life.

Caregiver-infant synchrony

While attunement, through mentalizing skills, contingency and sensitivity, are important skills for the caregiver which clearly influence dyadic interactions, the quality of these interactions relies on bi-directional influences. For the caregiver to develop their skills, the infant must also learn to communicate their needs, with each party's development relying on the skills of the other. This leads to a unique communication style within each caregiver-infant dyad. Research highlights some debate over the theoretical models of dyadic interactions (Beebe, 2000; Murray et al., 2016; Steele et al., 2017). For example, *maternal contingency*, focusing on the matching of the mother's response to the infant's cue, and *functional architecture*, focusing on the preparedness of each party to provide specific responses to specific cues, provide two different accounts for the structure of such communication (see Murray et al., 2016 for an overview). When considering the bi-directional nature of dyadic interactions, a further characteristic, synchrony, emerges, providing insight into the connection and coordination between the infant and the caregiver (Feldman et al., 2011; Feldman, 2012). According to Feldman (1999), when caregivers respond appropriately to the mental needs of their infant, they foster synchrony, relying on the higher order mentalizing skills described above (Feldman et al., 2011). Synchrony refers to dynamic processes in the caregiver-infant dyad whereby the caregiver and infant become aligned with one-another in response to cues exchanged between them, demonstrating temporal similarities (Feldman, 2012). Behavioural synchrony refers to temporal similarity of movements and behaviours in the caregiver-infant dyadic interactions (Provenzi et al., 2018). Several behaviours have been observed to quantify synchrony in caregiver-infant dyadic interactions, such as mirroring, turn-taking, eye contact, gaze following and joint attention (see

Provenzi et al., 2018 and Beebe et al., 2010). Such behavioural synchrony is well-documented in caregiver-infant dyadic communications, with behaviours indicating synchrony visible in the early months of life (Beebe et al., 2010). However, in addition to observable behavioural synchrony, below the surface caregivers and their infants also demonstrate physiological, neural and hormonal synchrony (Feldman et al., 2011; Feldman, 2012) and different forms of synchrony have been related with a variety of outcomes, as will be discussed next.

Physiologically, caregivers and their infants may demonstrate synchrony in several ways, including synchrony of heart rate, heart rate variability and thermal regulation (Feldman et al., 2011; Ludington-Hoe et al., 2006; C. G. Smith et al., 2022a; Van Puyvelde et al., 2015). Caregivers' and infants' heart rate variability has been found to synchronise during face-to-face interactions (Feldman et al., 2011), while infants' heart rates synchronise with their caregivers after even minimal skin to skin contact, such as the caregiver holding the infant's foot (Van Puyvelde et al., 2015). In addition, caregivers' bodies are able to provide thermoregulation that is tailored to the infant's need during feeding, even when feeding twins with different needs (Ludington-Hoe et al., 2006). Importantly, it has been proposed that the disruption and reparation of physiological synchrony supports the development of interoceptive processing in the infant, without the higher-order mentalizing skills considered essential in classical views of maternal sensitivity (Montirosso and McGlone, 2020). This appears to build on a previous theory, that of *parental embodied mentalizing*, in which non-verbal interpersonal communication takes place without explicit awareness (Shai and Belsky, 2011). Such non-verbal activity in the caregiver-infant dyad has been related with infants' socio-emotional development (Shai and Belsky, 2017). Interestingly, increased physiological synchrony between caregivers and their infants has been observed in anxious parents (C. G. Smith et al., 2022a). The authors observed increased synchrony in highly anxious caregivers during both low and high arousal, whereas in less anxious caregivers, synchrony increased specifically during peaks of arousal rather than calmer periods. Given the importance of reparation of physiological synchrony for interoceptive processing development proposed by Montirosso (2020), this brings into question whether increased physiological synchrony is always beneficial in cases of impaired mental health. In fact, it has been previously suggested that too much synchrony could indicate intrusive parenting (Beebe et al., 2010). Nonetheless and overall, physiological synchrony appears beneficial for the development of self-regulation in infancy and childhood (Depasquale, 2020).

Neural synchrony refers to similarity in brain activity in the caregiver and child when engaged in specific tasks (Leong et al., 2017; Nguyen et al., 2020) and increased neural synchrony has been observed in caregivers and their 5-year-old children when completing a problem-solving task together, but not when they undertake the same task concurrently but separately, indicating that when cooperating behaviourally, so brain activity becomes synchronised. Further, higher levels of synchrony predicted faster success at the problem-solving task. A similar synchronous effect during communication has been observed in infants, when they are engaged with watching their caregivers singing them a nursery rhyme (Leong et al., 2017). These studies indicate the potential for neural synchrony as a biomarker of interaction quality and highlight the multi-dimensional nature of caregiver-infant dyadic communication, potentially supporting the idea that interactive communication can facilitate brain connectivity, since neural synchrony suggests a transfer of understanding between the two parties that does not exist when they are not engaged with each other (Nguyen et al., 2020). Neural synchrony has been observed to be present between 10 - 18-year-old children and their caregivers, but not between children and a non-caregiver when comparing synchrony during the same tasks, suggesting interpersonal neural synchrony is unique within a caregiver-child dyad (Reindl et al., 2022). Further, the multimodal evidence collected in this study also distinguished neural synchrony from physiological synchrony, leading to the suggestion that they could represent different underlying processes. A recent study also supported the examination of neural synchrony in caregiver-infant dyads as a marker of interaction quality and, further, associated neural synchrony with attachment style (Nguyen et al., 2024). Interestingly, the association between neural synchrony and attachment was not demonstrated between behavioural synchrony and attachment.

In addition to physiological and neural synchrony, caregivers and their infants have also demonstrated synchronised hormone release. For example, mothers, fathers and their preterm infants all demonstrated a similar increase in salivary oxytocin following a period of skin-to-skin contact in a study of parent-infant bonding (Vittner et al., 2018). Oxytocin is considered important in the early bonding process between infants and caregivers (Abraham et al., 2019; Bosch and Young, 2018), but has also been associated with interoceptive processing (Quattrocki and Friston, 2014; Yao et al., 2018) and with anxiety (Hoge et al., 2008; Neumann and Slattery, 2016). This suggests that hormonal synchrony such as that described by Vittner et al. (2018) could be impaired in cases where caregivers are experiencing elevated anxiety levels, potentially influencing not only the bonding processing, but also bringing into question whether this relates to interoceptive processing development in the infant, should early dyadic interactions be compromised by hormonal differences in this way.

The research reviewed in this section highlights that caregivers and their infants synchronise with one another in several ways. While behavioural synchrony can be observed, through mirroring, turn taking, etc, caregivers and their infants also synchronise beneath the surface, neurally, physiologically and hormonally. There is some evidence that these different forms of synchrony are independent from one another. A study of the effects of affective touch revealed an association between touch and neural synchrony, but not physiological synchrony, in caregiver infant dyads (Nguyen, Schleihauf, et al., 2021). This not only demonstrates the different channels involved in interactions leading to a unique connection between the caregiver and the infant, but also suggests the important role of dyadic interaction in the infant's development (Atzil et al., 2018). Importantly, the caregiver's role in these early exchanges would appear fundamental, with the potential to directly influence the infant's development. This raises an important question: does variation in caregivers' engagement in dyadic interactions relate to variation in the infant's development and, if so, what factors might influence the caregiver's ability? Factors influencing the caregiver's role in dyadic interactions will be discussed next.

Factors influencing the caregiver's behaviour towards their infant

Given the importance of the caregivers' skills, such as mentalizing, in order to become attuned with their infant in dyadic interactions, it is important to consider what factors may influence these behaviours. As mentioned above, emotional inference is required in mentalizing. This requires the caregiver to be able to recognise and regulate their own emotional state and, as discussed in Section 1.2.3 above, this ability relates to the caregivers' own interoceptive abilities and mental health. Therefore, differences in caregivers' interoceptive abilities, as well as their own mental health, could influence their behaviour in dyadic interactions with their infant and, hence, the early development of interoceptive processing. While this is yet to be researched directly, indirect evidence has shown the influence of these factors on caregiver behaviour in dyadic interactions. For example, the extent to which caregivers use touch in interactions with their infant has been associated to caregiver interoception. Caregivers reporting greater focus on their interoceptive signals also reported engaging in more stroking and rocking behaviours with their infants (Donaghy et al., 2024). Previous theories have suggested that caregivers' own interoceptive abilities directly relate to their infant's interoceptive processing development by facilitating simultaneous monitoring of their own bodily signals and their infant's arousal state to enable sensitive caregiving (Abraham et al., 2019; Montirosso and McGlone, 2020). Caregiver interoception has also been associated with developmental outcomes for the child. For example, maternal interoceptive knowledge has been found to better predict emotion regulation abilities and social skills in older children than other types of emotional knowledge(MacCormack et al., 2020). fMRI data suggests maternal interoceptive processing, observed through increased activity in the anterior insula and amygdala, predicts fewer somatic problems in their children at age 6, moderated by greater sensitivity towards the child at age 4 (Abraham et al., 2019). In this case, the relationship was found to be modulated by parental oxytocin levels, believed to provide a protective buffer for the child in cases of maternal depression (Pratt et al., 2015). Based on this evidence, it is reasonable to speculate that reduced interoceptive abilities in caregivers may hinder their ability to promptly respond to an infant's cues, potentially affecting the infant's developing interoceptive abilities.

Caregiver mental health has also been found to relate directly to their behaviour during dyadic interactions. Stepakoff and Beebe (2023) observed that caregivers with higher levels of depression used less affectionate touch with their 4-month-old infants compared to non-depressed caregivers. Depressed caregivers were also more likely than non-depressed caregivers to use toys and objects to touch their infants (Stepakoff and Beebe, 2024). Similarly, Mercuri et al. (2023) found that less depressed caregivers engaged in more frequent affectionate touch with infants (Mercuri, Stack, Mantis, et al., 2023). In addition to touch, caregivers' speech has also been related to their mental health. Latency of caregivers' interactive speech has also been found to be altered in depression, with depressed mothers responding to their infant 11% more slowly than non-depressed mothers (N. Smith et al., 2022).

Evidence of a link between caregiver anxiety and dyadic behaviour has also been widely demonstrated, overall suggesting that anxious caregivers display a specific set of behaviours when interacting with their infant. Kaitz et al. (2010) reported that anxious mothers behave differently from non-depressed controls, by demonstrating greater engagement with their 6-month-old infants and showing exaggerated behaviours in dyadic interactions (Kaitz et al., 2010). The authors suggested that this type of behaviour is related to hyper-arousal associated with anxiety. Indeed, Smith et al. (2022) reported that anxious caregivers use more intense vocalisations with their 12-month-old infants in naturalistic settings. This behaviour was associated with higher physiological arousal in both caregivers and infants (C. G. Smith et al., 2022a). This study did not describe the intense clusters of vocalisations as either positive or negative, so it is difficult to compare this directly with the findings of Kaitz et al. (2010). Less anxious caregivers in this study exhibited an additional skill: the ability to downregulate their own arousal during high-arousal moments in the dyad. This skill was absent in more anxious caregivers. Murray et al. (2012) reported that anxious caregivers displayed reduced engagement with their infants, but that was only visible in a stressful task, relative to a non-stressful task (Murray et al., 2012), again suggesting that caregiver behaviour relates to physiological arousal. Highly anxious mothers tend to demonstrate less sensitive responsivity and emotional tone than less anxious mothers during interactions (Nicol-harper et al., 2007). However, Reck et al. (2018) found no behavioural differences between anxious and non-anxious mothers (Reck et al., 2018). These mixed findings may be attributed to the heterogeneity encompassed within the broad term "anxiety". Indeed, Murray et al. (2012) highlighted the anxiety disorder-specific nature of altered parenting. In this study, caregivers of 4- to 5-year-old children were observed when their children were asked to complete a social threat task (give a speech), a non-social threat task (explore scary objects), and a non-threat task (play with play-dough). Caregivers' behaviour differed between groups for each task, with caregivers showing reduced engagement with the child on the task that was related to their own anxiety disorder (Murray et al., 2012). In a separate between-groups study of mothers with social anxiety disorder and generalized anxiety disorder, mothers with social anxiety disorder were less positively engaged, and more anxious during the interactions, but equally as sensitive as control mothers, while no effect of generalized anxiety disorder was observed (Murray et al., 2007). Inconsistencies highlight the need for specificity and replication, in order to clarify whether behavioural differences are due to characteristics of different anxiety presentations, or, as another possibility, due to trans-diagnostic characteristics based on somatic, emotional and cognitive aspects of different mental health difficulties. Either way, it would appear that caregiver mental health can impact on dyadic interactions, with the potential to influence the development of interoceptive processing in the infant. As discussed in Section 1.2.3, impaired interoceptive abilities have been associated with psychopathology in adulthood (e.g. Khalsa et al., 2018; Nord and Garfinkel, 2022). Therefore it could follow that, if poor mental health in caregivers leads to them providing sub-optimal care in dyadic exchanges, this could lead to impaired interoceptive processing development in the infant, thus presenting a risk for psychopathology. Caregiver mental health is considered a risk factor for child mental health difficulties, as is already widely recognised in clinical research and practise, with parental mental health difficulties considered among Adverse Childhood Experiences, or ACEs, a list of widely accepted risk factors for childhood psychopathology (e.g. Elmore and Crouch, 2020; H. Y. Lee et al., 2020; Racine, 2020; Vostanis et al., 2006). A relationship between caregiver mental health, their behaviour towards their infant and the infant's interoceptive processing development could offer insight into a specific mechanism behind this statistical risk.

While the research presented here demonstrates that caregiver interoception and mental health can influence the quality of dyadic interactions, there is also empirical evidence of their direct relationship with emotion regulation within the infant. For example, infant vagal tone has been found to correlate positively with maternal sensitivity, suggesting greater sensitivity relates to higher vagal tone (Rattaz et al., 2023), which is associated with better emotion regulation (e.g. Porges et al., 1994). In addition, reduced infant vagal tone is associated with higher symptoms of maternal depression and lower levels of caregiver-infant synchrony in dyadic interaction (Feldman and Eidelman, 2007). Parental anxiety has also been associated with autonomic hyper-arousal of their 4-month-old infants, which in turn predicts more fearful temperament at two to three years old (de Vente et al., 2020), offering some direct insight into the mechanism behind intergenerational anxiety transfer.

In this section I have highlighted some important aspects of the role of the caregiver in dyadic interactions, specifically attunement-based skills, such as mentalizing and mind-mindedness and their relationship with behavioural skills, such as contingency. The evolving dyadic communication between caregiver and infant can be likened to a language unique to them, but the quality of these early interactions appears important for the development of interoceptive abilities and emotion regulation abilities in the infant. The research I have described highlights how caregivers' skills could be influenced by their own interoceptive abilities and mental health, with some direct evidence of this influence on physiological evidence of emotional development in their infants, such as vagal tone. Theoretical approaches to the development of interoceptive processing highlight the importance of the caregiver's skills. When those skills are compromised by poor interoceptive abilities or mental health, it can pose a risk to their infant's future mental health. While some empirical studies support the theories proposed in Section 1.3.1, this evidence remains sparse and predominantly indirect. In this thesis, I seek to address this research gap by focusing on caregiver contingency during dyadic interactions. I use the term contingency as defined by Crucianelli et al. (2019), referring to the degree to which a caregiver's behaviour aligns with the infant's needs as indicated by the infant's behaviour (Crucianelli et al., 2019). In the next section, I will present data on the wider context of child mental health and the role of interoception in older childhood, highlighting the immediate need for more research on this topic.

1.4 Interoception and mental health in childhood

The research presented thus far has highlighted the important role of the caregiver in early caregiver-infant dyadic interactions. In addition, this review exposes the need for further empirical studies of factors influencing caregivers' skills, to shed light on the developmental origins of the relationship between risk of psychopathology and interoceptive processing development. Greater understanding of this development is both important and urgent, since child mental health in the UK is currently in crisis.

An NHS report recently demonstrated a staggering rise in childhood mental health problems in the UK. The percentage of 7-16-year-olds with a mental health problem rose from 12.1% in 2017 to 18.0% by 2022. Anxiety disorders are the most prevalent mental health disorders in children and adolescents, affecting over 8% of children (Newlove-Delgado, 2023). In parallel, referral waiting times continue to rise (10 months on average), with only 25% of children referred to Child and Adolescent Mental Health Services, CAMHS, being seen at all (England and Mughal, 2019; National Audit Office, 2018; National Audit Office, 2023). Although it is widely recognised that early intervention and treatment of anxiety is beneficial to the patient and the efficient use of resources (Brakoulias et al., 2017; Blakey et al., 2017; Lydiard et al., 1996), intervention is often triggered on presentation of symptoms severe enough to necessitate immediate action. The goal of optimal mental health care therefore faces several challenges: deeper understanding of the developmental mechanisms predicting anxiety, recognition of symptoms early enough to enable intervention at the appropriate time, and sufficient healthcare resources to minimise waiting times on presentation of symptoms. Against this backdrop, understanding early developmental influences on interoceptive processing and its association with mental health is of critical importance, potentially facilitating earlier risk assessment, diagnosis and intervention (Murphy, Brewer, Catmur, and Bird, 2017b).

Several studies of interoception in older children provide insights into the development of interoception and its relationship with emotion regulation and mental health. For example, 9- to 12-year-old children demonstrate a positive correlation between scores on self-reported scales of interoceptive awareness and emotion regulation (Cheung et al., 2023). Oldroyd et al. (2019) found a relationship between attachment styles and interoception in older children and adolescents, with the children whose mothers are less accepting of negative emotions (consistent with disorganised attachment) demonstrating lower congruence between their physiological arousal and self-reported emotional state (Oldroyd et al., 2019). Interestingly, the opposite relationship was not observed, i.e. higher acceptance of negative emotion in mothers did not predict greater congruence in their children. Importantly, this study indicates a relationship between interoceptive abilities in older children and their early social environment, highlighting the potential enduring effects of early environment on the relationship between interoception and mental health later on. This evidence supports the theoretical arguments for interoceptive processing development being rooted in early social interactions (Atzil et al., 2018; Fotopoulou and Tsakiris, 2017a; Filippetti, 2021). Like adults, children aged 8 to 11 years with symptoms of panic disorder have been shown to exhibit high interoceptive accuracy on a heartbeat tracking task (Eley et al., 2004). At this age, children's self-reported interoceptive accuracy is negatively associated with internalising behaviours, a potential marker of depressive symptoms (Brand et al., 2024). By adolescence, the relationship between interoception and emotion regulation discussed in relation to adults in Section 1.2.3, appears to be established. For example, in 13-year-olds, De Witte et al. (2016) observed higher interoceptive accuracy related to reduced maladaptive emotion regulation behaviours, such as rumination, while higher HRV related to greater use of external emotional regulatory behaviours, such as support seeking (De Witte et al., 2016). The authors also examined the relationship between these measures and parental psychopathology, observing that increased HRV but decreased interoceptive accuracy in the children were associated with maternal internalising behaviours and child externalising emotion regulation, suggesting a possible protective role for higher HRV. Similarly, higher vagal tone was associated with better emotion regulation among 14-year-olds (Braet and Braet, 2024), consistent with the adult literature (see Section 1.2.3).

Taken together, the studies discussed in this section provide glimpses into the evolving relationship between interoception, emotion regulation and mental health in childhood. While they do not provide a complete picture, they do indicate the concurrent and potential long-term impact and importance of the early environment in the development of interoceptive processing, by relating children's interoceptive abilities and mental health with some factors in their caregivers and early experiences, supporting the theoretical approaches to interoceptive processing development discussed in 1.3.1 above. The research reviewed so far also highlights some similarities between the relationships among interoception, emotion regulation, and mental health in children, and those described in adulthood in Section 1.2.3. The link between interoception and mental health in childhood is already evident from this literature. Yet, these studies highlight the need for further research on interoception from a developmental perspective to address gaps in our understanding of the developmental trajectories of dimension of interoception and provide a more comprehensive understanding. In the next section I will provide a summary of the research questions I am seeking to address within this thesis, based on the gaps revealed in this literature review.

1.5 Summary and research questions

In the sections above, I have outlined the current state-of-the-art on interoception and what is known of its relationship with mental health and anxiety. I then considered interoception from a developmental perspective and examined the factors that could be influencing its development. This review has revealed several gaps in the current literature, which I will summarise here.

Firstly, there is very little empirical evidence of interoceptive processing in infancy. It is therefore unclear when the relationship between interoceptive processing and mental health begins to develop and whether early experiences influence both the development of interoceptive processing and an infant's risk for psychopathology. While several studies indicate relationships between caregiver mental health, caregiver interoception and mental health and interoceptive abilities in children, these issues are yet to be addressed in infancy. From these gaps, several questions emerge, which I seek to address in this thesis. Firstly, do caregiver interoception and/or their mental health influence the development of interoceptive processing in their infants and, secondly, to what degree does any such influence endure through childhood? To investigate these broad questions, I considered several more specific questions in the studies I present in this thesis:

1. How do caregiver mental health and interoception relate to caregiver behaviour in naturalistic caregiver-infant dyadic interactions? (Study 1)

2. How does touch influence physiological evidence of emotion processing in infants? (Study 2a)

3. Do caregiver mental health and/or interoception relate to caregiver behaviour in a structured interaction task? (Study 2b and 2c)

4. Do caregiver mental health and/or interoception relate to infant vagal tone? (Study 2c)

5. Do caregiver interoception and/or mental health relate to child interoception and anxiety risk? (Study 3)

In addition to these research gaps, a further limitation that I identified from reviewing the literature is the use of inconsistent terminology and the use of several different models which refer to different specific processes, particularly in the field of interoception. Table 1.1 provides a glossary to clarify the definitions and terminology I have used within this thesis.

To answer these questions outlined above, I conducted 5 studies which will be presented in Chapters 3, 4 and 5. Studies 1, 2a, 2b and 2c focused on caregivers' interactions with their 6 - 8-month-old infants, while Study 3 focused on caregivers and their children aged 5 - 14 years old. In Study 1, I examined caregivers' use of touch and the contingency of their behaviours

Table 1.1
Glossary

Glossary	
Caregiver Contingency	The degree to which caregivers' behavioural responses to their infants' cues match the apparent needs of the infant. This ability depends on caregivers' mentalizing skills to be able to infer their infant's needs from their behavioural cues (Crucianelli, 2018).
Electrodermal activity, EDA	Changes in the electrical conductance of the skin associated with changes in the sweat glands. Electrodermal activity is associated with changes in emotional state (Critchley, 2002).
Heart rate variability, HRV	The degree of variation between the time period of each heartbeat. The root mean square of successive differences, RMSSD, is one measure of HRV and is considered a proxy for vagal tone (Laborde, 2017).
Interoception	The processing of internal bodily signals (Brewer, 2021).
Interoceptive accuracy	Either 1) the objective accuracy in detecting internal bodily sensations, such as one's own heartbeat as measured in a heartbeat detection task (Garfinkel, 2015) or 2) a score on the Interoceptive Accuracy Scale, a self-report questionnaire (Murphy, 2019). Both definitions are used in this thesis, with the definition specified each time.
Interoceptive attention	The degree to which one focuses on interoceptive sensations, as measured by the Interoceptive Attention Scale, IATS, a self-report questionnaire (Gabriele 2022).
Interoceptive awareness	Metacognitive awareness of interoceptive accuracy (Garfinkel, 2015).
Interoceptive sensibility	Self-perceived dispositional tendency to be internally self-focused and interoceptively cognisant (Garfinkel, 2015). Interoceptive sensibility is measured via a confidence rating in Study 5.
Vagal tone	The activity of the vagus nerve, part of the parasympathetic nervous system, in regulating several bodily functions, such as heart rate and digestion. High vagal tone is associated with better emotion regulation ability (Porges, 1992).

when interacting with their infants. I then explored the relationships between these factors and caregivers' self-reported anxiety and interoceptive abilities. In Study 2, I explored the relationships between caregiver mental health and interoception and their interactive behaviours with their infant alongside physiological evidence of interoceptive processing in response to emotional experience in the infants. In Study 2a, I examined changes to infant physiology during emotion processing and had planned on comparing these changes, between groups, with and without affective touch from the caregiver (this study was halted due to the COVID-19 lockdowns). Study 2b focused on caregiver behaviour in a structured task, again alongside their self-reported anxiety and depression levels and interoceptive abilities. This study was conducted online during lockdown. Study 2c repeated study 2b in a laboratory setting, and included an analysis of infant vagal tone. Finally, Study 3 considered whether caregiver anxiety and interoceptive abilities related to the interoceptive abilities of their children and whether this was also associated with the child's susceptibility to anxiety. In conducting these studies, I examined different dimensions of interoception. I used different models of interoception described in 1.2.2 above, depending on the circumstances of each study. In Studies 1, 2b and 2c, I have adopted Murphy's two factor model which distinguishes between interoceptive accuracy and interoceptive attention. These dimensions are measured separately, by detailed self-report (Gabriele et al., n.d.; Murphy et al., 2020), enabling comparison between accuracy and attention, in order to explore whether either or both of these dimensions are important factors in caregivers' mental health and/or behaviour towards their infant. More practically, these measures are also suitable for use when conducting studies remotely. In study 3, which was conducted in person, I adopted Garfinkels' model of interoception (Garfinkel et al., 2015). I assessed interoceptive accuracy and sensibility, using a modified heartbeat detection task (Schaan et al., 2019) and a self-report confidence measure, respectively, in accordance with this model. The different models and measures of interoception I chose to use are summarised in the glossary above. As suggested by the findings of the literature review (e.g. Nord and Garfinkel, 2022), the studies I conducted consider different dimensions of interoception and their relationship with mental health and behaviour, adopting multi-method designs that combine behavioural, physiological, and self-reported methods with caregivers, their infants and children. In the next chapter I provide a detailed overview of the methods and measures used.

Chapter 2

Methods and Measures

2.1 Introduction and rationale

The studies within this thesis are concerned with factors influencing the early development of interoceptive processing, in the context of the infant's future mental health, given the relationship between interoception and mental health discussed in detail in Chapter 1. My research is based on theoretical proposals that caregiver-infant interactions are at the core of the infants' emerging interoceptive processing (Atzil et al., 2018; Filippetti, 2021; Fotopoulou and Tsakiris, 2017b). In order to examine the developmental origins of the relationship between anxiety and interoception, in this thesis I have adopted a comprehensive multi-method approach that allowed me to measure both caregivers' and infants' factors in a variety of ways. Specifically, the methods I employed comprise physiological measures, behavioural observations and self-reported measures, to provide a rich illustration of factors influencing dyadic interactions between the infant and their caregiver in the early months of life. This chapter provides an overview of the methods and measures that I have adopted in my PhD.

The chapter begins with a description of physiological measures that have been used for the investigation of self-regulation and interoceptive processing in the literature. For the purpose of the studies in this thesis, I have employed measures of electrodermal activity (EDA, Study 2a), along with measures extracted from recorded cardiac data, including heart rate (Study 2a), heart rate variability and vagal tone (Study 2c). Previously, these measures have been used as indicators of arousal (Wass et al., 2015), or as evidence of interoceptive processing (Paulus, 2013), or as a marker, in the case of vagal tone, of emotion regulation abilities (Porges, 1992;

Porges, 1995b; Porges, 2001).

Next, behavioural observations of caregiver-infant interactions are considered. The studies presented in this thesis make use of several tasks to examine caregiver and infant behaviour, such as parent-infant interactions using traditional observations (Study 1) as well as a new adapted version of the Still Face Paradigm (Studies 2b and 2c) (Tronick et al., 1978). In this section of Chapter 2, I also provide a comprehensive overview of how these behaviours can be systematically assessed using established behavioural coding methods, such as that used in Study 1 (see Chapter 3).

Finally, self-report measures are discussed. The specific influence of the primary caregiver is assessed to add a final dimension to the emerging picture of the development of interoceptive processing in relation to the infant's early environment. The studies presented in my thesis therefore examine caregivers' self-reported anxiety levels (Studies 1, 2b, 2c and 3), dimensions of their interoceptive abilities (Study 1, 2b and 2c), and their perception of their infant's temperament (Study 2b and 2c).

By using this multi-method approach to examine factors influencing early dyadic interaction, this thesis builds on previous theoretical and empirical studies of the early development of interoceptive processing, thus providing a more comprehensive picture of the important relationships between caregivers' behaviour, mental health and infant physiology. The findings of this thesis will contribute to the body of research investigating the relationship between caregiver and child mental health and the precise mechanisms behind that relationship, taking interoception into account. A summary of methods and measures used in the studies in this thesis is provided in Table 2.1.

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2.2 Physiological measures

2.2.1 Rationale

Physiological information is very important in the consideration of the early development of interoceptive processing in infants and its relationship with mental health, for several reasons. Firstly, as discussed in 1.2.1, interoception relays information on our physiological state between

Table 2.1
Summary of Methods and Measures

Study	Method	Measure
1	Self-report questionnaires	Caregiver anxiety (Stat Trait Anxiety Index) Caregiver interoceptive accuracy (Interoceptive Accuracy Scale) Caregiver interoceptive attention (Interoceptive Attention Scale)
	Behavioural observation of caregiver-infant interactions in free play and story tasks	Caregiver contingency Caregiver use of instrumental, affectionate and playful touch
2a	Physiological measures, electrocardiogram (ECG) and electrodermal activity (EDA)	Changes in infant heart rate (ECG) Changes in electrodermal activity (EDA)
2b	Self-report questionnaires	Caregiver anxiety (Generalized Anxiety Disorder - 7) Caregiver depression (Patient Health Questionnaire -9) Caregiver interoceptive accuracy (Interoceptive Accuracy Scale) Caregiver interoceptive attention (Interoceptive Attention Scale) Infant temperament (IBQ – R, IBQ – VS - R)
	Behavioural observation of caregivers in an interactive task (online)	Duration of still face period in a modified Still Face Paradigm
2c	Self-report questionnaires	Anxiety (GAD-7) Depression (PHQ-9) Interoceptive Accuracy Interoceptive Attention Infant temperament (IBQ)
	Behavioural observation of caregivers in an interactive task (laboratory)	Duration of still face period in a modified Still Face Paradigm
3	Self report	Anxiety (GAD-7) Interoceptive accuracy (Heartbeat detection task) Threat detection task
	Physiological	Heart Rate Jumping Jack paradigm

the body and brain, for the purpose of homeostatic balance (Craig, 2009). While much of this activity takes place subconsciously, some interoceptive activity relates to the sensation and perception of changes in state that require our attention, such as hunger, thirst and tiredness. As well as helping us to attend to our physiological needs, perception of our physiological state also contributes to our emotional state (Critchley and Garfinkel, 2017; Tsakiris and Critchley, 2016). Understanding the perception of physiological state can, therefore, help to inform our understanding of emotion and emotion regulation. Secondly, as discussed in detail in 1.2.3, physiological responses characterise many mental health difficulties, such as the experience of anxiety, panic and stress (Hoehn-Saric and McLeod, 2000). However, even at sub-clinical levels, the body's healthy, normal response to perceived threat involves physiological changes. The body's physiological response to a perceived threat or danger is often referred to as the 'fight or flight' response (Porges, 2001). This response is driven by activity in the sympathetic nervous system and is characterised by increased heart rate and blood pressure, increased respiration, pupil dilation and sweating (Hoehn-Saric and McLeod, 2000). Measurement of these changes can, therefore, assist in the observation of response to specific stimuli, as in the study of emotional responses including anxiety. Finally, physiological changes have been established as measures in research relating to interoceptive processing and emotion regulation (Porges, 1995b; Garfinkel et al., 2015). The polyvagal theory, discussed in detail in 1.2.3, describes how the parasympathetic nervous system, specifically activation of the vagus nerve, plays an important role in restoring balance in response to activation of the sympathetic nervous system, as in the fight or flight response (Porges, 1992; Porges et al., 1994; Porges, 2021).

Since this thesis seeks to understand factors influencing the development of interoceptive processing and its relationship with anxiety in infancy, several of these measures are utilised in the studies presented in the chapters that follow. Study 2a examines infants' heart rate changes and electrodermal activity while observing different facial expressions, while study 2c considers infants' vagal tone in relation to their caregivers' mental health, interoception and interactive behaviour. While such measures were initially used with adults (e.g.Cheng et al., 2022), more recently, methodological studies have demonstrated their suitability for use with children and infants, opening up vast opportunities in developmental research (e.g. Ham and Tronick, 2008;Huffman et al., 1998 Wass, 2021). Methods for collecting electrodermal, cardiac, and vagal tone measure, including their specific use with infants, are all discussed in detail below.

2.2.2 Electrodermal activity

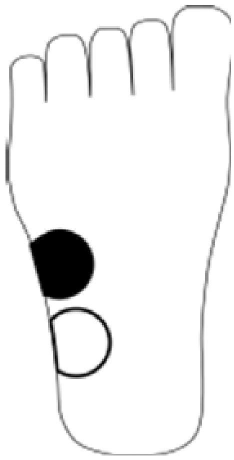
Electrodermal activity (EDA) measures changes in the natural electrical conductance of the skin. Skin conductance increases as we sweat and sweat gland activity is triggered by the sympathetic nervous system responsible for the fight or flight response (Posada-Quintero and Chon, 2020). While there are two kinds of sweat glands in the human body, apocrine and eccrine, it is the eccrine glands that are primarily responsible for thermoregulation. Despite this primary function, eccrine glands on the plantar surfaces of the hands and feet have been found to be more responsive to psychological than thermal stimuli (Ellaway et al., 2010). Electrodermal activity comprises both tonic and phasic changes. Tonic changes relate to the natural changes of physiological state during the course of a day, whereas phasic changes are more rapid, occurring in response to emotions such as surprise or fear. Phasic changes are observable in real time, with the duration of spikes typically less than two seconds (Benedek and Kaernbach, 2010). EDA is considered to be an indicator of emotional arousal, such as anxiety, and is therefore a useful measure in the study of emotion processing and regulation (Critchley, 2002). Changes to skin conductance have been measured in studies of emotion for over 100 years, since the French psychologist, Georges Fere, first observed that emotional reactions are accompanied by electrical changes in the human body in the late nineteenth century (Peterson, 1908). Since then, empirical studies have made use of changes to skin conductance as a quick and simple, non-invasive measure of arousal in psychophysiology (e.g. Christopoulos et al., 2019, Critchley, 2002, Storm, 2008, Fusar-Poli et al., 2009), as well as clinical studies (Novak, 2019).

EDA in adults is usually recorded via sensors placed on the fingers or hand. Two electrodes are required, connected to a recording device. A harmless low electrical current is then applied while the resistance is measured, enabling its inverse, conductance, to be calculated (Posada-Quintero and Chon, 2020). Despite its ease of use in laboratory studies, collection of EDA data requires several important considerations - especially in the context of infant research. Firstly, this measure is highly sensitive to movement artifact as EDA data can be contaminated by noise if the participant is prone to movements (Ham and Tronick, 2008). This is especially important to consider in studies involving young infants, as they are generally unable to follow instructions and remain still. Secondly, it is essential to ensure that the task duration aligns with the short attention spans of infants. This is important, since electrodermal activity recordings comprise both short, tonic, fluctuations and longer, phasic fluctuations, meaning recordings must be sufficiently long in order to extract meaningful data that takes both of these components into account (Ham and Tronick, 2008; Wass et al., 2018). Finally, electrodes must provide firm adhesion while minimising irritation to delicate infant skin. Ham and Tronick, (2008) addressed all three of these issues, i.e. movement sensitivity, recording duration and suitability of adhesive electrodes, when they proposed and validated a procedure for the measurement of skin conductance in 5-month-old infants. In the first study to record infant skin conductance in an interactive task, the authors elicited a skin conductance response proportional to arousal levels triggered by clap startle (Ham and Tronick, 2008). Firstly, the authors found that a reliable signal could be obtained from the plantar surface of the infant's foot. This positioning may help to address movement artifacts as it moves the distraction caused by the presence of the electrodes a little further out of sight for the infant. Yet, care is still required to prevent the infant from kicking or scraping off the electrodes. In this sense, a sock or bandage placed over the electrodes was found to be helpful. Giving some time to the infant to familiarise themselves with the sensation of the electrodes, and introducing some simple distraction with toys and soothing from the caregiver, also enabled the infant's attention to be captured elsewhere and reduced movement artifacts. Secondly, to maximise valid data within a short time frame, the authors used multiple trials of very short tasks. This strategy also enabled tasks recordings containing movements to be identified and removed from the data easily. By introducing short breaks in between tasks, the infant could be soothed if needed and re-engaged between trials. Finally, the authors provided recommendations on electrodes to ensure that the infant's sensitive skin is considered by the researchers. Several manufacturers produce disposable electrodes with low tack, so as not to irritate delicate skin. The down side of using low-tack electrodes is that they tend not to stay in place for long, but, with infant studies, this is not usually a problem, since recordings need to be very brief, either to keep the infant's attention or to be completed while the infant remains still (see above). Paediatric electrodes also allow for positioning to be checked regularly, e.g. between trials, in case the infant's movements have disturbed them.

Due to previous practical difficulties and a perception that collecting EDA data in infants is very difficult (Ham and Tronick, 2008), early results involving EDA from studies of infants were few, so the methodological changes recommended by Ham and Tronick (2008) represented a key milestone in the use of EDA measures with infants. Indeed, EDA has since been used in several studies of infant arousal, following these recommendations. For example, infant EDA responses have been found to differ in the processing of happy versus angry faces (Nava et al., 2016). Differences in the duration of increases versus decreases in arousal have also been observed when EDA data was examined alongside heart rate changes and head movements from 12-month-old infants while they observed static and dynamic images (Wass et al., 2018). Increases and decreases in arousal were measured, along with their duration, with arousal associated with negative emotions lasting longer than changes in response to positive emotions. Skin conductance is also considered an indication of pain during procedures such as routine heel pricking in newborns (Munsters et al., 2012). Hernes et al. (2002) provided a useful longitudinal overview of changes to skin conductance in the first year of life, indicating spontaneous skin conductance response amplitudes and wavelengths both increased significantly in the first 10 weeks of life, then stabilised up to one year of age (Hernes, 2002). Low skin conductance has also been associated with poor regulation of aggression in infancy and more aggressive behaviour in toddlerhood (Baker et al., 2013). In these studies, the plantar surface of the infants' foot was used to successfully collect both tonic and phasic EDA data, as per Ham and Tronick (2008)'s method (see Figure 2.1). Such studies emphasise the useful role of EDA data in studies of infant physiological arousal in relation to emotion processing and stress.

In Study 1 (Chapter 3), I conducted a pilot test recording of physiological arousal in infants to examine emotion processing in response to different facial expressions. EDA was recorded, along with heart rate data, while infants observed videos depicting differing emotional expressions. Variations in EDA responses to the different emotions were to be compared, between groups, with one group receiving affective touch from the caregiver and the other group not, in order to observe whether affective touch influenced the physiological response to the infant's processing of emotions. However, due to laboratory closure during the COVID-19 pandemic, this study was halted before completion.

Figure 2.1
Positioning of Paediatric Electrodermal Electrodes



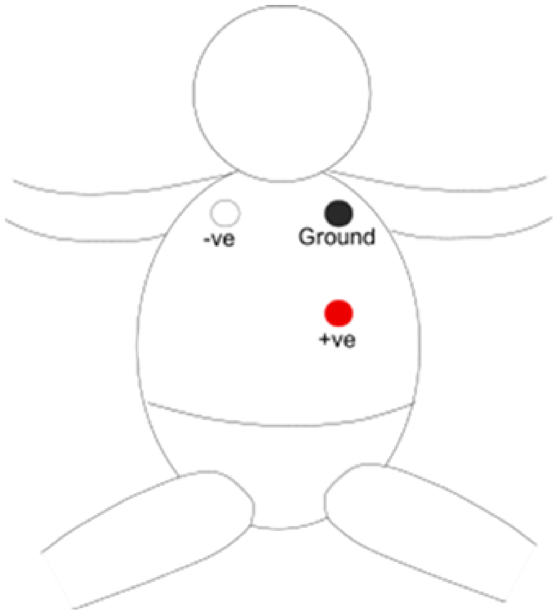
Note: Positions of electrodermal electrodes proposed by Ham and Tronick (2008), on the plantar surface of the foot. Electrodes are then secured with an elasticated bandage.

2.2.3 Cardiac measures

The connection between heart rate measures and anxiety within the field of interoception stands as a crucial area for investigation, offering insights into how our body's responses relate to our subjective experience of physiological states. By studying changes in heart rate and individual differences in ability to detect and interpret such changes, we can better understand how our body's automatic functions connect to the conscious perception of these physiological sensations. This link is particularly apparent in psychiatric conditions, such as anxiety, although more research is needed to understand the specific link between anxiety and interoception across different domains (see Adams et al., 2022 for a review and meta-analysis). Sensations relating to heart rate changes are common when experiencing worrying thoughts, anxiety, excitement, etc. at sub-clinical levels, as well as in clinical presentations of anxiety, with increased heart rate associated with stress and anxious arousal (Hoehn-Saric et al., n.d.).

To collect cardiac data, a cardiac waveform is produced, usually via electrocardiogram, ECG, a non-invasive technique which has been in use for well over a century. Medical doctor and physiologist, Einthoven, presented the first images of the heart's waveform in 1893. Since then, the ECG equipment has shrunk considerably enabling cardiac activity to be easily monitored and studied in both medical and research settings (AlGhatrif and Lindsay, 2012; Billman, 2011). ECG uses sensors placed on the skin to detect electrical signals from the heart, enabling the heart's rhythm to be observed while conducting a variety of different activities. Figure 2.2 shows a typical ECG setup used to record infant cardiac data. Alternatively, a simple recording of heart rate can also be obtained by use of a pulse oximeter. This relies on a measure of fluctuating blood oxygen levels obtained by sending infrared light through the capillaries via a clip, usually applied to the participant's or patient's finger.

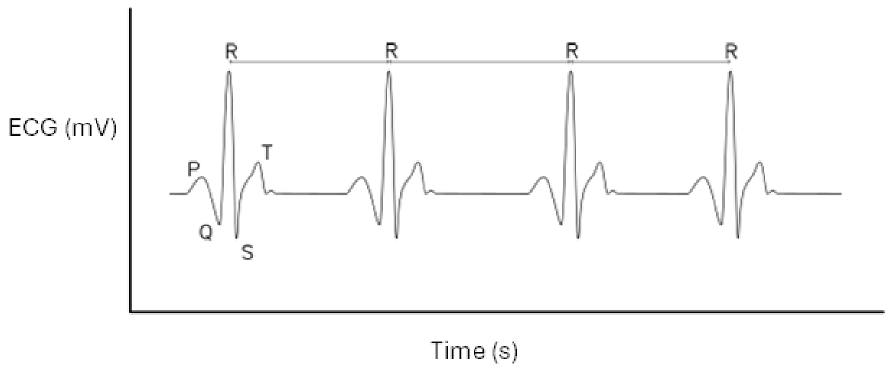
Figure 2.2
Paediatric Lead-II Electrocardiogram (ECG) Setup



Note: Positions of positive (usually red), negative (usually white) and ground (usually black) electrodes in a conventional paediatric Lead-II ECG setup are displayed.

A healthy waveform comprises three primary components. Firstly, the P wave depicts depolarisation of the atria. This is followed by the QRS complex, characterised by the R peaks, the maximum amplitude in the QRS component, representing depolarisation of the ventricles. Finally, the T wave represents repolarisation of the ventricles. The time period between the R peaks is referred to as the inter-beat interval, or IBI. Each heartbeat is characterised by two phases, diastole and systole. Diastole refers to the period when the heart relaxes and fills with blood (the period between T and R on the waveform), while systole refers to the contraction and emptying of the heart (R - T) on the waveform). Figure 2.3 provides a diagram of this basic waveform, highlighting the R peaks and the IBI, as well as diastolic and systolic phases. Once a basic waveform has been obtained, the heart rate, i.e. the number of heartbeats per minute, as well as further metrics, such as heart rate variability (HRV), can be extracted.

Figure 2.3
Components of the Electrocardiogram (ECG) Output



Note: Components of the electrocardiogram (ECG) waveform are indicated along with R – R intervals, used in the extraction of heart rate variability.

In a cardiac waveform, HRV refers to variability of the time between the R peaks. HRV can be calculated in several different ways (see F. Shaffer and Ginsberg, 2017 for a comprehensive overview). These methods are primarily based in either the time domain, in which the amount of variability in a time period is quantified, or frequency domain, in which the distribution into ultra-low, very low, low and high frequency bands is estimated. Measures of HRV are typically extracted from ultra-short (less than 5 minutes), short (approximately 5 minutes), or 24-hour cardiac recordings. Importantly, HRV recordings of different duration are not comparable with one another, due to differences in slower, underlying influences on their values (F. Shaffer and Ginsberg, 2017). For example, short duration recordings are dominated by increases and decreases in blood pressure during respiration, due to the baroreflex, whereas longer duration recordings, such as 24-hour recordings are subject to circadian rhythms, body temperature, metabolism and sleep. As a result, longer recordings typically result in higher HRV. Several time domain measures of HRV relate to standard deviations of intervals between components of the ECG trace. The distance between heartbeats, the R-R or N-N intervals, is often associated with the variation of these intervals over time, defined by the metrics of SDRR (standard deviation of R-R interval) and SDNN (standard deviation of N-N interval), respectively. Additionally, the pNN50 refers to the proportion of successive NN intervals that differ by more than fifty milliseconds, while the NN50 refers to the number of adjacent NN intervals differing by more than 50ms. As these metrics demonstrate, there are many ways to assess HRV from and ECG recording (see F. Shaffer and Ginsberg, 2017 for an overview of metrics and norms). One measure of heart rate variability is the RMSSD, or the root mean square of successive differences, in which the differences in successive IBIs in a time period are calculated and squared. The mean is then calculated before the square root of the mean is calculated. RMSSD correlates strongly with pNN50 over longer recordings and high frequency power in frequency domain metrics of HRV (F. Shaffer and Ginsberg, 2017). Use of RMSSD is widespread and offers two particular advantages. Firstly, it is suitable for use in short-duration recordings, which is particularly useful in studies with infants. Secondly, RMSSD is considered to also represent vagal tone (Laborde et al., 2017) as described in 2.2.4, below. In the frequency domain, Fast Fourier transformation enables HRV to be resolved into its ultra low, very low, low and high frequency rhythms. Whichever metric of HRV one adopts, Shaffer and Ginsberg (2017) pointed out the importance of context in the measurement and interpretation of HRV data, since different recording periods, detection methods and sampling frequencies are all associated with differences in the resulting HRV (F. Shaffer and Ginsberg, 2017).

HRV is influenced by autonomic nervous system functioning, thus relating to stress arousal and emotion regulation, with higher HRV associated with better adaptive ability to cope with stress (F. Shaffer and Ginsberg, 2017). Studies have found that high frequency heart-rate variability in adults relates to emotion processing, (Gaebler et al., 2013, Howells et al., 2014, Lane et al., 2009), emotion regulation, (Lane et al., 2009; Shahrestani et al., 2014), and response to stress, (Cheng et al., 2022), demonstrating the potential importance of heart rate variability in emotional development early in life. HRV has been examined alongside emotional wellbeing in many studies with adults (e.g. Beauchaine and Thayer, 2015, Cheng et al., 2022, Gorman and Sloan, 2000, Porges, 1995a, Porges, 2021), leading to a consensus that higher resting HRV is associated with better emotional wellbeing (Cheng et al., 2022, F. Shaffer and Ginsberg, 2017). Similarly, lower HRV has been observed in those individuals diagnosed with anxiety disorders, (Chalmers et al., 2014, Cheng et al., 2022, Beauchaine and Thayer, 2015), with high frequency HRV being recognised as a direct biomarker of mental ill-health (Beauchaine and Thayer, 2015).

While these studies of HRV relate primarily to adults, more recent (although sparse) developmental studies relating to stress arousal suggest that HRV is also a valid indicator of developmental psychopathology in infants and children (e.g. Cainelli et al., 2022, Dierckx et al., 2009, Fiskum et al., 2018, Shahrestani et al., 2014). Collection of ECG data from infants is relatively straightforward, due to its non-invasive nature and short duration. However, when using ECG to collect cardiac data from infants, some additional considerations must be taken, as for the collection of EDA data described above. Firstly, low-tack infant electrodes must be used, to minimise skin irritation and maximise ease of removal. Secondly, a vest or top can be worn over the electrodes to prevent the infant from trying to remove them. Finally, study design needs to consider that the infant might need a short while to get used to the electrodes being in place, requiring some soothing and/or distraction before the study begins.

Infant HRV has been used in developmental research studies investigating a variety of topics. For example, it has been found to be positively correlated with several aspects of cognitive development, as measured on the Bayley Mental Development Index, MDI, a measure designed to assess cognition through evaluation of sensory-perception, knowledge, memory, problem solving, and early language, with higher variability associated with more advanced development (Richards and Cameron, 1989). Infant HRV is also considered to be a useful metric of physical wellbeing, both in medical observations of, for example, post-operative pain (e.g. Lavanga et al., 2021, Verweij et al., 2021), indication of sepsis (e.g. Joshi et al., 2020, Leon et al., 2021) or developmental progress of neonates (e.g. de Souza Filho et al., 2021, Recher et al., 2021). However, two important factors make infant HRV an extremely important measure when considering early development of interoceptive processing in the context of early environment and mental health. Firstly, maternal psychopathology has been associated with infant HR and HRV, with historical diagnosis of a psychiatric disorder, postnatal anxiety and postnatal depression all associated with increased mean HR and reduced HRV (Dierckx et al., 2009). Secondly, HRV in infants has been shown to be adaptable. For example, studies have indicated that infant HRV can be increased by skin-to-skin contact, (Cong et al., 2009), affective touch (Della Longa et al., 2019) and massage (S. L. Smith et al., 2013). Critically, these forms of touch are fundamental aspects of early caregiver-infant interaction. Together, these results relating higher HRV with improved outcomes, alongside its relationship with early environment and its malleability, highlight the importance of infant HRV when examining early emotional development against a backdrop of caregiver mental health and early dyadic interaction.

Cardiac data is utilised in several of the studies in this thesis. Study 2a (Chapter 3) examines changes to infant heart rate in relation to processing of different emotions. Study 2c considers differences in infant heart rate variability and vagal tone and their association with caregiver's interoception, mental health and behaviour in an interactive task. These studies make use of ECG in a lab setting. Study 5 relies on simple heart rate data collected via a pulse oximeter to record changes in heart rate in children and their caregivers. Absolute and perceived changes are then compared, to provide a measure of interoceptive accuracy in both the caregiver and the child, before considering whether this relates to the child's performance in a threat-detection task or their caregiver's anxiety levels.

2.2.4 Vagal tone

The vagus nerve plays a central role in conveying interoceptive information from the body to the brain. The vagus nerve is a fundamental cranial nerve and the primary nerve of the parasympathetic nervous system. Vagal activation is involved in the subconscious regulation of bodily systems such as heart rate, respiration, appetite and thermoregulation, important in homeostatic maintenance and physical health. However, this physiological regulation also serves a crucial purpose in how we respond to threat. The parasympathetic nervous system works to restore a state calm, i.e. to perform the reverse action of the sympathetic nervous system, activated in the fight or flight response discussed in 1.2.3. Vagus nerve activity is referred to as vagal tone, an indicator of the adaptive performance of the vagus nerve, with higher vagal tone believed to relate to better emotion regulation abilities as well as better physical health (Porges, 1995b). Recording baseline vagal tone, even in the absence of specific stimuli, therefore provides a useful measure of one's regulatory abilities. Vagal tone describes the performance of the vagus nerve in terms of the relationship between HRV, as discussed in 2.2.3 above, and Respiratory Sinus Arrhythmia (RSA). RSA refers to the variation of heart rate synchronised with the inspiration and expiration phases of the breath. The R-R interval on an ECG, see 2.2.3, is shortened during inspiration and prolonged during expiration.

Porges' Polyvagal Theory (Porges, 1995b) offers an explanation of the importance of vagal tone from an evolutionary perspective on the mammalian nervous system, stating that physiological state limits our range of behaviour and psychological experience, important for basic survival in the face of physical threat. Porges compared vagal regulation of the stress response to a brake, which is released when we are required to undergo a physiological response to threat, as in fight or flight. Building on the Polyvagal Theory, Porges also proposed a mechanism for quantifying the performance of the vagus nerve in this role, so called cardiac vagal tone (Porges, 1995a). RSA has an identifiable underlying neural mechanism reflecting ventral vagal control of the heart (Yasuma and Hayano, 2004), so by measuring vagal function, it becomes possible to observe evidence of autonomic adjustments to threat and safety (Porges, 2021).

One simple way to assess vagal tone is to extract RMSSD data from an ECG trace, as described in 2.2.3 above, since RMSSD is considered to represent vagal tone as it accounts for variation due to RSA (Laborde et al., 2017). However, the contribution of RSA to RMSSD has also been described as uncertain by others (F. Shaffer and Ginsberg, 2017). While RMSSD, a measure of heart rate variability, provides a convenient representation of vagal tone, it is important to highlight here that HRV and vagal tone are not identical. Vagal tone refers specifically to functioning of the vagus nerve and, although it contributes to the regulation of heart rate, HRV in its own right is also a distinct biomarker of physical health and adaptive autonomic regulation. As discussed next, however, use of vagal tone as a measure for research purposes, especially in infants, is not as straightforward as it might appear.

Extracting RMSSD from an ECG as a measure of vagal tone is relatively simple across developmental ages. It is non-invasive, it does not require any verbal or cognitive skills, and methods for the collection of cardiac data via ECG in young infants are well-established and frequently used, as previously discussed (See Section 2.2.3). However, despite the ease of data collection, the analysis and interpretation of vagal tone is more complex and have been the subject of debate (e.g. Laborde et al., 2017, Li et al., 2019, Poliakova et al., 2014). Methods for calculating vagal tone have been proposed by both Porges (Porges, 1995a) and Grossman, (Grossman and Taylor, 2007), resulting in some debate over its use and interpretation in psychology research (Poliakova et al., 2014). Specifically, the source of the debate appears to be the differing theoretical approaches to the role of vagal tone, developed in response to different research topics (Laborde et al., 2017). While Porges' Polyvagal Theory is concerned with the relationship between vagal tone and social and emotional functioning, Grossman's biological behaviour model, (Gross and Thompson, 2007) focuses on the role of vagal tone in the synchronisation of respiratory and cardiovascular processes during metabolic and behavioural changes. Other theoretical approaches include the neurovisceral integration model (Thayer and Lane, 2000), the resonance frequency model (Fisher and Lehrer, 2022), and the psychophysiological coherence model (McCraty, 2011), (see Laborde et al., 2017 for a more detailed theoretical review). These differing theories have led to different ways of analysing vagal tone, in both the time domain, for example by looking at the root mean square of successive differences (RMSSD) of the inter-beat interval (IBI) between R peaks, (F. Shaffer and Ginsberg, 2017), as well as in the frequency domain, by spectral analysis, (Li et al., 2019). In addition to the variety of approaches used by researchers to calculating and analysing vagal tone, a further important consideration is the sensitivity of HRV to methodological variation and a number of individual factors that are difficult to control for, including diet, medication, caffeine, nicotine, alcohol consumption and physical activity, as well as current physiological state, in terms of when the subject last ate, for example (Laborde et al., 2017). When recording vagal tone data from infants, of course not of all these individual factors become relevant. However, working with infants brings additional complications. For example, infants vagal tone increases during feeding and falls shortly afterwards (Porges, 1992). It is therefore important to control experimental conditions around feeding times. Infant vagal tone is also related to infant temperament, with higher baseline vagal tone relating to fewer observed negative behaviours (Huffman et al., 1998). While this helps us to understand the early development of vagal tone in relation to socio-emotional development, when temperament is not the focus of the study, variation of vagal tone in relation to temperament needs to be taken into account. In addition, vagal tone appears to mature in the first six months of life (T. Field et al., 1995). This means that observed differences of vagal tone in very young infants must be interpreted with caution, since it would be difficult to disentangle whether the differences were due to experimental conditions and response to stimuli or individual differences in brain development. The variety of vagal tone measures utilised in the literature to date, combined with the methodological sensitivity of HRV described above, highlights the need for caution and replication in the interpretation of results as well as for consensus regarding reporting methods (Quintana et al., 2016).

Despite these different theoretical approaches to vagal tone, consistent empirical findings suggest that vagal tone is a useful metric in the study of interoceptive processing and emotional wellbeing in both adults and children (e.g. Porges et al., 1994; Santucci et al., 2008). In recent years, many studies have related vagal tone to aspects of childhood emotional wellbeing. For example, research suggests that vagal tone relates to stress levels in preschoolers (Messerli-Bürgy et al., 2020), childhood emotion regulation strategies, (Santucci et al., 2008) and childhood behaviour (Calkins, 1997). Earlier in life, infant vagal tone appears open to some influence from the caregiver, for example from maternal mental health (T. Field et al., 1995; Somers et al., 2021), with lower infant vagal tone observed in infants of depressed mothers (Somers et al., 2021). In a between-groups longitudinal study, vagal tone in infants increased between the ages of 3- and 6- months of age. However, this same increase was not observed in infants of depressed mothers (T. Field et al., 1995). Infant vagal tone has also been associated with parental sensitivity, with greater parental sensitivity associated with higher infant vagal tone (Rattaz et al., 2023). Converging evidence suggests that maternal postpartum behaviour towards newborns is associated with the vagal tone of the newborn (Feldman and Eidelman, 2007). Caregivers' behaviour has also been associated with their own vagal tone, with higher caregiver vagal tone relating to increased emotional support being provided to their preschool offspring (Ravindran et al., 2022). Taken together, these findings suggest that the association between infant vagal tone and caregiver's vagal tone are at least partly accounted for by differences in caregivers' behaviour in dyadic interactions.

Given these early influences, it is essential to consider how the resulting developing vagal tone in the infant further affects the infant's development, in terms of their future emotion regulation abilities and longer-term wellbeing. It can therefore be seen that infant vagal tone is an extremely important early measure of their social and emotional development, with the potential to highlight differences in the development of interoceptive processing. Building on this idea, Study 2c in this thesis (Chapter 4), investigates associations between infant vagal tone, caregiver-infant interactive behaviour, caregiver interoception and caregiver mental health.

2.3 Behavioural observations

2.3.1 Rationale

Direct observation of behaviour has provided an important foundation for studies with preverbal infants and their relationship with their caregiver (e.g. Beebe et al., 2010;Crucianelli and Filippetti, 2018; Kaitz et al., 2010 Puura et al., 2019; Seifer and Schiller, 1995). Behavioural observations are important in studies with infants for several reasons. Firstly, we cannot ask infants to follow specific task instructions, nor to tell us how they feel, so instead we need to observe what they do and how they interact with others in naturalistic or structured tasks. Secondly, the infant's early environment has been associated with important developmental characteristics, such as attachment (Beebe et al., 2010; Pauli-Pott and Mertesacker, 2009), highlighting the importance of early caregiver-infant interactions for infant social, emotional, and cognitive development. Thirdly, observing interactions between infants and their caregivers has enabled characteristics of caregiver behaviour, such as caregiver sensitivity, to be observed, measured, and examined in relation to other developmental outcomes (Beebe and Steele, 2013; Seifer and Schiller, 1995). The development of interoceptive processing, central to this thesis, is proposed to begin very early in life, with environmental factors interacting in this process and shaping its development (Atzil et al., 2018; Filippetti, 2021; Fotopoulou and Tsakiris, 2017a). To examine factors influencing interoceptive processing development, it is therefore essential to observe caregiver-infant interactions.

2.3.2 Caregiver-infant dyadic interactions

Observation of dyadic interaction

Previous studies of caregiver-infant interaction have highlighted how the infant must learn to recognise their own needs and communicate those needs to their caregiver, while the caregiver must get to know her infant in order to adapt to their individual characteristics, resulting in each learning from the other, as they gradually develop their own unique style of communication (e.g. Beebe et al., 2010;Crucianelli and Filippetti, 2018; Kaitz et al., 2010 Puura et al., 2019; Seifer and Schiller, 1995). During dyadic interactions, a broad range of behaviours contribute to caregiver-infant exchanges and communication, including vocalisations, facial expressions, directed gaze, eye contact, physical movements, joint attention, touch, etc. In addition, infants display their emotions through different behaviours, such as bodily movements, in addition to facial expressions and vocalisations (Weinberg and Tronick, 1994; Weinberg et al., 1999). Opportunities for the development of interactive behaviour are plentiful and varied in the early months of life, since the infant is completely dependent on their primary caregiver. Bathing, changing, feeding, and playing are just some examples of the daily activities that facilitate the use of different forms of communication from both parties. Importantly, both the caregiver and the infant must use such behaviours to communicate clearly with the other. For example, the infant must gain the attention of their caregiver in order to have their physical needs met, e.g. to be fed, to be clean, to be dry, to be soothed, etc. For the infant, these interactions are a source of considerable information about the surrounding environment and about their own physiological state, but what the infant learns through these interactions depends on whether their needs are met appropriately. For example, an infant whose cues are correctly interpreted by their caregiver, who then responds appropriately, will have a very different learning experience from an infant whose cues go unnoticed or are repeatedly misinterpreted. Thus, the actions of each party within the dyad are interconnected and influenced by the other's behaviour, which, in turn, is affected by their personality traits, characteristics, and emotional state. This dynamic interaction shapes the creation of their distinctive way of interacting and makes each dyad unique. This chain of interactive behaviour has been described as a 'dance' (Cerezo et al., 2021), with each party taking turns to respond to the previous behaviour of the other. This dance has been proposed to inform future behaviours and interactions (Fogel, 2011; Fotopoulou and Tsakiris, 2017a; Mundy and Newell, 2007).

By examining behaviour, we can gain insight into the emotional state of the infant. This is considered a valuable source of information in the search for evidence of interoceptive processing in the absence of verbal communication. Therefore, behavioural observation is an essential research tool for the studies presented here, where the role of caregiver mental health and interoception are considered as influencing factors on the behaviours demonstrated by both caregiver and infant. In addition, employing a suitable method to quantify these behaviours, as well as the overall quality of the interactions, becomes imperative. Hereafter, I will discuss different methods of observing and quantifying interactive behaviour.

For quantitative research purposes, it is important to be able to compare observed behaviour between participants. For this reason, specific tasks can be used to direct certain activities, thus eliciting behaviours which can be quantified and compared between dyads. Observations can be categorised as either naturalistic, designed to replicate the dyad's natural style of interaction, or controlled, designed to elicit specific behaviours. While naturalistic tasks enable observation of realistic behaviours with high ecological validity, there is also a risk that the objectives of the study go unmet, should the participant not demonstrate the behaviours of interest. In addition, measurement validity may be compromised by the presence of many complex or extraneous factors, such as interruptions from siblings, pets or visitors, or distractions from the equipment used, such as laptops (Connors and Glenn, 2006). On the other hand, structured tasks are designed with specific behaviours of interest in mind, enable precise measurement, variable manipulation and experimental control (e.g. Ainsworth and Bell, 1970; Gagne et al., 2011; Tronick et al., 1978). However, structured tasks do not necessarily reflect the behaviour that would occur naturally, perhaps compromising their ecological validity. In addition, simply knowing they are being watched is enough to cause some participants to change their behaviour, due to shyness, fear of judgement, or desirability bias (Abels et al., 2017). Asking caregivers to allow us to observe how they behave and interact with their infant is a particularly sensitive subject, and the pressure associated with having one's parenting skills observed could easily introduce behavioural modifications. To mitigate for this factor, it is important to provide clear information regarding the purpose of the study and to remind participants that their parental skill is not being the subject of judgement, but that the behaviours observed are contributing to a pool of data from which trends might be extracted. Despite these limitations, observing dyadic interactions is a necessary step in understanding the relationship between early interactions and the physiological and self-reported measures of interest within this thesis, providing a rich set of data that could not be collected in any other way. In addition to considering the task itself as either naturalistic or structured, the same can be said about the environment in which the task takes place. Attempting to observe the natural behaviours of an unstructured task in a laboratory setting will not provide a perfect reflection of the natural environment. The unusual surroundings can be distracting for the infant, while caregivers are reminded that they are being observed. For example, caregivers who know their behaviours are being recorded use a higher frequency of behaviours than those who do not (Abels et al., 2017). By contrast, observing caregivers and infants in their home environment can reduce distractions and discomfort for the infant and the caregiver (e.g. Crucianelli et al., 2019), but come at a cost of reduced experimental control. Just as naturalistic tasks can be undertaken in the laboratory or the home, so can structured tasks. While some studies involve researchers visiting participants at home, the use of webcams and the internet allow for studies to be undertaken without a researcher even present, such as those conducted online via the ChildrenHelpingScience.com website. This has been very useful during COVID-19 related lockdowns, which affected several of the studies in this thesis. Given these considerations, the choice between structured and naturalistic tasks, therefore, often involves a compromise between ecological and measurement validity (Kominsky et al., 2022). Next, I will discuss examples of naturalistic observations in infant studies, followed by the use of structured observations.

Naturalistic observations

One might expect the most natural of all behaviours should be elicited while caregivers and their infants interact in a 'free play' task, i.e. with no structure at all. Here, the caregiver and infant communicate with one another as they normally would, and their communication methods can be observed without any influence from performing tasks under instruction. However, for some, the lack of direction in an unfamiliar setting such as a laboratory setting could be uncomfortable. In addition, for research purposes, there are no guarantees that a specific question about a particular aspect of interactive communication could be answered. For example, if one is interested in different kinds of touching behaviours and the pair engages in free play on the floor, there is no guarantee that any opportunities for touch will arise within the time frame of the study. Of course, this does not necessarily mean that touch is not a big part of natural communication in this particular dyad, but simply that it did not occur on this occasion. Despite this risk, observing an unstructured interaction does provide an opportunity to observe the unique communication style that is developing within each dyad, providing a valuable richness to the data collection. A semi-structured approach can also be taken, whereby a simple task is requested, but still within a naturalistic environment. Examples include asking caregiver-infant dyads to share a story (e.g. Crucianelli et al., 2019), or play a familiar game, such as 'peek-a-boo,' (e.g. Miller and Commons, n.d.). Variations to the positioning of caregiver and infant can further be utilised to encourage different categories of interaction. For example, with an infant on their caregiver's lap, it is likely that one can observe the frequency of different kinds of touch, while, with the infant in a highchair facing their caregiver, one can observe and quantify eye contact, joint attention or directed gaze. In a direct comparison of a structured versus free play task with toddlers, Kwon et al. (2013) observed differences in both caregiver and toddler behaviours between the two tasks. Toddlers used a broader variety of verbal communications and language in the free task, while caregivers demonstrated reduced negative parenting behaviours in free play than the structured task (Kwon et al., 2013). This distinction is important when selecting tasks for observational studies. Taking this into consideration, Study 1 (Chapter 3) utilises both a 'free play' observation alongside a more structured 'story time' observation, to provide an opportunity to observe both the natural style of each dyad and the specific behaviours of interest, touch and caregiver contingency.

Structured observations

In contrast to naturalistic tasks, several structured tasks have been developed and validated, to provide standardisation between studies and to replicate specific situations or elicit specific behaviours in the participants. Perhaps one of the most famous structured tasks in developmental research is the Strange Situation (Ainsworth and Bell, 1970), which represents the basis for assessing attachment styles. In this task, the infant's behaviour is observed while a series of separations and reunions between the infant, the caregiver and a stranger take place. First, the infant and caregiver enter the room and play together. They are then joined by the stranger, before the caregiver leaves the room. Next, the caregiver returns and the stranger leaves. This is followed by the caregiver leaving the infant alone in the room. The stranger returns, before, finally, the caregiver returns. The infant's responses are observed throughout, to determine attachment styles. The Strange Situation has become a popular task, with attachment styles being studied in relation to many aspects of caregiver behaviour and child development (Beebe and Steele, 2013; Koehn and Kerns, 2018; Pauli-Pott and Mertesacker, 2009). For example, caregiver and infant expressions of emotion when the infant is 4-, 8- and 12-months-old were found to be associated with attachment style according to the Strange Situation at 18months (Pauli-Pott and Mertesacker, 2009), with greater caregiver openness of emotion associated with secure attachment. Another commonly used set of structured tasks are The Laboratory Temperament Assessment Battery, Lat-TAB. The Lab-TAB was initially developed for use with young children, (Gagne et al., 2011), while an infant version was subsequently developed (Planalp et al., 2017). The battery of tasks in the Lab-TAB are designed to replicate everyday situations likely to elicit a reaction across five dimensions of temperament: fearfulness, anger proneness, joy/pleasure, interest/persistence and activity level. Examples include the Stranger Approach task in the fearfulness domain, whereby a stranger (a previously unseen researcher) enters the room and slowly approaches the infant. In the use of such tasks, the infant's behavioural response is recorded and coded after each of the tasks. The Lab-TAB tasked have been used in the study of many aspects of development, such as behavioural inhibition (Faísca et al., 2021) and emotional expression differences in autism spectrum (Macari et al., 2018).

Another structured task widely used to investigate infant emotion processing and regulation is the Still Face Paradigm, SFP, (Tronick et al., 1978), in which the caregiver abruptly stops interacting with their infant for a fixed time period. This provides an opportunity to examine how the infant responds when their communication needs are no longer being met, shedding light on infants' abilities to process and regulate their emotional state. Since its development in the late 1970s, the SFP has been used in many studies of infant emotion regulation (see Mesman et al., 2009 for a meta-analysis). In the SFP, the caregiver is instructed to interact as they would normally do with their infant. When they have their infant's attention, the caregiver is instructed to suddenly adopt a fixed, neutral expression for a fixed period. This is followed by a reunion period, where the caregiver resumes interacting with their infant. Changes in infant behaviour observed consistently across studies using the SFP are now referred to as the "Still Face effect" and include increased negative affect, reduced positive affect, increased gaze aversion (Mesman et al., 2009). Some carry-over effects are also usually observed at the beginning of the reunion phase of the task, and these have been the subject of research attention in relation to emotion regulation (Mesman et al., 2009). In two of the studies in this thesis, I asked caregivers to engage in a novel modification to the Still Face Paradigm (Tronick et al., 1978), which I named the Responsive Still Face Paradigm, RSFP. In this case, the focus is on the caregiver's behaviour rather than that of the infant. In this modification, caregivers were asked to hold the still face period for an undefined period of time (in contrast to the fixed still face period in the classic version), then to re-engage with their infant when they chose to do so, based on what felt right to them. This task is designed to provide a measure of the caregiver's comfort when resisting interacting with their infant. This could relate to a naturally occurring situation when the caregiver is engaged with a task and they see or hear their infant communicating some need to them. In this situation, the caregiver would need to decide how quickly to respond to their infant, given their engagement in another task. As explained in more detail in Chapter 4, in Studies 2b and 2c, I expected the duration of the still face held by the caregiver during the RSFP to be associated to their own interoceptive abilities and mental health.

Within this thesis, both naturalistic and structured tasks have been used in the observation of caregiver-infant interactive behaviour. Study 1 asked caregivers to engage in two naturalistic tasks. Firstly, caregivers were asked to engage in 'free play' with their infant within their own homes. This was followed by a 'story time' task where caregivers were asked to read a familiar book with their infant. In order to maintain measurement validity, a strict coding protocol was developed in order to measure the duration of difference categories of touch (see Chapter 4, Studie 2b and 2c). These were observed and coded offline, enabling frame by frame analysis. Studies 2b and 2c made use of a novel structured task, the Responsive Still Face Paradigm, described above. This was conducted in the familiar home environment in Study 2b, and in the Essex Babylab in Study 2c. Data from these behavioural observations were then examined in relation to caregiver interoception and mental health measures, to explore whether behaviour differed with different anxiety and depression scores and interoceptive abilities. The studies within this thesis were completed, in part, during the COVID-19 pandemic. During this time, laboratories were closed due to social distancing regulations in the UK, forcing data collection to be undertaken online. Thankfully, several platforms, such as the ChildrenHelpingScience.com website, were developed for this specific purpose and Studies 1 (Chapter 3) and 2b (Chapter 4) utilised this platform to enable data collection during COVID-19 lockdowns.

Behavioural coding of caregiver-infant interactions

Once interactive behaviour has been captured, the task of coding the individual behaviours of interest begins. Several coding systems have been developed for coding dyadic interactions, each of these serving different purposes. Methods for quantifying the infants' behaviours can include simple labelling and counting of the number of occurrences of a certain behaviour, as in the AFFEX coding system (Izard et al., 1980), grading the intensity of a behaviour during each time interval (e.g. Morris et al., 2011), or counting units of time spent on each particular behaviour, as in the Mother-Infant Touch Scale, MITS (Crucianelli et al., 2019).

One specific measure of interest within this thesis is caregiver contingency, described in detail in Section 1.3. Contingency refers to the adaptive appropriateness of the caregiver's response to their infant, which requires the caregiver to demonstrate their understanding of their infant's emotional and physiological states in order to respond to their needs appropriately (Crucianelli et al., 2019). The method used for assessing caregiver contingency builds on the method described in the development of the Mother Infant Touch Scale, MITS (Crucianelli et al., 2019). The MITS was developed to examine both caregiver and infant behaviours, considering both the caregiver and infant as active agents within the interaction. Working on the assumption that the infant is directing the interaction based on their own need, the caregiver's response to the infant's cue is assessed in terms of whether it is appropriate to the infant's need, i.e. contingent, or not. Therefore, as well as analysing the frequency and variety of behaviours employed by the caregiver, such as talking to, looking at, and touching their infant, one can also categorise their behaviour as either contingent, or non-contingent, in response to the needs demonstrated by the infant. For example, an infant might stretch or move towards a toy. A contingent response would be to help the infant to reach for the toy, or to hand it to the infant. A non-contingent response, however, could be to distract the infant with some other behaviour, such as a tickle, or a different object from the one the infant was reaching for. Once a caregiver responds to their infant's cue in a contingent way, the infant's need is satisfied and their change in behaviour can be interpreted to confirm contingency of the caregiver's response. However, should the caregiver respond in a non-contingent way, the infant's need would remain unmet and their subsequent behaviour may highlight, for example, their strategies for clarifying their need, e.g. continuing to vocalise, moving towards the toy of interest, etc. In this latter scenario, the caregiver might make a second attempt to respond contingently, thus creating a chain of interaction until the infant's need is met. The overall contingency of the caregiver's behaviour can then be assessed by calculating the proportion of caregiver responses observed as contingent, in terms of number of occurrences, units of time, or proportion of total time the behaviour was observed. In the studies presented here, I was primarily interested in caregivers' responses to the communications demonstrated by their infant. The contingency of the caregiver's response was therefore assessed, along with the variety of touch employed by the caregiver, given the relationship between touch and interoception discussed in Chapter 1. Following the suggestion by Crucianelli et al. (2019), I considered the infant as the instigator of interactions. The caregiver's response to the infant's cue was then assessed in terms of how well it matched the (observable) need of the infant and considered contingent, if it satisfied the infant's need. Study 1 (Chapter 3) used a measure of caregiver contingency and use of touch based on the MITS (Crucianelli et al., 2019).

2.4 Self-reported measures

2.4.1 Rationale

Self-reported information provides a vast pool of data from which many psychology studies extract statistics and trends. However, the use of self-report measures has undergone considerable scrutiny, highlighting several potential pitfalls including bias, the role of self-awareness, considerations of self-presentation, and individual differences in tolerance thresholds (Haeffel and Howard, 2010). Despite these limitations, self-reported measures are often essential, offering a practical method for gathering data that may otherwise be impossible to collect, such as attitudes and beliefs. Similarly, understanding individual perceptions of cognitive and somatic experiences, such as anxiety symptoms, requires the participant to tell us about their own experience. This can be done via questionnaires such as the State Trait Anxiety Inventory (Spielberger, 1983) or the Generalised Anxiety Disorder Assesment-7 (GAD-7, Spitzer et al., 2006).

When collected alongside physiological and behavioural data in a multi-method design, the use of self-reported data becomes even more meaningful, providing a more comprehensive picture of the processes of interest. In addition, this approach also enables us to consider the role of the perception demonstrated by participants when answering questions. For example, when comparing caregivers' reports of their infants' behaviour, one must be mindful of the limitations and variation between how caregivers perceive and report their data. However, when considered alongside data on their physiological arousal and mental health, factors influencing how caregivers perceive their infants' behaviour can be examined more deeply, for example to explore whether caregiver depression levels relate to a more negative perception of their infant behaviour.

The studies presented in this thesis rely on several self-reported measures. I used the Interoceptive Accuracy Scale, IAS (Murphy et al., 2020 alongside the Interoceptive Attention Scale, IATS (Gabriele et al., 2022), in Studies 1, 2b and 2c. In study 3, I used a heartbeat detection task (Schaan et al., 2019) alongside a measure of interoceptive sensibility (Garfinkel et al., 2015). I also employed several mental health scales; the State-Trait Anxiety Inventory (STAI; Spielberger et al., 1970) was used in Study 1, the Generalised Anxiety Disorder Assesment-7 (GAD-7, Spitzer et al., 2006) was used in Studies 2b, 2c and 3 and I included a depression screening, the Patient Health Questionnaire-9, or PHQ-9 (Kroenke et al., 2001) in Studies 2b and 2c. I employed the revised Infant Behaviour Questionnaire, IBQ-R (Gartstein and Rothbart, 2003), a caregiver-reported scale of infant's temperament to quantify caregivers' perceptions of their infants' behaviours (Studies 2b and 2c). These measures are all discussed in detail below.

2.4.2 Measuring interoception in adults

Growing understanding of interoception has resulted in recent calls for new, updated measures of interoception, taking the different dimensions into account (Desmedt, Luminet, Maurage, and Corneille, 2023; Garfinkel et al., 2022). Although differences in the underlying processes involved in different tasks and different dimensions of interoception are becoming more widely understood, there is still ongoing wider debate on the definition of interoception as well as residual confusion from the historic use of different terminology (Desmedt et al., 2018; Desmedt, Luminet, Walentynowicz, and Corneille, 2023; Desmedt, Luminet, Maurage, and Corneille, 2023; Murphy, 2023). The relationship between mental health and interoception provides a good example of the importance of using appropriate measures. For example, considerable literature is dedicated to the role of interoception in a variety of mental health conditions (Khalsa et al., 2018), yet associations between scores on heartbeat detection tasks do not consistently relate to anxiety (Adams et al., 2022). It therefore behoves researchers in the field to be as precise as possible when deciding exactly what to measure and how to measure it, as well as to take great care in their interpretation of results.

While self-report data may be relatively straightforward to collect, the interpretation of self-reported interoceptive data has been the subject of much discussion and debate (Desmedt, Luminet, Maurage, and Corneille, 2023). Ongoing debates and developments in the field of interoception were discussed at length in Section 1.2. For the purpose of this thesis, I focused on dimensions of interoception that relate to how *accurately* an individual can detect their internal sensations, how *confident* they are in their perception of these sensations, and how much *attention* they pay to these. Interoceptive accuracy, confidence and attention most closely relate to the dimensions proposed in the *Three-Dimensional Model* of interoception (Garfinkel and Critchley, 2013) and the *Factorial Model* (Murphy, Bird, and Catmur, 2019). In the three-dimensional model, interoceptive accuracy refers to the objective performance in a heartbeat detection task, while interoceptive sensibility considers how confident the participant feels about their ability to detect their heartbeat (Garfinkel and Critchley, 2013). In the Factorial Model, accuracy and attention refer to self-reported measures obtained via questionnaires. These dimensions are discussed in more detail in Section 1.2.2. In the present chapter, I expand on methodological considerations surrounding the measures that have been developed to capture these dimensions of interoception.

Behavioural tasks to measure interoceptive accuracy

Initial attempts to measure and quantify interoceptive accuracy initially focused on the heartbeat, for largely practical reasons (e.g. Schandry, 1981; Wiens et al., 2000). Perception of heartbeats is usually familiar to adults and older children, enabling the straightforward instruction of attending to and reporting on one's heartbeat to be followed. Reported perception of heartbeats can then be compared with actual heart activity, recorded with a pulse oximeter or via ECG (see Section 2.2.3), as in the well-established heartbeat detection task, (Schandry, 1981). Heartbeat detection ability has previously been associated with the intensity of emotional experience (Wiens et al., 2000) and so heartbeat detection ability would appear important when considering both anxiety susceptibility (Hoehn-Saric et al., n.d.) and dimensions of interoception (Garfinkel et al., 2015). It is important to acknowledge that converging evidence suggests interoception is not unitary, i.e. that cardiac, respiratory and gastric interoception are not all equal (see Chapter 1). As the perception of heartbeats and interpretation of the changes in heart rate are important characteristics in the experience of anxiety (Hoehn-Saric et al., n.d.), a focus on cardiac interoception is justified here, since this thesis is focused on the relationship between interoception and anxiety.

Several different methods to measure *interoceptive accuracy* have been proposed to date, based on heartbeat detection (Schandry, 1981) and heartbeat discrimination (Brener and Kluvitse, 2018; Katkin et al., 1983; Whitehead et al., 1977). One of the first studies developed to quantify heartbeat detection abilities is that by Schandry (1981). Schandry set out to examine differences in the experience of emotion in relation to individual differences in the ability to detect internal sensations. The Schandry heartbeat counting task (Schandry, 1981) requires participants to count their heartbeat for periods of 25, 35 and 45 seconds, with rest periods in between. Participants are instructed not to take their pulse, but to focus on internal sensations that may be related to their heart. Simultaneously, their actual heartbeat is recorded via ECG or pulse oximeter, to enable a direct comparison between participants' perceived number of heartbeats and their actual number of heartbeats within each period. The difference between actual and perceived heartbeats is then divided by the actual number of heartbeats to produce an error score between 0 and 1. The closer to 1, the lower the difference between the two, indicating higher accuracy, while scores close to zero reflect poorer accuracy.

Despite widespread use, the Schandry task does have several limitations. Firstly, our knowledge of heart rates means that we have an expectation of when our heart should be beating. Studies have found this expectation to have an influence on the results of heartbeat counting, due to participants including different sensations they feel when they expect their heart to beat or reporting a number of heartbeats they believe to be appropriate, even if they don't actually feel those heartbeats (Ferentzi et al., 2018; Körmendi et al., 2021). A second limitation relates to the interaction between cognitive and interoceptive processes involved when concentrating, counting and reporting on the sensation of heartbeats, since it is difficult to separate these contributing processes (Ferentzi et al., 2018). In addition, methodological differences concerning variation in the precise instructions provided to participants have also been questioned

(Desmedt et al., 2018; Schillings et al., 2022). To help overcome these limitations, studies have undertaken a more strict approach, with very precise instructions to only count the heartbeats actually perceived, has led to lower, but perhaps more reliable, scores of interoceptive accuracy (Desmedt et al., 2018).

At a similar time to the development of Schandry's heartbeat counting task, an alternative approach was developed to measure interoceptive accuracy. In the heartbeat discrimination task or Whitehead task, participants are asked to discriminate whether auditory tones or visual signals are either synchronous or asynchronous with their heartbeat (Katkin et al., 1983; Whitehead et al., 1977). Several variations of this discrimination task have since been used, all requiring the participant to detect synchronicity between perceptual cues and their heartbeat. Variations include, for example, the use of different numbers of forced choice procedure, or a continuous tone (e.g. Brener and Ring, 2016; Brener and Kluvitse, 2018). In addition to the heartbeat counting task and the heartbeat discrimination task, other tasks have involved heartbeat tapping, adjustment and perturbation methods (e.g.Carroll and Whellock, 1980; Gannon, 1980; Khalsa, Rudrauf, Sandesara, et al., 2009). For example, Carroll et al. (1980) asked participants to adjust the pulse of a flashing image to match their heartbeat, but turning a dial. Gannon et al. (1980) asked participants to estimate the interval between heartbeats by adjusting an on-screen vertical line. Khalsa et al. (2009) administered adrenaline to induce changes to heart rate, before asking participants to report on the change they experienced. More recently, the use of wearable devices and mobile phones has facilitated further development of the measurement of cardiac interoception, such as with the Cardiac Elevation Detection Task, in which participants receive regular automated requests to report on whether they feel their heart rate is higher or lower than previously, along with a confidence rating (Ponzo et al., 2021).

Understandably, the emergence of different measures of cardiac interoception has brought with it much discussion over the meaning and interpretation of such data (e.g. Adams et al., 2022; Desmedt et al., 2018; Garfinkel et al., 2015; Hickman et al., 2020). A meta-analysis of twenty-two studies indicated only a small relationship between task scores of heartbeat detection and heartbeat discrimination, suggesting that these methods are not interchangeable and that caution is necessary when comparing results between studies utilising different methods of measuring cardiac interoception (Hickman et al., 2020). These recent developments have led to the understanding of interoception becoming more refined. However, researchers must still apply great care in their selection of measures and interpretation of results, since different dimensions of interoception, such as accuracy, awareness and sensibility, measured with different methods, such as objective versus self-report, have been suggested to rely on different underlying processes (Desmedt et al., 2018;Desmedt, Luminet, Maurage, and Corneille, 2023). For example, according to these suggestions, the measurement of interoceptive accuracy using heartbeat detection, as referred to by the three-dimensional model (Garfinkel et al., 2015), will not necessarily produce a comparable result with scores on a self-report questionnaire asking participants how accurate they believe their perception of bodily sensations is, as in the Interoceptive Accuracy Scale (IAS) Murphy, Bird, and Catmur, 2019), even though both measures are referred to as 'interoceptive accuracy.' Despite these discrepancies, self-report measured of interoception do offer an insight into individuals' perception of their own bodily sensations, offering a practical measure for use when an objective measure, e.g. heartbeat detection tasks, is not practical.

Self-reported interoceptive abilities

Several self-report questionnaires have been designed to measure interoception by asking participants about their bodily sensations. Self-report measures offer a practical alternative when objective measures of interoception, such as the heartbeat detection tasks described above, are not possible. However, due to a lack of rigorous psychometric testing, early examples of such subjective measures of bodily sensation and internal signals were the subject of criticism (Mehling et al., 2009). Since then several scales have been rigorously tested and published, and are now used frequently in psychology research. There is an important point to note, however; non-significant correlations have been observed between different self-report measures of interoception (Vig et al., 2022) and between subjective and objective measures (Garfinkel et al., 2015; Vig et al., 2022). This has led to further debate in the field of interoception research, which has gradually led to greater specificity in the terminology used and improved understanding of the underlying processes involved (e.g. Desmedt, Luminet, Maurage, and Corneille, 2023; Murphy, 2023). As a result, it has been suggested that future studies of interoception make use of multiple measures, encompassing implicit and explicit measures, in order to enable a more specific understanding of findings (Nord and Garfinkel, 2022). Please see Section 1.2 for a comprehensive discussion of these issues.

Porges' Body Perception Questionnaire, BPQ, is one example of a frequently-used self-report measure (Porges et al., 1993). The BPQ was originally developed to assess the subjective experiences of the function and reactivity of target organs related to activation by the autonomic nervous system. With a total of 122 items, the length of the original BPQ triggered subsequent development of short (26 item) and very-short (12 item) forms, which focus on the body awareness subscales of the original questionnaire (Cabrera et al., 2018). Participants are asked to rate their awareness of sensations such as 'Muscle tension in my arms and legs' on a 5 point scale from never (1) to always (5). Good internal reliability was reported, with categorical omega scores of .96 for the short form, BPQ-SF and .91 for the very short form, BPQ-VSF.

The Multidimensional Assessment of Interoceptive Awareness, MAIA (Mehling et al., 2012), was developed in response to increasingly complex theoretical approaches to body awareness. A thirty-two item questionnaire, the MAIA provides body awareness scores across eight categories, including noticing, attention regulation, emotional awareness, body listening and trusting. (Mehling et al., 2012). In the MAIA, participants rate statements such as 'I try to ignore pain' or 'I notice where in my body I am comfortable' on a 6-point Likert scale, from 'Never' (0) to Always (5). Due to low internal consistency, i.e. the MAIA was subsequently refined resulting in publication of the MAIA-2, which includes 5 additional items leading to improved psychometric properties over the original questionnaire, (Mehling et al., 2018; Rogowska et al., 2023), i.e. internal consistency of .76.

Murphy et al.'s two-by-two factorial model of interoception focuses on the dissociation between interoceptive awareness and attention, (Murphy, Bird, and Catmur, 2019), leading to the development of two new carefully worded questionnaires. These scales differentiate between an individuals' awareness of their bodily signals and sensations and the attention they pay to those signals, namely the Interoceptive Awareness Scale, IAS, (Murphy et al., 2020) and the Interoceptive Attention Scale, IATS, (Gabriele et al., 2022). The IAS comprises 21 items concerning the consistent accuracy of perception of sensation, e.g. 'I can always accurately perceive when I am thirsty.' Participants are asked to rate items on a 5 point Likert scale from 'strongly agree' (5) to 'strongly disagree' (1), with total scores ranging from 21 to 105. Higher scores indicate greater self-reported interoceptive accuracy. The items of the IAS are based on sensations previously reported as interoceptive, or relating to activation of the insula, one of the brain regions associated with the processing of interoceptive information. The authors reported good internal consistency, with Cronbach's alpha of .90. The IAS was reported to demonstrate a significant correlation with an objective measure of cardiac interoception, a heartbeat counting task (Schandry, 1981), but not with scores on the BPQ. This indicated a valid distinction between interoceptive accuracy and interoceptive attention, leading to the subsequent development of the IATS. The IATS follows a similar structure to the IAS, again asking participants to rate 21 items using a 5 point Likert scale. In the IATS, the items are worded to focus on how much attention is paid to sensations, e.g. 'Most of the time my attention is focused on whether I am breathing fast.' Good internal consistency was reported, with Cronbach's alpha of .91 and no relationship between the IATS and IAS was found, supporting their dissociation.

More recently, the Three-domain Interoceptive Sensations Questionnaire, THISQ, has been developed with the objective of distinguishing between cardiac, gastric and respiratory interoception Vlemincx et al., 2023). The THISQ asks participants to rate 18 items, six in each of the three domains, describing their perception of bodily sensations (e.g. 'When I am moderately physically active I feel that my heart beats fast') on a 5 point Likert scale, from 'never' to 'always.' Good internal consistency was reported, with Cronbach's alpha for the total score of .84, with values of .71 for Cardiorespiratory Activation, .82 for Cardiorespiratory Deactivation, and .75 for Gastroesophageal Sensations.

Researchers are often interested in how confident participants are in their interpretation of bodily sensations. This is referred to as *interoceptive sensibility* in Garfinkel's three-dimensional model of interoception (Garfinkel et al., 2015). Porges' BPQ, described above, is suggested as a measure of interoceptive sensibility. However, a straightforward confidence rating is also suggested as an alternative measure of interoceptive sensibility within this model.

Questionnaires relating to interoception form an important part of the data collected within the studies presented in this thesis. Studies 1 (Chapter 3), 2b and 2c (Chapter 4) focused on the relationships between caregiver interoception and caregiver mental health and examined associations between these factors and differences in caregiver-infant interactive behaviour. In addition, Study 2b extended Studies 2 and 3 by further examining infant cardiac data and vagal tone alongside caregiver interoception, to examine whether the same caregivers' factors included in Studies 2 and 3 relate to their infant's physiological responses.

2.4.3 Measuring anxiety and depression in adults

Several questionnaires have been developed to assess anxiety and depression in adults. While some of these scales can be used for diagnostic purposes, such as the Generalised Anxiety Disorder Assessment - 7 (GAD-7, Spitzer et al., 2006), or Patient Health Questionnaire, PHQ-9 (Kroenke et al., 2001), others have been developed to detect sub-clinical symptoms of mental health issues within the research environment (such as the State-Trait Anxiety Inventory, Spielberger, 1983).

The GAD-7 requires the participant to think about how they have felt over the previous two weeks, then rate the frequency of symptoms experienced on a Likert scale questionnaire, with each item scored from 0 (not at all) up to 3 (nearly every day). The GAD-7 scale combines questions on physiological (e.g. restlessness, nervousness), cognitive (e.g. worrying) and emotional (e.g. feeling afraid) aspects of anxiety to produce a GAD-7 score out of 21 based on 7 items. Clinical cut-offs are 5, 10 and 15 for mild, moderate and severe anxiety, respectively. Despite its brevity, the GAD-7 has been found to correlate with the State-Trait Anxiety Inventory, STAI, described below (Manzoni et al., 2018. Spitzer et al. (2006) reported Cronbach's alpha of .92 for the GAD-7 scale as a measure of generalised anxiety in clinical samples and, subsequently, Lowe et al. (2008) reported a Cronbach's alpha of .89 when the scale is used in the general population Löwe et al., n.d.), indicating good internal validity. Despite its clinical origins, in a research setting, the GAD-7 anxiety scale offers two particular strengths. Firstly, it is quick to administer and can be used easily in studies alongside other measures, both in person and remotely. Secondly, the focus on current symptom presentation enables a direct comparison between the anxiety experienced over the previous two weeks and the behaviour and other measures observed during the same visit to the lab.

In contrast to the clinically-derived GAD-7, one of the most well-known scales for measuring anxiety in psychology research is the State-Trait Anxiety Inventory (STAI; Spielberger et al., 1970), which has been used in countless psychology studies since the 1970s. The STAI differentiates between two dimensions of anxiety: the temporary state of anxiety, based on how the participant is feeling right now, or state anxiety, and the longer term tendency towards anxiety described as trait anxiety, based on how they feel more generally. In psychology studies, this differentiation can be useful to take account of short-term, temporary fluctuations or consider more stable, longer term tendencies. The STAI is a 40-item self-report questionnaire, with 20 items each dedicated to measure current anxiety (state anxiety), asking participants to rate how they *currently* feel, versus how they *generally* feel (trait anxiety). Participants are asked to rate their symptoms based on a 4-point scale from "not at all" to "very much so". Scores above 40 are considered to indicate clinical levels of anxiety. Studies of the psychometric properties of the STAI have reported good internal consistency, test-retest reliability and (Ortuño-Sierra et al., 2016; Spielberger et al., 1970).

Scales of anxiety used in psychological research, such as the STAI, can be very different from scales of anxiety used in a clinical setting, such as the widely used GAD-7, (Spitzer et al., 2006). GAD-7 uses the frequency of current symptoms over a two week period, in terms of the number of days a patient is affected by specific symptoms, along with a measure of disruption to daily function caused, in order to gauge severity. The STAI, on the other hand, relies on a subjective estimate of strength of a variety of perceived feelings and sensations which relies much more on individual perception. Of course, reports of symptom frequency in the GAD-7 are also subject to patient perception, but by being directed to count the number of days they have been affected (such as in the GAD-7), participants are able to provide a very specific picture of their symptom frequency and how debilitating their condition is when compared with how strong a patient might consider their feelings to be (such as in the STAI).

As for anxiety, when it comes to choosing a scale for measuring depression symptoms, several choices are available. The Patient Health Questionnaire-9, or PHQ-9 (Kroenke et al., 2001) scale works similarly to the GAD-7, asking participants to rate symptom frequency during the previous two-week period, but is based on 9 items to produce a score out of 27. Clinical cut offs are 5, 10, 15 and 20 for mild, moderate, moderately severe and severe depression, respectively. In clinical settings, clinicians regularly screen for anxiety together with low mood, or depression. The PHQ-9 is used most frequently for initial screening of depression, both within the NHS and private sector healthcare. Like the GAD-7 for anxiety, the PHQ-9 collects information regarding symptom frequency over a two week period. Once the presence of depression is suspected, more detailed measures may be used, such as the Beck Depression Inventory, BDI (Beck' et al., 1961). Mental health patients in the UK quickly become accustomed to completing the GAD-7 and PHQ-9 questionnaires regularly, when attending therapeutic appointments or medication reviews. Kocalevent et al. (2013) reported a Cronbach's alpha of .87 for the PHQ-9 when used as a screening tool in the general population(Kocalevent et al., 2013), indicating good internal consistency. Excellent test-retest reliability has also been reported (Kroenke et al., 2008).

The studies presented in this thesis make use of both the STAI and the GAD-7 in the measurement of anxiety levels, along with the PHQ-9 depression screening. The relationships between caregivers' self-reported anxiety, interoceptive accuracy and interoceptive attention and their behaviour in dyadic interaction with their infants is examined in Studies 1 (Chapter 3), 2b and 2c (Chapter 4). In addition, Study 2c examines their relationship with infant physiology during a behavioural task. In Study 5, caregiver anxiety is examined in relation to their and their child's interoceptive accuracy measured in a heartbeat detection task, and their child's performance in a threat detection task.

2.4.4 Infant and child scales

Measuring Infant Temperament

The quantification of infant temperament is useful in early developmental psychology research, since emerging differences in personality and behaviour for each infant provide a useful backdrop against which to consider behavioural responses observed in the lab. However, measuring infant temperament poses specific challenges. We cannot ask a pre-verbal infant to answer questions or complete a questionnaire themselves, so we must rely on their caregiver's perception of their child's behaviour. This raises the additional consideration, that a caregiver's perception of their infant's behaviour may be influenced by several factors such as their own experiences, beliefs, as well as their physical and emotional wellbeing, since maternal anxiety and depression have been associated with altered cognition in dyadic interactions (Stein et al., 2012). For example, a happy, well-rested parent might notice and interpret their infant's behaviours differently from an exhausted, worried parent.

The assessment of infant temperament underwent significant methodological development during the 1970s and 1980s. However, early attempts to measure infant temperament developed during that period, such as the Carey Infant Temperament Questionnaire (Carey, 1970, Carey and McDevitt, 1978), were criticised for assessing the caregiver rather than the infant (Vaughn et al., 1981). Vaughn et al. (1981) suggested the Carey Infant Temperament Questionnaire provided a measure of caregiver attitudes towards their infant's behaviour, rather than the behaviour itself. Such criticism provided an important consideration in the further advances of measures aiming to assess infant temperament, leading to a considerable change in approach(Vaughn et al., 2002). The Infant Behaviour Questionnaire (IBQ, Rothbart, 1981) addresses some of the criticisms. Rather than asking caregivers to interpret their infant's behaviour, the IBQ provides an extensive list of specific infant behaviours and asks the caregiver to rate their frequency over a one week period. Of course, the caregiver's attention to their infant's behaviours is still an important influencing factor in the resulting IBQ scores, since the infant's behaviour is quantified through the lens of the caregiver's perception in any caregiver-reported measure. The original version of the IBQ assessed behaviours in six categories, activity level, fear, distress to limitations, smiling and laughter, soothability, and duration of orienting (Rothbart, 1981). Since its development, the IBQ has been used extensively in developmental psychology research and, in 1998, underwent subsequent development to create the revised form, IBQ-R (Gartstein and Rothbart, 2003). The IBQ-R included eight new domains, to create 184 items across 14 domains, providing an increased level of differentiation and enabling researchers to focus on those subscales most relevant to their area of interest. More recently, short (91 items, 14 scales) and very short (37 items, 3 broad scales) forms of the IBQ-R have also been developed (Putnam et al., 2014). These are designed to take account of developments in temperament research, requiring an increased number of characteristics to be considered within temperament, but at the same time producing a practical tool that does not place too great a demand on participants (Putnam et al., 2014. The IBQ-R has been found to demonstrate good internal consistency. Factor analyses resulted in a three-factor model, with Cronbach's alpha reported as 0.92 for Surgency/Extraversion, and 0.91 for both the Negative Affectivity and Orienting/Regulation factors. While reported Cronbach's alphas reported for the short and very short forms are slightly reduced, they are still above .7 for all scales, demonstrating that good internal consistency has been maintained in these more practical forms of the IBQ (Putnam et al., 2014).

Despite attempting to remove caregiver bias by asking caregivers to rate behavioural frequency, the IBQ-R, just like other self-reported measures, is still open to influence from the person assessing the frequency of such behaviours. In the studies presented in this PhD thesis, this potential bias is of interest in itself, raising questions of how caregivers' mental health might affect their perception of, their infant's behaviours. For example, an anxious caregiver might be more sensitive to their infant's crying, believe it to signal something serious or urgent and feel a need to provide a solution quickly, while a depressed caregiver, on the other hand, might be distracted, preoccupied or lacking in energy and, perhaps, less likely to register their infant's cry in the same way. Indeed, several studies have reported differences in caregivers' perception of their infants' behaviour in relation to caregiver mental health (Kertz et al., 2008; Mäntymaa, Tamminen, et al., 2006 Morrell and Steele, 2003). Given the theoretical arguments behind the importance of dyadic interaction in how infants learn to recognise and regulate their emotions (Fotopoulou and Tsakiris, 2017a; (Atzil et al., 2018; Filippetti, 2021), influences on caregivers' perception of their infants' behaviour, and their infants' response to their caregivers' actions, are important factors in the consideration of early emotional development. The studies presented here employ caregiver-reported information, alongside assessments of caregiver mental health, to examine the combination of these influences on infant development.

Self-reported heartbeat detection and perception in children

As for adults, self-reported heartbeat detection and perception tasks have also been used with children. However, these studies are sparse. A few of the existing studies have used heartbeat detection tasks based on Schandry, 1981 in children aged six and over (e.g. Palser, Fotopoulou, et al., 2018a; Palser, Fotopoulou, et al., 2018b). In some studies, the original task was used in children aged 8 (Eley et al., 2007), aged 8 - 11 (Eley et al., 2004) and with children aged 11 (Schmidt and Trakowski, 2004). In other studies, the task was adapted to the child's age to ensure that it could be understood and completed. For example, building on the work of Eley et al. (2004), Koch and Pollatos reduced the time intervals used in the original heartbeat detection task to take children's attention and concentration into account, using the task with children aged 6 - 11, (Koch and Pollatos, 2014a, Koch and Pollatos, 2014c). This method was then adopted in further studies, e.g. Georgiou et al., 2015. For younger children, an alternative method of asking about their perception of their heartbeat relies on the child choosing a pictorial representation, rather than counting their heartbeats (Opdensteinen et al., 2021; Schaan et al., 2019). In the original Jumping Jack Paradigm children aged 4-6 years were asked to indicate the strength of their heartbeat before and after exercise, using four different sized circles (Schaan et al., 2019). Changes in the circle the child chooses before and after exercise can then be compared with the actual change in their heart rate, measured with a pulse oximeter. A further adaptation of the Jumping Jack Paradigm included the addition of repeated trials of jumping jacks along with a fifth circle in the choices of magnitude estimation, aimed at improving reliability and sensitivity, respectively (Opdensteinen et al., 2021).

The use of heartbeat detection tasks with young children requires some caution. This is because rapid cognitive development in the early years leads to individual differences in ability, such as numerical representation, which can have a confounding effect on the collection of interoceptive data (Koch and Pollatos, 2014b; Opdensteinen et al., 2021; Schaan et al., 2019). For example, asking children to pay attention to their heartbeat requires them to understand what their heartbeat is and feels like in the first place. Even when that is clear, using a suitable representation of the speed of their heartbeat requires the child to have the ability to associate the mental representation of speed with its representation in pictures or numbers. For this reason, one could expect the resulting interoceptive accuracy recorded to be positively associated with the child's age. Indeed, this was the case in a study using a heartbeat detection tasks with children aged 4-6 years (Schaan et al., 2019), highlighting the need for researchers to take age into account when using such tasks. In addition to the cognitive factors, emotional factors could also confound results. For example, a child might understand about their heartbeat but want to provide the 'right' answer and therefore provide what they believe to be an appropriate response, even if this is not what they were actually able to feel. To mitigate for this, the researcher would need to reinforce that everyone is different with respect to perception of their heartbeat and that they are interested in these differences, reminding the child that it is important to focus on what they can actually feel.

Study 3 (Chapter 4) employed a heartbeat detection and estimation task, the Jumping Jack Paradigm (Schaan et al., 2019) to establish a measure of interoceptive accuracy in children between 5- and 16-year-old, and their caregivers, along with a measure of interoceptive sensibility. The data are then considered alongside caregiver mental health and child performance in a threat detection task.

Chapter 3

Study 1: Interoception and Anxiety Influences on Caregivers' Contingency and Use of Touch in Dyadic Interactions

3.1 Introduction

In Chapter 1, I outlined the relationship between interoception and anxiety, highlighting the scarcity of research into the early development of interoceptive processing. Emerging theories suggest that the development of interoceptive processing takes place during infancy and is facilitated by early caregiver-infant interactions (Atzil et al., 2018; Filippetti, 2021; Fotopoulou and Tsakiris, 2017b). Fotopoulou and Tsakiris (2017b) suggested that a primary purpose of caregiver-infant dyadic interaction is the maintenance of the infant's homeostasis and that the matching of internal experience, such as visceral sensations, and external information, such as contingent care from the caregiver, facilitates both the development of the infant's interoceptive processing and their understanding of those around them. Atzil et al. (2018) proposed that social care facilitates the development of not only the neural pathways relevant for social development, but all brain development, likening early social interactions to "wiring instructions" (Atzil et al., 2018 p624) for the brain. These connections are proposed to be formed as infants associate interoceptive information with exteroceptive information from their caregivers, resulting in conditioned associative learning. Thus, the infant's brain is prompted to regulate their internal milieu in the development of allostatic regulation by responding to social information (Atzil et al., 2018). Building on these accounts, Filippetti (2021) focused on the intimate environment of feeding interactions to explain how both infant and caregiver factors play a role in the interplay of infant cues and caregiver responses (Filippetti, 2021). Montirosso and McGlone (2020) similarly highlighted the importance of touch and close proximity in the caregiver-infant dyad. They suggested that the repairing of communication via physiological synchrony between the caregiver and infant when there are inevitable breaks helps to improve attunement between them and is important for the infant's development of a sense of self. These theoretical accounts of the development of infants' interoceptive processing, discussed in more detail in Chapter 1 (1.3), highlight the important role the caregiver plays. In more practical terms, these accounts raise questions regarding individual differences in caregiving approaches. Specifically, if caregivers' abilities in these early interactions directly relate to differences in the development of their infants' interoceptive processing, what are the factors that could contribute to differences in these caregiving behaviours? In the study presented in this chapter, I attempted to answer this question by examining caregiver interoception and anxiety, and its relation to their behaviour in dyadic interactions with their infant.

Caregiver contingency

Theories have suggested that infants begin to recognise their own bodily state in response to consistent, appropriate, caregiver responses, whereby both the infant and caregiver alike generate increasingly accurate models of interoceptive inference based on their previous responses to one another (Fotopoulou and Tsakiris, 2017b). For example, the caregiver will learn to recognise the different cries of the infant, eventually understanding which cry refers to hunger rather than a wet nappy or tiredness. The more consistently the caregiver responds to the infant, the more efficiently the infant learns to make sense of their internal state (Fotopoulou and Tsakiris, 2017b). This adaptive appropriateness of the caregivers' behaviour to the infant's need during infant-caregiver dyadic interactions is referred to as *contingency* and is proposed to facilitate the developing ability of the infant to detect and interpret their own bodily signals (Atzil et al., 2018; Filippetti, 2021; Fotopoulou and Tsakiris, 2017b). Before being associated with interoceptive development, maternal contingency has long been considered a determinant of attachment, since the seminal work of Mary Ainsworth (Ainsworth, 1972). In her work, Ainsworth (1972) described contingency in terms of maternal sensitivity, the timely and appropriate response to the infant. More recently, contingency has referred to the degree to which caregivers' responses fit the needs of the infant (Beebe et al., 2010;Crucianelli et al., 2019). This definition aligns with the work of Gergeley and Watson (1999), who emphasised the ability of the infant to detect whether the caregiver's response matches their need, thereby placing the infant in charge of the communication. This is because it is the infant's responsibility to first communicate their need and then to assess whether this has been met. In this respect, contingency implies an adaptive quality in the caregiver, since Gergely and Watson (1999) proposed that the infant learns to better recognise the contingency of their caregiver's response as their sense of self develops. Clearly, contingent behaviour from the caregiver is highly important, not only for optimum physical care of the infant, but potentially as an important factor in the infant's interoceptive processing development, in turn influencing their cognitive, social and emotional development. But what makes a caregiver contingent?

Contingent caregiving relies not only on provision of a timely response which accurately satisfies the infant's need, but, firstly, on their ability to notice, attend to, and infer meaning from their infant's behavioural cues, such as crying. This process relies on several different skills. Firstly, the caregiver needs to be able to infer what their infant is experiencing, recognising this as separate from what they themselves might be experiencing. This process has been referred to as mentalising (Fonagy et al., 2018). Caregivers' mentalising abilities have been directly related to attachment (Meins et al., 2001). Next, the caregiver needs to attribute the correct mental state to their infant, referred to as mind-mindedness (Meins et al., 1998; Meins et al., 2001). Inevitably, communication between caregiver and infant may break down. While this could appear detrimental, Montirosso and McGlone (2020) suggested that the reparation following such breakages in communication actually plays an important role in reinforcing the infant's ability to recognise their own physiological state. This would suggest that, while contingent behaviour from the caregiver is clearly highly important for overall optimal care for the infant, the imperfections in contingency that naturally arise from periods where the caregiver is unattuned also provide valuable developmental opportunities too, through this reparation process. Differences in caregiver contingency have been related to different factors within the caregiver, such as their own interoceptive abilities (Abraham et al., 2019; Montirosso and McGlone, 2020) and their mental health (Murray et al., 2012; Turner et al., 2003), as will be discussed next.

Caregiver interoception

Fotopoulou and Tsakiris (2017) described the process of integrating multisensory information within the self as an important skill for us to understand the emotional and physical state of others. They suggested our own interoceptive awareness helps us to understand how others' states make us feel for us to infer how the other is feeling (Fotopoulou and Tsakiris, 2017b). This theoretical approach suggests that caregivers' own interoceptive skills influence their ability to act contingently in the first place. Indeed, as discussed in detail in Section 1.3, previous research has indicated that caregivers' own interoceptive abilities relate to their infant's interoceptive processing development, suggesting that it is caregivers' interoceptive abilities that facilitate simultaneous monitoring of their own bodily signals and their infant's arousal state to enable sensitive caregiving (Abraham et al., 2019; Montirosso and McGlone, 2020). In addition, caregivers' interoceptive abilities have been related with their own interactive behaviour and with outcomes for their child (Abraham et al., 2019; MacCormack et al., 2020; Suga et al., 2022). For example, mothers with higher interoceptive sensibility report noticing more positive feelings in their infant (Suga et al., 2022). Caregiver interoception is also associated with outcomes in older children. For example, eight-year-old children whose caregivers show greater interoceptive knowledge demonstrate better emotion regulation abilities and better social skills (MacCormack et al., 2020).

Together, these theoretical approaches and empirical studies suggest that caregivers' interoception plays an important role in their ability to engage contingently with their infant. However, as discussed in Chapter 1, interoception is a broad term, with ongoing debate within the field over the precise processes involved and their categorization (Desmedt et al., 2018). With different terms for the various dimensions of interoception currently in use, it is important to understand which dimensions are involved when considering the caregiver's role in interactive behaviour. As discussed above, consistent, appropriate behaviour depends on the caregiver's mentalising skills and corresponding contingent behaviour. These skills rely, first of all, on the caregiver's ability to interpret their own bodily sensations accurately, since this is thought to relate to their understanding and experience of their own emotional state (e.g. L. F. Barrett, 2017; Critchley and Garfinkel, 2017; Seth, 2013). According to the theory of mentalising, this ability then informs our ability to infer the mental state of others (Fonagy et al., 2018). This is essential for caregivers if they are to respond to their infant contingently. In Section 1.2.2, I discussed models of interoception, including the three-dimensional model (Garfinkel et al., 2015) and the factorial model (Murphy, Bird, and Catmur, 2019). Both models refer to *interoceptive accuracy* as how accurately an individual detects their bodily sensations, either as measured with an objective task, such as a heartbeat detection task (Garfinkel et al., 2015) or as a self-reported measure of how accurately one usually interprets their bodily signals (Murphy, Bird, and Catmur, 2019). In addition to interoceptive accuracy, *interoceptive attention*, i.e., the extent to which individuals focus on internal sensation, as described by Murphy et al (2019), would also appear important in the context of caregiver behaviour in interactions with their infant. A focus on interoceptive signals in caregivers has been associated with caregivers' touching and stroking behaviours towards their infants (Donaghy et al., 2024). An increased focus on bodily sensations is also associated with mental health diagnoses, such as anxiety and panic disorders (Hoehn-Saric and McLeod, 2000). This distortion of attention on bodily sensations could, therefore, relate to both the caregiver's own emotional state and the state they attribute to their infant. This is important, as will be discussed next, since caregiver mental health has also been directly related to dyadic interactions.

Caregiver mental health

Caregiver mental health is another critical factor that has been shown to influence caregivers' ability to respond to their infants' cues and, consequently, the quality of caregiver-infant interaction. For example, latency of interactive speech has been found to be altered in depression, with depressed mothers responding to their infant 11% more slowly than non-depressed mothers (N. Smith et al., 2022). The effects of depression on dyadic interaction have been suggested to be moderated by attachment style (Flykt et al., 2010). In this study, preoccupied mothers with postpartum depression demonstrated greater difficulties interacting with their infant, but secure-autonomous attachment in the caregiver appeared to protect the quality of dyadic interactions to some degree. These findings highlight an association between maternal depression and maternal interactions with their infants. Similarly, maternal anxiety has also been related to dyadic interactions, however findings are inconsistent. For example, research has shown that anxious caregivers demonstrate reduced engagement with infants (Murray et al., 2012; Turner et al., 2003). In addition, highly anxious mothers have been observed to demonstrate less sensitive responsivity and emotional tone than less anxious mothers during interactions (Nicol-harper et al., 2007). However, Reck et al. (2018) found no difference in interactive behaviour in a between groups comparison of anxious versus non-anxious mothers (Reck et al., 2018). Kaitz et al. (2010) reported that anxious mothers demonstrate greater engagement and exaggerated behaviours in dyadic interactions relative to non-depressed controls (Kaitz et al., 2010), thought to be associated with hyper-arousal found with anxiety (Hoehn-Saric and McLeod, 2000). These mixed findings can be explained by the heterogeneity included within the broad term of anxiety. Indeed, Murray et al. (2012) highlighted the anxiety disorder-specific nature of altered parenting, with caregivers with generalised anxiety disorder behaving differently from those with specific phobias on a variety of observed behavioural tasks (Murray et al., 2012). For example, in a between groups study of mothers with social anxiety disorder and generalized anxiety disorder, mothers with social anxiety disorder were less positively engaged, and more anxious during the interactions, but equally as sensitive as control mothers, while no effect of generalized anxiety disorder was observed Murray et al., 2007). This highlights the need for consistency and replication in order to clarify whether behavioural differences are due to characteristics of different anxiety presentations, or, as another possibility, due to trans-diagnostic characteristics based on somatic, emotional and cognitive aspects of different mental health difficulties.

The importance of touch

If caregivers' interoception and mental health relate to differences in their interactive behaviour as suggested, which behaviours might be considered most important in the quality of dyadic interaction and, specifically, in the development of infants' interoceptive processing? While the pattern of behaviour that evolves within each dyad will be unique to them, touch is an essential component of early dyadic interaction for all dyads, since it is essential to the provision of basic instrumental care, such as feeding, bathing and soothing the infant. The soothing effects of touch and its role in how infants experience their environment has recently received much research attention (e.g. Della Longa et al., 2019; T. Field, 2019; Fotopoulou et al., 2022; McGlone et al., 2014). However, the use of touch in early dyadic interactions is also important when considering the early development of interoceptive processing.

Affective touch, a particular kind of slow, stroking, touch has been found to activate the same neural pathways, the C-T afferent system, as interoceptive information (Björnsdotter et al., 2010; Löken et al., 2009). This kind of touch is often administered instinctively by caregivers to soothe their infants (Croy et al., 2016). Infants have been observed showing different physiological responses to different kinds of touch from birth (Longa et al., 2021) and to specifically respond to affective touch from as early as 2 months of age (Jönsson et al., 2018). The activation of the CT-afferent system in response to affective touch once again raises the question of whether, and how, early tactile interaction facilitates interoceptive processing development. Affective touch has been demonstrated to enhance face processing in infants (Della Longa et al., 2019; T. Field, 2019), suggesting its influence for socio-cognitive development. Touch has also been related to other domains of infant development, such as autonomic regulation and immune function (see Carozza and Leong, 2021 for an overview). It is, therefore, important to consider to what extent early experiences of touch can specifically shape the developmental trajectories of interoception (Burleson and Quigley, 2021; Fotopoulou and Tsakiris, 2017b) and whether its use may vary between caregivers. Indeed, the extent to which caregivers use touch in interactions with their infant has been shown to relate to caregiver interoception. One recent study found that caregivers reporting greater focus on their interoceptive signals also reported engaging in more stroking and rocking behaviours with their infants (Donaghy et al., 2024). In addition to caregiver interoception, the use of touch has also been associated with caregiver mental health. Stepakoff and Beebe (2023) observed caregivers with higher levels of depression using reduced levels of affectionate touch with their 4-month-old infants. They were also more likely than non-depressed caregivers to use toys and objects to touch their infants (Stepakoff and Beebe, 2024). Similarly, Mercuri et al. (2023) also found less depressed caregivers engaged in more frequent affectionate touch with infants of the same age (Mercuri, Stack, Mantis, et al., 2023).

The theoretical accounts and empirical studies above suggest that early dyadic interactions facilitate the development of infants' interoceptive processing. In addition, previous empirical findings separately relate caregiver mental health and interoception to caregiver behaviour in dyadic interactions.

Considering these findings, with this study I sought to explore whether caregiver interoception and mental health influence caregiver behaviour during dyadic interactions. In this online study, I hypothesised that caregiver anxiety and interoception would be associated with 1) how caregivers touched their infant during interactive tasks and 2) their contingency in responding to their infant's cues. Specifically, I predicted that caregivers demonstrating greater interoceptive accuracy, lower interoceptive attention, and lower anxiety would demonstrate greater contingency in dyadic interactions. I also hypothesised that greater interoceptive accuracy would relate to increased use of touch, as a potential mechanism for facilitating the development of interoceptive processing in the infant.

3.2 Method

3.2.1 Participants

Fifty-five caregiver-infant dyads took part in this online study with their caregivers. Caregivers were recruited via the ChildrenHelpingScience.com website (Scott and Schulz, 2017). Participants were selected based on the child age, having already signed up to the website to take part in studies developed and promoted via the Children Helping Science website. Of the 55 dyads taking part in the study, 21 dyads failed to complete either the full questionnaires, the online behavioural components of the study, or both and so were excluded, resulting in a final sample of 34 healthy, full term 6- to 8-month-old infants (mean age = 210 days, 14 girls) and their primary caregivers (all female). Ethical approval was gained from the University of Essex Ethics Sub-Committee (2021-0125).

3.2.2 Measures

Caregiver interoceptive accuracy and attention

Caregiver interoceptive accuracy and interoceptive attention were measured using recently-developed self-report scales, The Interoceptive Accuracy Scale, IAS, (Murphy et al., 2020) and the Interoceptive Attention Scale, IATS (Gabriele et al., 2022). These scales differentiate between how accurately someone responds to their bodily sensations, and how much they focus on their bodily sensations, in terms of their interoceptive attention. The IAS has demonstrated a significant correlation with an objective measure of accuracy on the Heartbeat Detection Task, HDT, (Schandry, 1981), providing a suitable alternative to a measure of interoceptive accuracy that could have been utilised in the laboratory (see Chapter 2 for a detailed discussion on methods of measurement of interoception). The IAS offered a self-reported measure of caregiver interoceptive accuracy suitable for use in a remote, online study. This 21 item questionnaire asks participants to assess their own ability to accurately perceive a wide variety of bodily sensations and indicate their agreement on a 5-point Likert scale, from 1, Disagree Strongly, to 5, Strongly Agree. Caregiver IAS scores ranged from 68 to 105 (M=84.18, SD=10.72). Murphy et al. (2020) report a Cronbach's alpha of .88 indicating good internal consistency. In this study, Cronbach's alpha was .87. The Interoceptive Attention Scale, IATS (Gabriele et al., 2022) was also used, to measure how much attention caregivers paid to their bodily sensations. Like the IAS, the IATS asks participants the degree to which they agree with statements about how long their attention is focused on a variety of bodily sensations, again on a 5-point Likert scale. IATS scores ranged from 22 to 71 (M=44.35, SD=13.55). Gabriele et al. (2022) report a Cronbach's alpha of .91. In this study, Cronbach's alpha was .92.

Caregiver anxiety

Caregiver anxiety levels were measured using the State-Trait Anxiety Index, STAI (Spielberger et al., 1970). The STAI is a well-established measure of anxiety used in psychology research and has been found to correlate with the GAD-7 scale, an established initial clinical assessment of generalised anxiety (Manzoni et al., 2018). The STAI is a 40-item self-report questionnaire, with 20 items dedicated to measure current anxiety (state), and 20 items dedicated to measure general feelings of anxiety (trait). Participants are asked to rate their symptoms based on a 4-point scale from "not at all" to "very much so". Scores above 40 are considered to indicate clinical levels of anxiety. In this study, Cronbach's alpha was .94 for state anxiety and .90 for trait anxiety, in line with values previously reported, such as .92 and .90 respectively (Spielberger et al., 1970).

Caregiver behaviours in dyadic interaction

Caregiver behaviours were analysed during two interactive tasks. Firstly, caregivers were asked to play with their infant on the floor, without the use of toys, *as they normally would at home* (free play task). In the second task, caregivers were asked to read their infant a story from a book that the infant was already familiar with (story time task). This is because it was felt the novelty of a new story could alter the caregiver's and infant's usual behaviour, whereas a familiar story could give better insight into the usual pattern of established dyadic interaction, which is of greater interest in this study. These and similar tasks have been used previously as the basis for micro-analysis of interactive behaviour (Beebe et al., 2010; Beebe et al., 2016; Crucianelli and Filippetti, 2018; Kaitz et al., 2010).

Video recordings of these tasks were then coded offline, frame by frame, to measure behaviours with high precision. In this study, we coded caregiver touch behaviours by measuring the precise duration of each occurrence of touch and categorising the touch as either instrumental, affectionate or playful (see 3.1 for the precise behaviours coded). The method followed was based on the Mother Infant Touch Scale, MITS (Crucianelli and Filippetti, 2018). However, in this study, precise durations of each action were recorded, rather than whole one second blocks. Total durations were then calculated for each behavioural category, and divided by the total duration of the task, to produce standardised scores for each touch category during both the *Story* and *Play* tasks.

In addition to touch, contingency of caregiver behaviours towards the infant was also assessed. Caregiver behaviours *in response to their infant's behavioural cues* were categorised as either contingent or non-contingent. Contingency is a measure of the adaptable appropriateness of the caregiver's response to their infant's cues, and is therefore not categorised as either positive or negative, simply whether it matches the need demonstrated by the infant. In other words, the infant instigates the communication (Crucianelli and Filippetti, 2018). To judge a caregiver behaviour as either contingent or non-contingent requires both the infant's initial cue, and their response following the caregiver's action, to be considered. If the caregiver's action appears to satisfy the infant's need, confirmed by the infant's response, the action was coded as contingent. If the caregiver responded to their infant, but their action appeared not to satisfy the infant, the behaviour was coded as non-contingent. If the caregiver failed to notice or respond to the infant's cue within the following 5 seconds, the non-response was also marked as non-contingent. Contingency scores were produced by calculating the proportion of all responses that were coded as contingent. The scores for the two behavioural tasks were added together to produce a contingency score.

The offline coding and analysis of interactive behaviours in the free play and story time task were conducted using Eudico Linguistics Annotator, ELAN, version 6.8, a freely available download (Max Planck Institute for Psycholinguistics, 2024). Behavioural coding was conducted by CC and MO. Precise descriptions of the behaviours to be coded were provided by CC and coding was practised by both coders on the first 10 videos recorded. At this stage, any disagreements were discussed in order to produce a robust coding system before coding the rest of the videos. Inter-rater reliability was assessed on an additional 20% of the videos to ensure good internal consistency for the scales in question, i.e. contingency, instrumental touch, affectionate touch and playful touch. To assess the agreement between raters, a two-way random-effects model was used to compute Intraclass correlation coefficients (ICC). The ICC values obtained were: ICC = 0.898 (95% CI [$0.712 < ICC < 0.966$], $p < .001$) for affectionate touch, ICC = 0.870 (95% CI [$0.64 < ICC < 0.956$], $p < .001$) for playful touch, indicating good agreement between the raters. For instrumental touch, ICC = 0.505, (95% CI [$0.027 < ICC < 0.804$, $p < .02$) and for contingency ICC = 0.515, (95% CI [$0.015 < ICC < 0.812$], $p < .022$), indicating moderate agreement.

Table 3.1 summarises the coding protocol used for assessing caregiver touch and caregiver contingency.

3.2.3 Procedure

Caregivers taking part in the study had already signed up to participate in studies on the ChildrenHelpingScience.com website (Scott and Schulz, 2017). On beginning the study via the website, caregivers were provided on-screen instructions to arrange a suitable space for playing with their infant on their floor and their laptop so that both caregiver and infant were fully visible. Caregivers were instructed to hide their screen during the recording of the interactive tasks so as to reduce distraction for their infant. Caregivers were first asked to play with their infants for a period of 5 minutes, the beginning and end of which were indicated with a sound.

Table 3.1
Behavioural Coding Protocol for Observation Tasks

Caregiver behaviour	Method	Category	Brief Description
Contingency	Watch for 5 seconds from each of the infant's behavioural cues, then decide on one of the two possible codes. Code only a 0.5 second block, marked with the appropriate code. Mark as contingent, if the infant seems satisfied by the caregiver's response. Mark as non-contingent if the caregiver's behaviour appears not to match what the infant was requesting and the infant's need remains unsatisfied. Also mark as non-contingent if the caregiver does not respond to the infant's cue.	Contingent Non contingent	Caregiver behaviour satisfied infant's demonstrated need Does not satisfy infant's need or caregiver does not notice or respond to infant's cue
Touch	Code all physical touch from the caregiver, choosing one of the three possible codes. Code precise duration from beginning to end of contact. The end of contact is when either the infant moves away, the caregiver removes physical contact, or the category of touch changes – e.g. the caregiver may be wiping the baby (instrumental) but then start tickling the baby (playful) or kissing the baby (affectionate).	Affectionate Playful Instrumental	Stroking, cuddles, kisses, snuggles, etc. Tickles, swings, playful pats, etc. Moving, cleaning, supporting, restricting the infant, etc.

After a short break, they were then asked to read their infant a story from a book. Once the recordings were complete, the caregivers were asked to confirm their consent for their videos to be used in the study. They were then directed to a Qualtrics questionnaire. The questionnaire comprised the STAI, IAS and IATS described above. On completion of the questionnaire, caregivers were thanked for their participation and provided with a downloadable certificate for their infant.

3.3 Results

3.3.1 Descriptive statistics

Descriptive statistics of all variables are provided in Table 3.2.

Table 3.2
Study 1 Descriptive Statistics for all Variables

	Minimum	Maximum	Mean	Std. Deviation
State Anxiety	20.00	54.00	31.97	10.36
Trait Anxiety	24.00	61.00	38.56	9.04
Interoceptive Accuracy Score	68.00	105.00	84.18	10.72
Interoceptive Attention Score	22.00	71.00	44.35	13.55
Story Task				
Instrumental Touch	0.00	0.70	0.07	0.13
Affectionate Touch	0.00	0.11	0.02	0.03
Playful Touch	0.00	0.21	0.03	0.05
Contingency Score	0.00	1.00	0.77	0.27
Free Play Task				
Instrumental Touch	0.00	0.73	0.24	0.20
Affectionate Touch	0.00	0.21	0.06	0.05
Playful Touch	0.00	0.67	0.31	0.18
Contingency Score	0.50	1.00	0.85	0.12

Note: Touch scores are indicated by the proportion of the duration of the task, with a possible range of 0 – 1. Contingency is indicated by a score of contingent responses as a proportion of all caregiver responses, with a possible range of 0 – 1.

Anxiety Prevalence

In this study, State Anxiety scores ranged from 20 to 54 (M = 31.97, SD = 10.36), while Trait Anxiety scores ranged from 24 to 61 (M = 38.56, SD = 9.04). Twenty-six percent of caregivers scored above the cut-off score of 40 for clinical levels of state anxiety, while this figure rose to 44% for trait anxiety. The distribution of anxiety scores for caregivers is displayed in Table 3.3

Table 3.3
State-Trait Anxiety Scores of Caregivers

Score Range	20 - 29	30-39	40-49	50-59	60-69	> 70
State Anxiety Scores	17	8	5	4	0	0
Trait Anxiety Scores	6	13	11	3	1	0

Note: scores above 40 indicate clinically significant anxiety

Caregiver Contingency

The descriptive statistics indicated that caregivers demonstrated higher contingency scores in response to their infants' behavioural cues in the *Play* task than in the *Story* task. However, a paired samples t-test revealed this difference was not significant, t(34) = 1.847, p = .074, d = 0.24.

Caregiver Touch

The descriptive statistics indicated that caregivers demonstrated greater use of touch overall in the *Play* task than in the *Story* task. Paired samples t-tests indicated that these differences were significant for all categories of touch and total time caregivers spent touching their infant (instrumental touch ($t(34) = 4.949$, $p < 0.001$, $d = 0.24$), affectionate touch ($t(34) = 4.433$, $p < 0.001$, d = 0.05), playful touch ($t(34) = 8.682$, $p < 0.001$, $d = 0.50$), total touch ($t(34) = 10.487$, $p < 0.001$), $d = 0.28$. Based on these initial results indicating significantly different touch behaviours between the two tasks (Play and Story), I decided to keep the data from the story and play tasks separate for the remaining analyses.

3.3.2 Preliminary Analysis

Exploratory analyses were conducted using bivariate correlations between the variables of interest, to explore the relationships between them and to inform inferential analyses. Distributions of several touch variables within the data were skewed (*Play Task* instrumental touch D(34) = .175, $p = .01$, *Story Task*, instrumental touch D(34) = .301, $p < .001$, affectionate touch D(34) = .314, $p < .001$, playful touch D(34) = .306, $p < .001$), so Spearman's ρ correlations were calculated and are displayed in Figure 3.4, including Bonferroni-corrected significance level for multiple comparisons ($p < .005$).

Table 3.4
Correlations between Caregiver Anxiety, Interoception, Contingency and Use of Touch

		1	2	3	4	5	6	7	8	9	10	11
1	State Anxiety											
2	Trait Anxiety	.845**										
3	Interoceptive Accuracy Score	0.075	0.047									
4	Interoceptive Attention Score	0.063	0.261	-0.051								
5	Story Instrumental Touch	-0.275	-0.214	-.465*	-0.116							
6	Story Affectionate Touch	0.033	0.015	-0.210	-0.185	.354*						
7	Story Playful Touch	-0.290	-0.288	-.350*	-0.304	.420*	.413*					
8	Story Contingency Score	0.229	0.160	0.189	-0.180	-.610**	-0.122	0.022				
9	Play Instrumental Touch	0.219	0.101	-0.321	-0.054	.351*	0.254	0.077	-0.296			
10	Play Affectionate Touch	0.176	0.160	-.358*	-0.046	0.143	.348*	-0.046	0.106	0.270		
11	Play Playful Touch	0.131	-0.135	-0.077	0.052	-0.217	0.026	-0.043	0.272	-0.014	0.247	
12	Play Contingency Score	-0.338	-0.326	-0.115	-0.073	0.209	0.206	0.140	0.031	-0.092	-0.051	0.047

Note: * $p < .05$
** $p < .005$ (Bonferroni-corrected significance level)

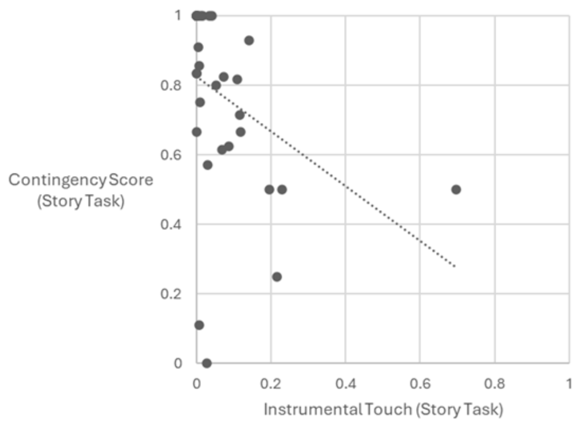
As expected, state anxiety was positively related to trait anxiety ($\rho = .845$, $p < .001$). Caregiver contingency was negatively associated with instrumental touch in the *Story* task

(ρ = -.610, p < .001) and this is illustrated in Figure 3.1. Several other correlations were observed at the $p < .05$ level, however these did not survive Bonferroni correction for multiple comparisons (see 3.4).

Interoceptive accuracy was negatively associated with instrumental touch in the *Story* task (ρ = -.465, p = .006) and also with playful touch in the *Story* task (ρ = -.350, p = .042). Interoceptive accuracy was also negatively associated with affectionate touch in the *Play* task (ρ = -.358, p = .038). I found a positive association between instrumental touch in the *Story* and *Play* tasks (ρ = 0.351, p = .042). Similarly, a positive association was also present between affectionate touch in the *Story* and *Play* tasks (ρ = .348, p = .044). However, playful touch in the *Story* task was not associated with playful touch in the *Play* task. I did not observe any associations between state anxiety, trait anxiety or interoceptive attention and any of the other variables of interest.

Figure 3.1

Scatterplot Demonstrating the Negative Relationships Between Caregiver Contingency and Instrumental Touch in the Story Task



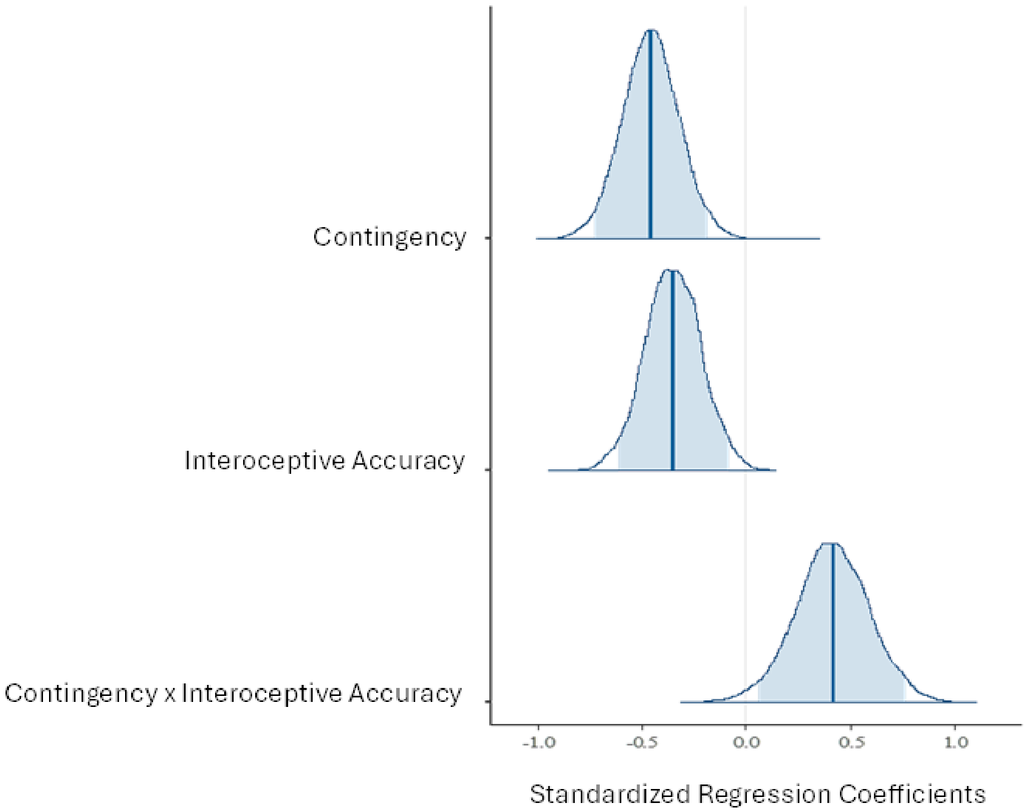
Note: Contingency score refers to the proportion of all responses that were contingent versus non contingent. Instrumental touch refers to the proportion of the total task duration which was spent using instrumental touch.

3.3.3 Bayesian Modelling

To further investigate the hypothesis, the relationship between instrumental touch, caregiver contingency and interoceptive accuracy in the *Story* task was examined using Bayesian linear modelling, using the Bayesian Regression Models using Stan (brms) package in R v4.0 (Bürkner, 2017). Caregiver interoceptive accuracy and caregiver contingency were examined as predictors of instrumental touch. The analysis indicated that both contingency and interoceptive accuracy had a clear effect on instrumental touch individually, each predicting reduced instrumental touch (contingency 95% HPDI [-0.58, 0.00], interoceptive accuracy 95% HPDI [-0.66, -0.06]). The analysis also indicated a clear interaction effect between contingency and interoceptive accuracy, predicting increased instrumental touch (95% HPDI [0.04, 0.75]).

Posterior distributions with medians and 95% confidence intervals are depicted in Figure 3.2.

Figure 3.2
Posterior Distributions of Caregiver Contingency and Caregiver Interoceptive Accuracy as Predictors of Instrumental Touch in the Story Task



3.4 Discussion

This study investigated whether caregiver anxiety and interoception are associated with caregivers' dyadic interactive behaviours. Specifically, I focused on how caregivers use touch in dyadic interactions and their contingency in responding to their infant's behavioural cues. Caregivers completed two interactive tasks in their own homes, *Play* and *Story*, to enable any differences between an unstructured (free play) and a structured (story) task to be observed.

Recordings of the tasks were observed and coded offline. I hypothesised that caregiver anxiety and interoception would be associated with 1) how caregivers touched their infant during interactive tasks and 2) their contingency in responding to their infant's cues. Specifically, I predicted that greater interoceptive accuracy, lower interoceptive attention, and lower anxiety among caregivers would be associated with greater caregiver contingency in dyadic interactions. I also hypothesised that greater interoceptive accuracy would relate to increased use of touch, as a potential mechanism for facilitating the development of interoceptive processing in the infant. The data collected in this study partially supported these hypotheses.

Firstly, I found that interoceptive accuracy and caregiver contingency were, indeed, both related to the way caregiver's used touch in interactions with their infants. However, this association varied between the kinds of touch and the tasks, and was not directly aligned with the hypotheses. Firstly, I found differences between how caregivers used touch in the *Play* and *Story* tasks. Caregivers used significantly less touch overall during the *Story* than in the *Play* tasks. This is consistent with previous studies of task-type in parent-child interaction studies (Kwon et al., 2013), with the quality of interactions being deemed higher in free-play than during more structured tasks. Similarly, in studies of touch specifically, task and context have highlighted behavioural differences in caregivers (Brzozowska et al., 2021). In this study, caregivers touched their 6- to 8-month-old infants less when engaged in a simultaneous activity, such as a conversation, than when their focus was directly on the infant. Free play tasks require the caregiver to play with their child as they normally would, enabling complete freedom for the caregiver. The story task, on the other hand, provides an instruction for the caregiver to follow, to read the book with their infant, which could lead to conflicting needs within the caregiver and between the infant and the caregiver. Despite differences in the amount of touch used, there were strong, positive correlations between the proportions of instrumental and affectionate touch between the tasks, suggesting that caregivers were somewhat consistent in their use of the different categories of touch across the two tasks.

Both interoceptive accuracy and caregiver contingency were associated with reduced instrumental touch in the *Story* task, but were not related to affectionate or playful touch. This association was not observed in the *Play* task. While interoceptive accuracy and caregiver contingency were not directly associated with increased touch overall, as per the hypothesis, their association with reduced instrumental touch is of interest. Instrumental touch in this study was coded as any touch that fulfilled a necessary function, such as moving the infant, restricting the infant, cleaning, changing the infant's position, etc. Instrumental touch was neither affectionate nor playful and could be contingent, such as moving the infant towards an item they expressed interest in, or non-contingent, such as restricting the infant to prevent them from doing something deemed inappropriate by the caregiver, such as crawling away or grabbing the laptop being used to record the task. Anecdotally, many caregivers appeared to use non-contingent, restrictive touch during the story task, appearing to want to keep their infant in one place while completing the story book. This observation of one kind of instrumental touch could suggest this finding hints at an underlying mechanism whereby caregivers with higher interoceptive accuracy or contingency were less inclined to restrict their infants, despite the task at hand, perhaps feeling more confident to prioritise their infant's needs and preferences over the instructions in the study. This speculation would need closer examination in a laboratory setting, to fully understand the caregivers' responses in this situation.

Interestingly, a significant interaction effect between interoceptive accuracy and contingency led to a change in direction in the relationship with instrumental touch, with higher interoceptive accuracy combined with higher contingency predicting increased, rather than decreased, levels of instrumental touch. While this partially supports our hypothesis of increased touch associated with higher interoceptive accuracy and higher contingency, this effect is only visible in the interaction. The small sample size and the skewness in the data render it difficult to interpret these results fully. However, a possible explanation for the combined effect of contingency and interoceptive accuracy on instrumental touch could be that as contingency increases, the negative association between interoceptive accuracy and instrumental touch weakens. This finding could, therefore, indicate that caregivers that are good at inferring the needs of their infant and acting accordingly, prioritised the infant's need over their own feelings in the moment.

Differences were also observed between tasks in the observation of caregiver contingency. In the Story task, mean caregiver contingency scores were significantly lower than in the *Play* task. As explained in the discussion of instrumental touch above, several caregivers were observed using non-contingent, restrictive behaviours with their infant in the story task, perhaps due to prioritising completing the task requested, i.e. following the instructions to read a story together, even if the infant had other ideas, such as crawling away. While restrictive touch was not coded as a separate category in this study, it was one of the behaviours included in the instrumental touch category and regularly contributed to non-contingency counts. This difference in caregiver behaviour between tasks raises an important real-life issue, whereby often-time caregivers' attention is split between caring for their infant and carrying out other tasks. Indeed, divided attention occurs commonly for new parents, who rarely sit and wait for a behavioural cue from their infant (Ablow and Measelle, 2019). A study of caregivers' responses to their infants' cues while undertaking a separate task has revealed that communication is, indeed, impaired when the caregiver is engaged in a non-infant directed task (Chamam et al., 2024). In the present study, the structured story telling task required the caregivers to follow the instruction to read a book to their infant. It is plausible that caregivers' focus on completing the task led to either reduced attention towards the needs of their infant, or their prioritising the need to complete the study over the preferences of the infant, in turn leading to increased restrictive (non-contingent) touch. To explore this, future studies should code restrictive touch separately from other types of instrumental touch.

The current findings did not indicate a significant direct relationship between caregivers' interoceptive accuracy and contingency and did not, therefore, support the hypothesis that greater interoceptive accuracy would relate to greater contingency. This is in contrast to the theoretical accounts relating caregiver interoception with their ability to understand their infant's cues and respond appropriately (Fotopoulou and Tsakiris, 2017b; Montirosso and McGlone, 2020). However, our data remain preliminary and further large-scale studies should examine the association between caregivers' responses and different measures of interoception in a controlled laboratory setting. The use of self-report scales of interoceptive accuracy and attention required the caregivers to think about how well they process different interoceptive sensations. Measuring implicit interoceptive processing, such as heartbeat-evoked potentials could reveal a different picture. Indeed, as discussed in Chapter 1, interoception is a broad term relating to sensations from different sources within the body, at both conscious and subconscious levels (Garfinkel et al., 2015; Herbert et al., 2012; Murphy, Brewer, Catmur, and Bird, 2017b; Whitehead and Drescher, 1980;Steptoe and Vögele, 1992). In this respect, a self-reported measure of interoceptive accuracy could be considered several steps removed from the processing of interoceptive information that could inform caregiver contingency.

In the data presented above, I found no relationship between interoceptive attention and touch behaviours. This is in contrast to a recent study in which greater focus on interoceptive information was associated with more stroking and rocking behaviours (Donaghy et al., 2024). However, there are important differences between Donaghy et al. (2024)'s and the current study. First, Donaghy et al. (2024)'s study relied on self-reported touch behaviours, rather than direct observation of interactions between caregivers and their infants, which I collected for the present study. Discrepancies between self-report data and direct observations could account, at least in part, for the difference in findings between these two studies. A study comparing self-reported caregiver touching behaviours with those observed in a laboratory study found a correlation between the two but also acknowledged the influence of context for the observations, as well as the influence of beliefs and memory (Brzozowska et al., 2021). Second, Donaghy et al. (2024) used *The multidimensional assessment of interoceptive awareness*, version 2 (MAIA-2, Mehling et al., 2018) to measure interoceptive awareness whereas in the present study, I separately assessed caregivers' interoceptive accuracy and attention using the recently developed Interoceptive Attention Scale and Interoceptive Accuracy Scale (Gabriele et al., 2022; Murphy, Bird, and Catmur, 2019). Like Donaghy et al. (2024), the present study relied on self-reported measures of interoceptive dimensions from caregivers. However, the distinction between interoceptive accuracy and interoceptive attention in the present study enabled a clear comparison between both dimensions of interoception, which have been found to be dissociated (Murphy et al., 2020). While the MAIA-2 questionnaire (Mehling et al., 2018) provides useful insight into several categories of interoceptive awareness, these measures of interoception are not directly comparable. In light of the evolution of models of interoception discussed in 1.2, the study of interoception must now focus on the specific dimensions of interoception, acknowledging the different cognitive processes involved in each dimension. Ideally, future studies of this topic should be explored using a combination of implicit and explicit measures of interoception, as recommended in recent discussions on the study of interoception (Desmedt, Luminet, Maurage, and Corneille, 2023; Nord and Garfinkel, 2022), along with direct observation of touching behaviours.

I did not find any association between caregiver anxiety and any of the variables of interest.

This is in contrast to previous analyses of caregiver-infant interactions in which maternal anxiety was also considered (Beebe et al., 2011; Kaitz et al., 2010). In these previous studies, Beebe et al. (2011) found that anxious caregivers demonstrate increased visual vigilance, but reduced emotional contingency towards their infants, while Kaitz et al. (2010) observed exaggerated behaviours by anxious caregivers during free play, consistent with hyper-arousal. Similarly, Smith et al (2022) reported that anxious caregivers use more intense vocalisations than non-anxious caregivers when interacting with their 12-month-old infants in naturalistic settings. This was associated with higher physiological arousal in both the caregivers and their infants (C. G. Smith et al., 2022a). The lack of effect of anxiety in our data could be explained by the fact that the study relied on a non-clinical sample of caregivers, who's anxiety levels were skewed towards lower anxiety scores. This did not allow for a between-groups comparison of anxious versus non-anxious caregivers comparable with previous studies (Kaitz et al., 2010; C. G. Smith et al., 2022a).

One important limitation of this study is that the infant's temperament was not considered. The focus was on the role of caregivers' factors, i.e. their own interoception and anxiety, in examining differences in interactive behaviour through touch and contingency. In reality, the development of individual dyadic communication is bidirectional in nature, with both the infant and the caregiver contributing to the interaction, as they both detect and respond to the other's cues (Beebe et al., 2010; Filippetti, 2021). Previous studies of caregiver-infant dyadic interactions highlight the uniqueness of dyadic communications (e.g. Beebe et al., 2010; Provenzi et al., 2018). In addition to the caregivers' part in this process, individual differences in infant temperament are also likely to influence the use of different behaviours and, therefore, the dyadic interaction as a whole. For example, while touch features prominently in some dyads, vocal exchanges might be more dominant in other dyads. By definition, contingent caregiver behaviours vary depending on the cues provided by the infant. Therefore, the behavioural patterns that evolve within any caregiver-infant dyad will depend on factors from the infant as well as those from the caregiver, as I have considered in the observation of contingency in the present study.

Additional limitations related to the methodologies used for the study. First, the study took place online due to COVID-19 forcing laboratory closures. This prevented the researchers from checking participants' understanding of instructions. Consequently, the interpretation of the instructions varied a little between dyads. For example, in free play, some caregivers chose to hold their infant while other dyads chased each other around the floor. In this respect, a laboratory setting would enable greater methodological control and consistency on the one hand, but could also limit the individual differences of expression and behaviour. When assessing the touch used by caregivers, the remote nature of the study meant I could not observe *affective* touch specifically, since this would require caregiver training and greater experimental control to ensure touch was CT-optimal. While this could provide useful insight into potential mechanisms of infant interoceptive processing development, in the present study I focused on more broad categories of touch. Another methodological limitation of the study concerns the inconsistencies in coding caregiver contingency, as evidenced by low inter-rater reliability. Unfortunately, extensive training of the coders was not possible and this may have impacted the reliability of the coding.

In summary, this study explored whether caregivers' interoception and mental health related to their behaviour in dyadic interactive tasks with their infant. I found that caregiver interoceptive accuracy and contingency, but not anxiety levels or interoceptive attention, relate to caregiver interactive behaviour, partially supporting my hypotheses and providing some consistency with previous literature. The study was conducted against a theoretical backdrop proposing that contingent dyadic interactions early in life provide a facilitating framework in which infant's interoceptive processing develops. While here I looked at factors that might influence the caregivers' behaviour in early interactions, this study did not address whether observed differences in caregiver behaviour are directly associated with infants' interoceptive processing. To explore this question requires an approach that considers evidence of infant interoceptive processing as well as caregivers' factors, which are investigated in Chapter 4.

Chapter 4

Studies 2a, 2b, 2c: Caregiver Anxiety, Interoception, and Infant Physiology in Caregiver-Infant Interactions

4.1 Introduction

In Chapter 3, I demonstrated an association between both caregivers' interoceptive accuracy and the contingency of their behaviours, and their use of different kinds of touch in dyadic interactions. This partially supported my hypotheses and provided some consistency with previous literature, including theoretical proposals that contingent dyadic interactions early in life shape the development of infants' interoceptive processing (Atzil et al., 2018; Filippetti, 2021; Fotopoulou and Tsakiris, 2017a). Chapter 3 focused on factors that might influence the caregivers' behaviour in early interactions, but did not address whether observed differences in caregiver behaviour were associated with infants' interoceptive processing. With the studies presented in this chapter, I sought to further explore the relationship between caregiver behaviour, mental health and interoceptive abilities, this time alongside physiological evidence of interoceptive processing in the infants.

As discussed at length in Chapter 1, considerable research in the last two decades has established a relationship between interoception and mental health in adulthood (see Khalsa et al., 2018 for an overview). Despite increasing research on this relationship, the developmental origins of interoceptive processing and its association with mental health across the lifespan are still not well understood. This is an important gap because early interoceptive processing could play a crucial role in an infant's future mental health. Theoretical accounts of interoceptive processing have proposed that early interactive behaviour in the caregiver-infant dyad facilitates its development (Atzil et al., 2018; Filippetti, 2021; Fotopoulou and Tsakiris, 2017a), although this is yet to be supported directly by empirical studies. Fotopoulou and Taskiris' *Mentalizing Homeostasis* (Fotopoulou and Tsakiris, 2017a) suggests that a primary purpose of caregiver-infant dyadic interaction is maintenance of the infant's homeostasis. Atzil et al. (2018) propose that infants associate interoceptive information with exteroceptive information from their caregivers, resulting in conditioned associative learning that prompts the development of allostatic regulation by responding to social information (Atzil et al., 2018). Building on these accounts, Filippetti (2021) focused on how the intimate environment of feeding interactions facilitates the interplay of infant cues and caregiver responses, determining the distinction and blurring of the infant's interoception (Filippetti, 2021). During such proximal interactions, the importance of nurturing touch within the caregiver-infant dyad was highlighted by Montirosso and McGlone (2020). They proposed that affectionate touch encourages physiological synchrony and that inevitable breaks in communication enable *embodied reparation*, a process whereby affectionate touch brings about interoceptive stability in the infant, helping them to develop a sense of bodily-self. These theoretical accounts of the development of interoceptive processing have been discussed at length in Chapter 1 (1.3.1).

The infant's early life involves very close physical proximity to their primary caregiver for much of their time. Physical touch plays a fundamental role in these early months, whether in the performance of physical care, such as feeding, bathing and changing their nappy, or socially, through affection and play. More specifically, the so-called affective, pleasant touch administered at 3 - 10 cms/s and often provided instinctively to infants by their caregivers, has been found to activate the same neural pathways as interoceptive information, the C-T afferent system (Björnsdotter et al., 2010;Croy et al., 2016; Fairhurst et al., 2014; Löken et al., 2009; McGlone et al., 2014). The activation of these pathways in response to touch suggests that affective touch plays a crucial role in the early relationship between interoceptive processing, emotion and anxiety, as affective touch has been shown to reduce arousal, lower heart rate, and enhance engagement (Beebe and Lachmann, 2002; Fairhurst et al., 2014; Kidd et al., 2023). Since most of the infant's experience of touch comes from their primary caregiver, this suggests that differences between caregivers in their use of touch could lead to differences in the development of interoceptive processing and self-regulation among infants. The role of touch was discussed in detail in 1.3.2.

If the emerging theoretical accounts introduced above are correct, the caregiver's role in early interactions is of fundamental importance to the development of the infant's interoceptive processing. Importantly, the caregivers' abilities in these tasks may depend on several cognitive and emotional skills: they must first divert their attention to their infant's behavioural cues, they then need to develop an understanding of the meaning of these behaviours, then demonstrate their understanding of their infant' emotional state by offering an appropriate response in a timely manner to meet their infant's need. Interoceptive abilities have been related to both cognitive abilities, such as attention and memory (Critchley and Harrison, 2013; Critchley and Garfinkel, 2015; Tsakiris and Critchley, 2016), and emotional awareness, such as empathy (Critchley and Garfinkel, 2017). When interacting with their infant, the caregiver must use these skills effectively to perform the specific tasks required. It therefore follows that the caregiver's interactive behaviour can be influenced by their own interoceptive abilities. Indeed, it has been suggested that caregivers' interoceptive abilities facilitate simultaneous monitoring of their own bodily signals and their infants' arousal state to enable sensitive caregiving (Abraham and Feldman, 2018; Montirosso and McGlone, 2020).

As described in the previous chapters, a rich developmental literature has established an association between caregiver's psychopathology and parental sensitivity towards their infants, with lower levels of parent-child interaction quality displayed in these dyads. For example, mothers with anxiety symptoms are more likely to show intrusive and controlling behaviours when interacting with their infants in the first nine months (Kaitz and Maytal, 2005; Stifter et al., 1993). In addition, their infants are more likely to demonstrate sleep disturbance and raised cortisol levels (Warren et al., 2003), potential risk factors for cognitive (Hernandez-Reif and Gungordu, 2022) and emotional (Reck et al., 2013) development later, since increased cortisol has been related to emotion regulation and susceptibility to stress (Hellhammer et al., 2009). Previous studies suggest that caregivers' mental health may directly affect their behavioural skills during interactions with their infants. For example, latency of interactive speech has been found to be altered in depression, with depressed mothers responding to their infant 11% more slowly than non-depressed mothers (C. G. Smith et al., 2022a). Caregiver-infant gaze and touch synchrony have been observed to be higher than controls in anxious caregivers, but lower than controls in depressed caregivers (Granat et al., 2017). The same study also related maternal mental health with infant behavioural differences, with infants of depressed mothers demonstrating higher levels of negative affect. Parfitt et al. (2013) found that fathers' mental health symptoms also related to the way they interact with their infants (Parfitt et al., 2013), with prenatal paternal symptoms of anxiety and depression predicting higher paternal unresponsiveness and baby passivity. These findings indicate that caregiver mental health influences how caregivers interact with their infants, which in turn affects infant behaviour. However, it is unclear whether these interaction differences are connected to the early development of interoceptive processing.

Research suggests that caregivers' mental health and interoception may influence how they interact with their infants, potentially shaping the development of interoceptive processing in infants through early interactions. Given the relationship between interoception and mental health, this developmental process could, in turn, influence a child's psychopathology risk. This potential mechanism could also shed light on the underlying causes of strong familial patterns in mental health, since research suggests mental health often follows generational patterns, with, for example, anxious caregivers being more likely to have anxious children (see Micco et al., 2009 for a meta-analysis).

In Chapter 1 (Section 1.3), I discussed the caregiver's role along with factors which could influence their behaviour in dyadic interactions. While much previous research focused on the relationship between caregiver anxiety and caregiver-infant interaction (e.g. Kaitz and Maytal, 2005; Murray et al., 2012; C. G. Smith et al., 2022a; Nicol-harper et al., 2007) and, to a lesser extent, the relationship between caregiver interoception and caregiver-infant interaction (Donaghy et al., 2024) and outcomes for the child (Abraham et al., 2019; MacCormack et al., 2020; Pratt et al., 2015), there is considerable evidence that interoception and mental health are fundamentally intertwined. For example, interoceptive awareness has been found to act as a mediator in the subjective experience of anxiety symptoms (Pollatos et al., 2007) and interoceptive sensibility has also been found to mediate reductions in self-reported anxiety levels following a brief mindfulness-based intervention (de Lima-Araujo et al., 2022). Considering the interaction between interoception and mental health, rather than the two variables in isolation, is therefore imperative.

It is also important to acknowledge that different, dissociable, dimensions of interoception (e.g. interoceptive accuracy, interoceptive sensibility) have been found to contribute differently to different mental health diagnoses. For example, misattribution of interoceptive signals is a characteristic of panic disorder, with the physiological sensation becoming a source of anxiety (Ehlers et al., 1995; Hoehn-Saric and McLeod, 2000). Similarly, enhanced attention to interoceptive signals is also widely associated with anxiety (Nord and Garfinkel, 2022). Research evidence of the relationship between the different dimensions of interoception and mental health is discussed in detail in 1.2.3. This complexity in the relationship between interoception and mental health means that, if we are to understand factors influencing the development of interoceptive processing, it is important to consider both caregivers' mental health and their different interoceptive abilities together.

When considering interoceptive processing in the context of emotion regulation and the experience of anxiety, the autonomic nervous system, responsible for regulating physiological arousal plays an important role (as discussed in detail in Chapter 1). The Polyvagal Theory, PVT, (Porges, 2001; Porges, 2007), offers an account for the development of the autonomic nervous system and interoceptive processing from an evolutionary perspective, with early social interaction proposed to provide, once again, a facilitating framework. PVT describes the role of the nervous system in terms of three distinct circuits: social engagement in a safe environment, fight or flight mobilisation in threatening situations and, finally, the shutting down of the nervous system as a second level of defence when a threat cannot be avoided. According to PVT, the subdivisions of the ANS, i.e. the ventral vagal, dorsal vagal, and sympathetic nervous system, provide pathways that regulate physiological states and influence social engagement, stress responses, and adaptive behaviour. In particular, the vagus nerve plays a crucial role in the subconscious collection of information from the environment, which is then communicated via interoceptive signalling, in order to bring about involuntary changes in state. PVT refers to the functioning of the vagus nerve in this role as 'vagal tone,' and suggests that the vagal tone is fundamental to one's regulatory abilities. More specifically, vagal tone is associated with interoception, endocrine, and somatosensory information, the integration of which enables the interpretation of danger and the regulation of emotion (Porges et al., 1994). PVT considers higher vagal tone to reflect better adaptability in the regulation of emotion. Porges (1992) described the role of vagal function as analogous to that of a brake, inhibiting the reflexes of the sympathetic nervous system in safe environments, and being released once danger is detected (Porges, 1992). Other models, such as the biological behavioural model (Grossman and Taylor, 2007), describe the role of vagal tone as an adaptive characteristic, performing the role of energy exchange, whereby respiration is synchronized with cardiovascular activity during behavioural changes. Importantly, both models indicate that higher resting vagal tone is more advantageous, serving as an energy reserve that can be utilised during more active states when action is needed.

In Chapter 1, I discussed the relationship between vagal tone and interoception in adults in detail . In infants, vagal tone has been associated with happiness and soothability, (Huffman et al., 1998) and co-regulation in the caregiver-infant dyad (Porter et al., 2022). Porges (1994) suggested that early social interactions facilitate the development of vagal tone, pointing towards the importance of investigating whether differences in the quality of early interactions may predict differences in vagal tone in the infant. Indeed, a review of the early development of the nervous system suggested that maternal stress may impair the development of vagal tone in the fetus and infant (Cerritelli et al., 2021). In addition, symptoms of maternal depression and levels of caregiver-infant synchrony in dyadic interaction have also been associated with infant vagal tone (Feldman and Eidelman, 2007). Conversely, maternal sensitivity has been associated with higher infant vagal tone measured by heart rate variability in 4-month-old infants (Rattaz et al., 2023). Such findings reinforce the suitability of infant vagal tone as a useful measure in studies of the development of interoceptive processing and emotion regulation. Indeed, infant vagal tone has been successfully used as a physiological measure of arousal in several studies of emotion regulation (see Rattaz et al., 2022 for a systematic review). Importantly, these findings support the idea that an infant's early environment and early social interactions are important in the development of the autonomic nervous system and emotion regulation ability.

In Chapter 3, I examined the association between caregiver contingency and use of touch during dyadic interaction, and their interoceptive abilities and mental health. To build on those findings, three studies are presented in this chapter. Here, I sought to look beyond behavioural observations of naturalistic caregiver-infant dyadic interaction and explore whether differences in specific caregiver behaviours are associated with differences in their mental health and interoceptive abilities and whether these, in turn, are associated with their infant's baseline vagal tone and physiological responses to emotion processing. In Study 2a I present a pilot study examining whether affective touch from the caregiver influences the infant's physiological response to different emotions. Study 2b explored how caregivers respond to their infant's cues by deciding how long to delay their response, using the Responsive Still Face Paradigm, RSFP, a novel adaptation to the previously-validated Still Face Paradigm, SFP (Tronick et al., 1978), and whether this behaviour relates to the caregiver's interoceptive abilities and mental health. Study 2c applied the RSFP in a laboratory setting alongside caregiver mental health and interoceptive abilities, whilst also considering the infant's heart rate response to the stages of the RSFP as well as their baseline heart rate variability (RMSSD) as a measure of vagal tone.

4.2 Study 2a: A pilot study examining infant physiological responses when processing different emotions

4.2.1 Introduction

This pilot study was conducted immediately before the first UK lockdown due to the COVID-19 pandemic, when laboratory testing was halted abruptly by the closure of laboratories. This prevented continuation of the study beyond the first pilot tests, forcing alternative research methods during closure of the Essex Babylab. The initial approach and progress up to the point of laboratory closure are described below.

As discussed in the chapter introduction above, early caregiver-infant interactions are important for social and emotional development and are believed to provide a facilitatory role in the development of interoceptive processing (Atzil et al., 2018; Filippetti, 2021;Fotopoulou and Tsakiris, 2017a; Montirosso and McGlone, 2020). Touch is a fundamental feature in the care of infants. Most of the touch experienced by the infant comes from the primary caregiver, essential when performing a variety of roles, whether functional, such as feeding or bathing, social, such as cuddling and tickling, or affectionate, such as stroking and kissing. Affective touch, a specific kind of touch administered at 3 - 10 cm per second, has been found to activate the C-T afferent pathways, and this particular kind of touch is often administered instinctively by caregivers to sooth their infants (Jönsson et al., 2018). Infants respond to this particular kind of touch very early in life. For example, 2-month-olds display stronger cortical activity in response to slow stroking than fast stroking (Jönsson et al., 2018), while 9-month-old infants demonstrate reduced heart rate and increased engagement when affective touch is administered, compared to faster or slower stroking (Fairhurst et al., 2014). Crucially, the C-T afferent system is also activated in the communication of interoceptive information, i.e. information on bodily states from the visceral organs (Björnsdotter et al., 2010; Löken et al., 2009). Activation of the C-T afferent pathways by affective touch raises several questions. Firstly, does affective touch from the caregiver play a facilitatory role in the development of interoceptive processing in the infant? Secondly, if so, does such an influence on interoceptive processing contribute to emotional development? Since interoceptive abilities in adults are believed to be related to susceptibility to anxiety risk, it is possible that the relationship between affective touch and the development of interoceptive processing in early life could shape individual differences in interoceptive abilities later on, potentially influencing the risk of developing psychopathology. If this is the case, then the caregivers' mental health, interoceptive abilities, and their ability to interpret their infants' needs could all be hypothesised to influence this developmental process. Indeed, differences in caregivers' abilities in understanding the needs of their infant have been shown to relate to differences in their use of touch in dyadic interactions, with verbal indications of maternal mind-mindedness predicting contingency of touch between caregivers and their 12-month-old infants (Crucianelli et al., 2019). The study presented here sought to explore the influence of affective touch on infant physiological response to emotion processing as a potential measure of interoceptive processing.

Emotion processing, emotional arousal and emotion regulation rely on interoceptive information, as was discussed in Chapter 1 (Section 1.2). The relationship between touch in the caregiver-infant dyad and emotion processing in the infant was first highlighted by Hertenstein and Campos (2001), who proposed that touch between the caregiver and their 12-month-old infant could influence the infant's emotional response, although this effect was specific to negative emotions. Consistent with this distinction between positive and negative emotion processing, Wass et al. (2018) observed that physiological responses (electrodermal responses and heart rate changes) to negative emotions had a longer duration than those associated with positive emotions in 12-month-old infants. Given the soothing effects of affective touch on infant physiological arousal (Fairhurst et al., 2014), together with the proposed association between affective touch and interoceptive processing development (Crucianelli and Filippetti, 2018; Montirosso et al., 2011; Tuulari et al., 2019), whether affective touch modulates the infant's physiological response to emotion processing would appear to an important consideration in dyadic interactions. In fact, affective touch has been shown to modulate social engagement in infants (Della Longa et al., 2021). In this study, affective touch administered to 4-month-olds synchronously with visual stimuli of different faces was associated with enhanced engagement, measured by increased looking time, with those faces which had been presented with affective touch. This suggests that affective touch not only enhanced visual attention, but is also involved in the salience of social cues.

To examine the effects of affective touch on pre-verbal infant emotional arousal and the processing of different emotions, suitable physiological correlates of emotion processing and ANS arousal are required. Heart rate and electrodermal response are two measures which have been associated with emotional arousal in response to ANS activity (Carlson and Birkett, 2017; Ham and Tronick, 2000; Wass et al., 2018). Methods for collecting both measures are non-invasive and simple to implement in a laboratory setting, rendering them suitable for use with infants. To investigate whether affective touch is associated with any changes to physiological responses during infant emotion processing, I conducted a between-groups pilot test to examine infant heart rate and electrodermal activity in response to the processing of different emotions. One group received affective touch from their caregivers while seated on their laps, while the other group sat on their caregivers' laps without receiving affective touch.

By asking caregivers to administer affective touch in a laboratory setting and observing their infants' physiological responses to the processing of different emotions, I hoped to provide more detailed insight into the regulatory role of affective touch across different emotional states, potentially shedding light on the role of affective touch and the influence of caregivers' behaviours in the development of interoceptive processing during infancy. I hypothesised that infants would demonstrate higher levels of arousal in response to negative, rather than positive or neutral emotions, consistent with previous studies (e.g. Wass et al., 2018). In addition, based on empirical studies of affective touch described above, I expected affective touch to have a regulatory (soothing) effect on ANS arousal and that this effect would be more visible in the processing of negative emotions than positive or neutral emotions (Beebe and Lachmann, 2002; Fairhurst et al., 2014; Kidd et al., 2023).

4.2.2 Method

Participants

For the pilot study, seven healthy, full term 6- to 8-month-old infants (5 girls, mean age 217 days) and their (all female) primary caregivers were invited to take part in this pilot study, via the University of Essex Babylab database of local families. Ethical approval was gained from the University of Essex Ethics Sub-Committee (CCo1901).

Measures

Electrodermal activity

EL512 low tack electrodes were attached to the plantar surface of the infant's foot, as per see Figure 2.1, above, then covered with an elasticated bandage and sock, as proposed in a previous methodological study (Ham and Tronick, 2008). Electrodermal activity was recorded using a Nexus10 MkII.

Infant heart rate

To record infant heart rate, three EL512 low tack electrodes were attached to the chest and abdomen in a conventional Lead II setup, see Figure 2.2. Cardiac data was recorded at a sampling rate of 2000Hz. The infants vest or t-shirt were then replaced over the electrodes and the infant distracted, to enable them to get used the sensation and to distract them from any attempts to remove the electrodes. Heart rate was recorded simultaneously with electrodermal activity, using the Nexus10 MkII.

Procedure

Once infants and their caregivers had been welcomed to the Babylab and briefed on the procedure, infants were seated on their caregivers' laps while electrodes were attached for the recording of cardiac and EDA data.

Infants were seated on their caregiver's lap approximately 90cm from a monitor adjusted to the infant's eye level. Twelve 3-second videos of actors portraying happy, sad, and fearful emotions were presented in random order. These target videos were alternated with another 12 videos of animals to serve as a baseline.

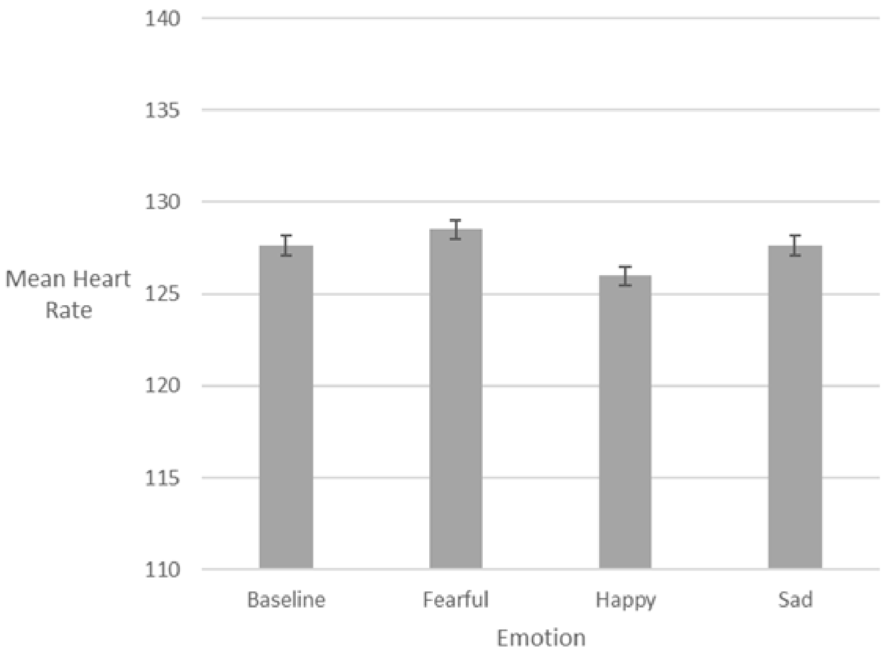
The videos were created using static images of facial expressions depicting neutral, happy, sad and fearful emotions. These images were used to create morphing videos using Abrasoft Fantamorph. The movies started with a neutral expression for one second, then gradually morphed into the target expression over the next one second, and paused on the target expression for one second. Four actors —two male and two female, from different ethnic backgrounds— were selected from the NimStim database (Tottenham et al., 2009).

Infants were to be randomly allocated to either the 'affective touch' or the 'no affective touch' condition to allow a between-group comparison. Caregivers in the 'affective touch' group were going to be provided with instructions and training on administering affective touch in the form of regular, slow stroking of their infant's arm, at approximately 7-8 cms/second, within the definition of affective touch described in the 1.3.2. However, the study was halted due to the COVID-19 pandemic before full testing began. By the time the Babylab closed, seven caregiver-infant dyads had participated in the pilot study, all of them being allocated to the 'no affective touch' condition. Therefore, the following results section presents heart rate data from the infants whilst watching videos of adult faces displaying fearful, happy, and sad emotions. Unfortunately, the short duration recordings in this pilot test rendered meaningful assessment of EDA responses impossible, due to their slower wave forms combined with their tonic and phasic components.

4.2.3 Results

Figure 4.1 displays changes in mean heart rate with each emotion watched by the infants. Infants' heart rates increased relative to baseline when processing sad and fearful faces, but decreased when observing happy faces. This pattern was observed in every participant in the pilot study.

Figure 4.1
Mean Heart Rate During Each Emotion



Note: Mean heart rates are calculated across all participants and trials. Error bars represent standard error.

4.2.4 Discussion

Due to the halting of this study at the beginning of the COVID-19 pandemic, the results presented here are only from the pilot stage of this study, in which only 7 participants took part, all without affective touch from the caregiver. No meaningful analysis could be conducted with such a small amount of pilot data. However, the testing protocol appeared valid and the minimal data that was collected supported feasibility of a full study using this methodology.

The small data set from this pilot study was consistent in indicating that infant heart rate increased when processing negative emotions relative to positive emotions. This is in line with previous research findings indicating larger magnitude responses to negative emotion and that such arousal is more long lasting than responses involving positive emotions (Maister et al., 2017; Wass et al., 2018). The consistent results relating changes in heart rate elicited during emotion processing using this method do justify further use of this method in the study of the role of affective touch on infant physiology during emotion processing. Once this pilot study had been halted due to the pandemic, it was necessary to consider alternative methods to address the research questions. As a result, studies were moved online, forcing a change in the measures which could be utilised during this time. Study 2b was conducted during COVID-19 lockdowns, while study 2c took place following the reopening of the Babylab once lockdowns were lifted.

4.3 Study 2b: The association between caregiver mental health, interoception and interactive behaviour in the caregiver-infant dyad

4.3.1 Introduction

This study sought to examine the factors which might influence the caregiver's behaviour in dyadic interactions. During dyadic exchanges, caregivers have to notice, interpret, and respond to their pre-verbal infant's behavioural cues. As described in the overall introduction to this Chapter, these tasks rely on several cognitive and emotional processes including attention, interpretation of emotional state, and inference of the infant's need or desire. The relationship between interoception, cognitive processing, and emotion discussed in Chapter 1 suggests that a caregiver's interoceptive abilities and mental health can significantly influence their behaviour during interactions with their infant. High interoceptive awareness allows caregivers to better regulate their own emotions and respond to their infant's needs more sensitively (Park and Blanke, 2019; Montirosso and McGlone, 2020). Conversely, mental health issues such as anxiety (Kaitz and Maytal, 2005; Murray et al., 2012; Nicol-harper et al., 2007; C. G. Smith et al., 2022a) or depression (Mercuri, Stack, De France, et al., 2023; N. Smith et al., 2022; Stepakoff and Beebe, 2024) may impair interoception and cognitive processing, leading to less attuned caregiving responses. These factors, in turn, affect the infant's emotional development and attachment (Abraham et al., 2019; MacCormack et al., 2020).

Since Mary Ainsworth's defining work on caregiver sensitivity, differences in caregivers' behavioural responses to their infant have long been studied in the context of infant temperament, behaviour, and attachment (e.g. Ainsworth, 1972). In addition to how sensitive, or responsive, a caregiver is to their infant, the contingency, or appropriate matching, of the caregivers response to the infant's need has also attracted considerable research in recent years (Crucianelli et al., 2019; Lohaus et al., 2001; Montirosso and McGlone, 2020). Firstly, caregiver contingency has been proposed to facilitate interoceptive processing development in infancy (Atzil et al., 2018; Fotopoulou and Tsakiris, 2017b; Filippetti, 2021). It represents an important feature of caregiver-infant dyadic interaction and varies between caregivers. Secondly, caregiver contingency requires the caregiver to infer their infant's need in order to provide an appropriately matched response to their infant. This requires the integration of cognitive skills, such as attention to their infant's cues, and memory of prior comparable experience, as well as emotional skills, such as empathy, which have in turn been hypothesised to relate to interoceptive ability (Fukushima et al., 2011). Further, caregiver responsiveness has previously been observed to relate to caregiver mental health, with higher levels of depression and anxiety being associated with reduced responsiveness (Nakić Radoš, 2021; S. L. Smith et al., 2013). Given the theoretical background of these studies, which suggest that early dyadic interactions are crucial for the development of infants' interoceptive processing, observing caregivers' responses to their infants in a controlled setting — along with assessing their own mental health and interoceptive abilities — could provide valuable insight into the factors influencing the infant's interoceptive development.

As discussed in Chapter 2 (Section 2.3), one method for examining dyadic interactions in a controlled laboratory setting is through use of behavioural paradigms allowing the manipulation of caregiver's behaviour. A frequently used structured task for this purpose is the Still Face Paradigm, SFP (Tronick et al., 1978). The SFP has been used in many studies of infant development (see Mesman et al., 2009 for an overview and meta-analysis) and I described and discussed this task in detail in Chapter 2 (2.3). However, my specific focus in the present study was on examining individual differences in caregiving behaviour. Specifically, could caregivers' mental health and interoceptive abilities shape their responses to their infant? To this aim, I developed an adapted version of the SFP. In this modified SFP, the Responsive Still Face Paradigm (RSFP) the focus is on each individual caregiver's decision over when to reinstate an interaction with their infant. As in the original SFP, the RSFP asks the caregiver to interact playfully with their infant, for a baseline period of 2 minutes. Then, again as in the classic SFP, the caregiver is asked to abruptly stop interacting with their infant and adopt a neutral expression, avoiding all interactive behaviours, such as eye contact, movement, touch and vocalising (the still face period). In a departure from the original SFP, the caregiver is then asked to hold the still face period for a duration *of their own choosing* based on their own comfort, rather than for a fixed duration (as in the original SFP). I wanted to examine whether a caregiver's comfort level while resisting interacting with their child and maintaining a still face — measured by the duration they chose to do so — was related to their mental health and interoceptive abilities. This modification to the SFP, the RSFP, requires the caregiver to make a decision about when to interact with their infant. This decision is likely to be influenced by the way each caregiver and infant normally interact, which requires some level of prediction of their infant's behaviour. Indeed, study of dyadic interaction has highlighted the uniqueness of each dyad's communication style (Provenzi et al., 2018). This is likely to relate to the infant's usual behaviour and reactivity, highlighting infant temperament as an important factor in how caregivers respond to their infants.

Infant temperament has previously been related with differences in caregiver behaviour (Mäntymaa, Puura, et al., 2006). At two to three months of age, infant distress and fussiness was related to increased distress in caregivers, increasing the caregiver's perception of their infant as difficult and, importantly, predicting reduced quality of dyadic interactions. This highlights the potential bi-directional influence between caregiver and infant in dyadic interactions. Infant temperament is also associated with infant vagal tone. For example, 12-week-old infants with higher baseline cardiac vagal tone demonstrate more positive temperamental behaviours than those with lower vagal tone (Huffman et al., 1998). This could indicate better emotion regulation consistent with the adult literature (e.g. Porges et al., 1994). In the present study, I deemed it important to consider the role of infant temperament in the caregiver's response during tasks such as the RSFP. For example, an infant who might be usually considered to be quite placid, who then becomes extremely upset in a behavioural task, might be considered to be responding differently from an infant that is usually considered to be more emotionally reactive who then shows only a small reaction to the same behavioural task. In other words, the infant's usual temperament is likely to be associated with the duration of the still face period that the caregiver is comfortable to maintain. The infant's signals to caregivers represent the primary method of achieving physiological regulation in infancy. If these signals are suboptimal, this can lead to incorrect responses from the caregivers. According to the theoretical accounts of interoceptive development (Atzil et al., 2018; Filippetti, 2021; Fotopoulou and Tsakiris, 2017a), frequent incorrect responses from caregivers could, in turn, hamper further interoceptive development, demonstrating a vicious cycle.

Caregiver mental health is considered a risk factor for child development (e.g. Elmore and Crouch, 2020; H. Y. Lee et al., 2020; Racine, 2020; Vostanis et al., 2006). The most prevalent mental health difficulties are anxiety and depression, both in wider society (Spytska, 2023; Steel et al., 2014) and among new parents (Parfitt and Ayers, 2014). In addition, mental health difficulties tend to follow family patterns (Beidel and Turner, 1997; Warren et al., 2003), although precise mechanisms for these patterns are unclear. Importantly, both anxiety and depression have been widely examined in the context of their influence over parenting behaviours (e.g. Kaitz and Maytal, 2005; Murray et al., 2007; Murray et al., 2012; N. Smith et al., 2022), but see Section 1.3.3. for discussion). In addition, caregiver mental health is related to impaired developmental outcomes for the child (e.g. Feldman and Eidelman, 2007; Hoffman et al., 2017). Taken together, these studies suggest the caregiver mental health is an important consideration in the development of interoceptive processing in their infants, since it can influence how they respond to them. This is especially important since contingent caregiving responses are proposed to be fundamental in interoceptive processing development (Atzil et al., 2018; Filippetti, 2021; Fotopoulou and Tsakiris, 2017a).

In addition to caregiver mental health, as explained in Chapter 1 (Section 1.3.3), caregiver interoception has also been related with caregivers' abilities in dyadic interactions (Fotopoulou and Tsakiris, 2017a; Montirosso and McGlone, 2020) and emotion regulation outcomes for their infant (e.g. MacCormack et al., 2020; Pratt et al., 2015). Interoceptive information informs the autonomic nervous system. In turn, parasympathetic regulation, facilitated by vagal activity informs emotion experience and emotion regulation (Porges et al., 1994), which relates to empathy. This is important for caregivers, since their own emotional experience and emotion regulation has been related to mentalizing abilities (Fonagy and Target, 1998). Mentalizing is an important skill for caregivers, since they must learn to attribute mental states to their infant, in order to provide contingent responses to their infant's behavioural cues. As discussed in Section

1.3.1, caregiver contingency is considered fundamental in the development of interoceptive processing in the infant (Atzil et al., 2018; Fotopoulou and Tsakiris, 2017a; Filippetti, 2021). Therefore, caregivers' interoceptive processing could underpin their interactive behaviour with their infant. Interoception has been described in terms of several, dissociable, dimensions (Gabriele et al., 2022; Garfinkel et al., 2015; Murphy, Bird, and Catmur, 2019; Nord and Garfinkel, 2022). These different dimensions of interoception have been found to relate to emotion regulation and mental health in different ways (Nord and Garfinkel, 2022), therefore it is important to consider them individually. I decided to focus on interoceptive accuracy and interoceptive attention in the studies presented here, since these two dimensions offer insights into one's ability to perceive bodily signals, as well as a behavioural aspect of interoception, in terms of how one attends to those sensations. In the RSFP, participants are asked to base their attention on how they are feeling. This requires them to be aware of their own arousal and emotional state, which, as discussed in 1.2.3, is related to their interoceptive information. Measuring caregivers' interoceptive accuracy as well as how much attention they usually pay to their interoceptive signals, i.e. their interoceptive attention, could therefore provide valuable insight into how caregivers decide when to re-engage with their infant.

In this study, caregiver interoceptive accuracy, interoceptive attention, anxiety, and depression were all considered as predictors of caregiver behaviour. To observe caregiver behaviour in a structured task, I used the modified version of the still face paradigm, the RSFP task described above. I hypothesised that (1) higher scores on caregiver mental health screening questionnaires would relate to a shorter duration of the still face period, suggesting greater emotional discomfort to resist interacting with their infant, (2) that caregivers with greater interoceptive accuracy and lower interoceptive attention would feel more comfortable during the still face period and therefore hold the still face longer and (3) that infant temperament would be related to the still face duration, due to caregivers' familiarity with their infant's temperament. Specifically, I hypothesised that higher surgency and lower negative affect would be associated with longer still face durations.

This study was developed and begun during the COVID-19 pandemic, with national lockdowns preventing working face to face with participants in the laboratory. As a result, this study was conducted online, using the Children Helping Science platform (Scott and Schulz, 2017).

4.3.2 Method

Participants

Primary caregivers and their six- to eight-month-old infants were recruited online, via the ChildrenHelpingScience.com website (Scott and Schulz, 2017). Participants were selected based on the child age, having already signed up to the website to take part in studies developed and promoted via the Children Helping Science website. Fifty-two (all female) primary caregivers and their full term, healthy infants (22 boys, 30 girls, infant mean age = 6.89 months, SD = 18.82 days) attempted to complete the study. However, of these, two caregivers did not complete the mental health questionnaire. Eight dyads failed to complete the follow-up questionnaire and six dyads failed to upload a video of their RSFP task resulting in a final sample of 36 caregiver-infant dyads. Ethical approval was gained from the University of Essex Ethics Sub-Committee (ETH2324-0590).

Measures

Caregiver interoception

Caregiver interoceptive accuracy and interoceptive attention were measured using recently-developed self-report scales, The Interoceptive Accuracy Scale, IAS, (Murphy et al., 2020) and the Interoceptive Attention Scale, IATS (Gabriele et al., 2022). These scales differentiate between how accurately someone responds to their bodily sensations, and how much they focus on their bodily sensations, in terms of their interoceptive attention. The Interoceptive Accuracy Scale, IAS (Murphy et al., 2020) is a 21-item self-report questionnaire which asks participants to assess their own ability to accurately perceive a wide variety of bodily sensations and indicate their agreement on a 5-point Likert scale, from 1, Disagree Strongly, to 5, Strongly Agree. The IAS demonstrated a significant correlation with an objective measure of accuracy on the Heartbeat Detection Task, HDT, (Schandry, 1981), providing a suitable alternative to a measure of interoceptive accuracy that could have been utilised in the laboratory (see Chapter 2 for a detailed discussion on methods of measurement of interoception). The IAS offered a self-reported measure of caregiver interoceptive accuracy suitable for use in a remote, online study. Caregiver IAS scores ranged from 61 to 101 (M=86.14, SD=9.27). Murphy et al. (2020) report a Cronbach's alpha of .88, indicating good internal consistency. In this study, Cronbach's alpha was .87.

The Interoceptive Attention Scale, IATS (Gabriele et al., 2022) was also used, to measure how much attention caregivers paid to their bodily sensations. Like the IAS, the IATS is a self-report questionnaire suitable for use in a remote, online study. It asks participants the degree to which they agree with statements about how long their attention is focused on a variety of bodily sensations, again on a 5-point Likert scale across 21 items. IATS scores ranged from 21 to 81 (M=40.33, SD=14.25). Gabriele et al. (2022) report a Cronbach's alpha of .91. In this study, Cronbach's alpha was .95.

Infant temperament - the Infant Behaviour Questionnaire (IBQ)

Infant temperament was assessed with the IBQ-Revised Very Short Form, IBQ-R VSF (Putnam et al., 2014) and the IBQ-Revised, IBQ-R (Gartstein and Rothbart, 2003). The IBQ-R VSF comprises 37 items separated to provide three broad scales: Surgency, Negative Affect, and Orienting/Regulatory Capacity(Putnam et al., 2014). Since the SFP and RSFP are designed to elicit a small stress response in the infant, in addition to these scales I also included the scales for Distress and Falling Reactivity from the IBQ-R (Gartstein and Rothbart, 2003). The temperament subscales of the IBQ questionnaires are discussed previously, in 2.5.4. The IBQ questionnaires ask caregivers to rate how often their infant has shown a specific behaviour during the past week by scoring the behaviour between 1, never and 7, always. Caregivers also have the option of NA, does not apply, and NA scores are excluded from analysis. Putnam et al. (2014) reported an average Cronbach's alpha of .75 or above for the three broad IBQ-R VSF scales. In this study, Cronbach's alpha for Surgency was .72, for Negative Affect it was .86 and for Orienting/Regulatory Capacity it was .73. An overview of a number of studies using different versions of the IBQ-R revealed that Cronbach's alpha for Distress and Falling Reactivity ranged between .74 and .79 (M = .76) and between .76 and .84 (M = .80), respectively, when using the short version of the IBQ-R (Putnam et al., 2014). In the current study, Cronbach's alpha for the Distress scale was .64 and for the Falling Reactivity alpha was .76.

Caregiver still face duration in the Responsive Still Face Paradigm, RSFP

For the RSFP, caregivers were asked to arrange their infant's highchair so they were sitting facing each other. As in the original paradigm, an initial interactive period of two minutes was recorded. During this interactive period, caregivers were asked to interact with their infant "as they would normally do." Once the two-minute interaction had been recorded, a bell sounded, to indicate the end of the interaction period. The caregiver was instructed to ignore the bell, but continue interacting with their infant, as I expected the infants could be distracted by the bell. The caregivers were instructed to wait until they had regained their infant's full attention after any such disruption. The caregivers were instructed to then abruptly stop interacting with their infant and adopt a still, neutral expression. The caregiver was instructed to slightly avert their gaze, thus avoiding eye contact with their infant, and to refrain from moving, and interacting in any way (e.g. talking or touching) their infant. Importantly, I modified the original paradigm by not specifying the duration of the still face period. Instead, I asked the caregiver to maintain the still face for "as long as they felt comfortable." Caregivers were told they were free to end the still face period at any point. Once the caregiver had resumed interacting with their infant, a further two minutes of interaction was recorded for the 'Reunion' period, back in line with the original paradigm. Videos of this task were uploaded and saved by the caregiver on the *ChildrenHelpingScience.com* website and the duration of the still face period was verified offline at a later stage. The offline coding and analysis of the still face duration was conducted using ELAN 6.4, a freely available download (Lausberg and Sloetjes, 2009). Behavioural coding was conducted by me and one other PhD candidate, PR. Precise descriptions of the behaviours indicating the beginning and end of the still face period were provided, along with training and practice. Intraclass correlation coefficients (ICC) were calculated to assess the agreement between raters coding the still face duration. A two-way random-effects model was used to compute ICC. The ICC value was 0.758 (95% CI [0.522, 0.887]), $p < .001$, indicating good agreement between the raters.

Caregiver mental health

After completing the RSFP, caregivers were asked to complete a mental health questionnaire, comprising the Generalised Anxiety Disorder Assessment - 7 (GAD-7, Spitzer et al., 2006) anxiety questionnaire and the Patient Health Questionnaire - 9, (PHQ-9, Kroenke and Spitzer, 2002) depression screening. These questionnaires are used frequently in healthcare settings as initial screening tools for anxiety and depression. They are relatively short and can be easily utilised in online studies. The participant is asked to think about how they have felt over the previous two weeks, then rate the frequency of symptoms experienced on a Likert scale questionnaire, with each item scored from 0 (not at all) up to 3 (nearly every day). The GAD-7 scale combines questions on physiological, cognitive and emotional aspects of anxiety to produce a GAD-7 score out of 21 based on 7 items. Clinical cut-offs are 5, 10 and 15 for mild, moderate and severe anxiety, respectively. Despite its brevity, the GAD-7 has been found to correlate with the STAI, a longer questionnaire often used in psychology research to distinguish between short-term fluctuations in anxiety *state* and longer-term, embedded *traits* of anxiety (Manzoni et al., 2018. Spitzer et al. (2006) reported Cronbach's alpha of .92 for the GAD-7 scale as a measure of generalised anxiety in clinical samples. Subsequently, Lowe et al. (2008) reported a Cronbach's alpha of .89 when the scale is used in the general population. In this study, Cronbach's alpha for the GAD-7 scale was .77.

The PHQ-9 scale works similarly to the GAD-7, asking participants to rate symptom frequency during the previous two-week period, but is based on 9 items to produce a score out of 27. Clinical cut offs are 5, 10, 15 and 20 for mild, moderate, moderately severe and severe depression, respectively. Kocalevent et al. (2013) reported a Cronbach's alpha of .87 when used as a screening tool in the general population. In this study Cronbach's alpha was .85 (Kocalevent et al., 2013).

Procedure

Given the online nature of the study, the caregiver required a PC or laptop with a webcam to participate. The caregiver was asked to seat their infant in a highchair and to sit facing their infant with the webcam positioned sideways on, so that both participants could be seen. Caregivers were first provided with a description of the study and an online consent form. Once happy to proceed, caregivers provided video-recorded consent via the ChildrenHelpingScience.com website. Instructions for carrying out the RSFP, as described above, were provided on screen, after logging in to the ChildrenHelpingScience.com website. Caregivers were able to stop and repeat the task, should their infant become fussy or in case of other interruptions. After completing the recording of the RSFP, the caregiver was asked to complete the GAD-7 and PHQ-9 brief clinical scales of anxiety and depression symptoms. Caregivers were then fully debriefed on the study. In the debrief, caregivers were informed that I would be analysing whether scores on the GAD-7 and PHQ-9 scales related to the duration of the still face. It was explained that the use of mental health scales was concealed until after the behavioural task, to prevent alterations to their behaviour during the interaction. Caregivers were then asked to re-confirm their consent in light of this additional information, along with being given the opportunity to withdraw their consent at this point. Safety and risk signposting regarding emotional wellbeing was provided and caregivers were then directed to the exit questionnaire. The exit questionnaire comprised the Interoceptive Accuracy Scale, (Murphy, Bird, and Catmur, 2019), the Interoceptive Attention Scale, (Murphy et al., 2020) and the Distress and Falling reactivity subscale of the Infant Behaviour Questionnaire-Revised - Very Short form, (Rothbart, 1981; Gartstein and Rothbart, 2003; Putnam et al., 2014). Caregivers attempting to complete the study were thanked for their time and sent an online US$5 Amazon voucher via email.

4.3.3 Results

Descriptive statistics

Descriptive statistics of all variables are provided in Table 4.1.

Table 4.1
Study 2b Descriptive Statistics for all Variables

	N	Minimum	Maximum	Mean	Std. Deviation
PHQ-9 Score	50	0.00	15.00	3.58	3.65
GAD-7 Score	50	0.00	18.00	3.34	3.79
Interoceptive Accuracy Score	43	61.00	105.00	86.14	9.27
Interoceptive Attention Score	43	21.00	81.00	40.33	14.25
Still Face Duration	46	0.49	115.13	34.06	27.82
IBQ Scale 1: Surgency	43	3.31	6.33	4.90	0.80
IBQ Scale 2: Negative Affect	43	1.92	5.92	3.98	0.95
IBQ Scale 3: Orienting/Regulatory Capacity	43	3.75	6.42	5.28	0.66
IBQ Scale 4: Distress	43	1.92	5.52	3.52	0.72
IBQ Scale 5: Falling Reactivity	43	3.38	6.92	4.86	0.76

Caregiver mental health

The GAD-7 screening tool was used as a brief measure of caregiver anxiety, (Spitzer et al., 2006). GAD-7 Scores ranged from 0 to 18 (M = 3.34, SD = 3.79). Nine caregivers scored above the clinical cut-off for mild anxiety, three caregivers scored above the clinical cut-off for moderate anxiety, and one scored in the severe anxiety category. The PHQ-9 screening tool was used alongside the GAD-7 questionnaire, as a brief measure of caregiver depression (Kroenke et al., 2001). PHQ-9 Scores ranged from 0 to 15 (M = 3.58, SD = 3.65). Eleven caregivers scored above the clinical cut-off for mild depression and two caregivers scored above the clinical cut-off for severe depression, with no caregivers scoring in the moderate category. The distribution of GAD-7 and PHQ-9 scores is displayed in Table 4.2.

Table 4.2
Caregiver Mental Health Scores

	None (0-4)	Mild (5-9)	Moderate (10-14)	Severe (15+)
Caregiver anxiety (GAD-7)	37	9	3	1
Caregiver depression (PHQ-9)	37	11	0	2

Preliminary exploratory analyses

Bivariate correlations were conducted between the variables of interest, to explore the relationships between them and to inform inferential analyses. Several variables of interest were not normally distributed (Still Face duration, $D(46) = .151$, $p = .011$, GAD-7, $D(50) = .196$, $p < .001$, PHQ-9, $D(50) = .263$, $p < .001$, IATS, $D(42) = .134$, $p = .051$), so Spearman's ρ correlations were calculated and are displayed in Table 4.3, including Bonferroni-corrected significance level for multiple comparisons ($p < .006$).

Table 4.3
Correlations between Caregiver Interoception, Caregiver Mental Health, Still Face Duration and Infant Temperament

		1	2	3	4	5	6	7	8	9
1	PHQ-9 Score									
2	GAD-7 Score	.590**								
3	Interoceptive Accuracy Score	-.215	-.130							
4	Interoceptive Attention Score	.056	-.100	-.376*						
5	Still Face Duration	-.077	-.154	-.063	-.036					
6	IBQ Scale 1: Surgency	.017	.230	.345*	-.198	-.274				
7	IBQ Scale 2: Negative Affect	.116	.119	.193	-.021	-.026	.482**			
8	IBQ Scale 3: Orienting/Regulatory Capacity	-.278	-.108	.321*	-.366*	-.190	.289	.269		
9	IBQ Scale 4: Distress	.201	.010	.121	.141	-.073	.168	.465**	-.038	
10	IBQ Scale 5: Falling Reactivity	-.074	.069	.006	-.183	-.035	-.014	-.470**	.089	-.396**

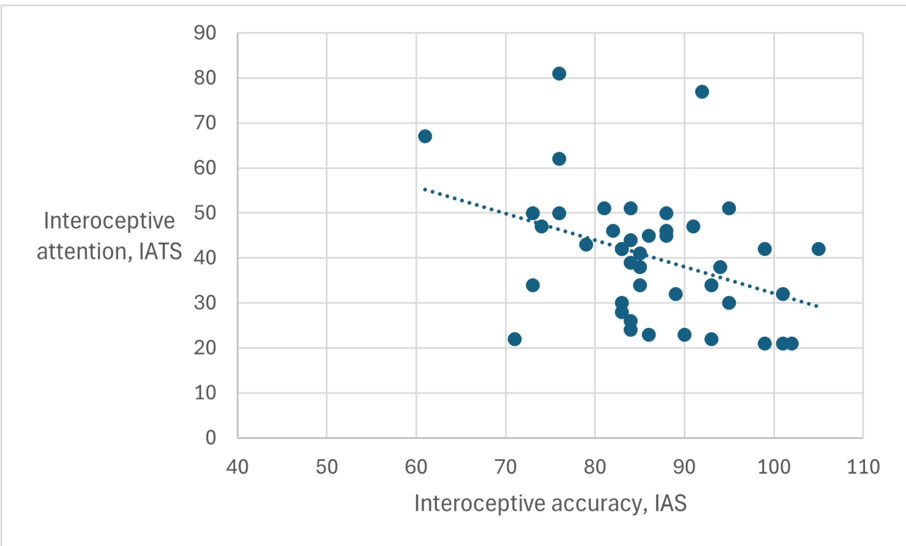
Note * $p < .05$
** $p < .006$ (Bonferroni-corrected significance level)

Several significant correlations were observed within the infant temperament data: Surgency was positively related with negative affect (ρ = .48, p < .001). Negative affect was positively related with distress (ρ = .47, p = .002) and negatively related with falling reactivity (ρ = .47, p = .001). Distress was negatively associated with falling reactivity (ρ = .40, p < .009)

Several further correlations were observed between caregiver interoception and infant temperament, however these did not survive Bonferroni correction. Caregiver interoceptive accuracy was found to be positively related with infant surgency, ρ = .35, p = .025. Interoceptive accuracy was also positively related with orienting/regulatory capacity, ρ = .32, p = .038, indicating infants of caregivers with greater interoceptive accuracy demonstrated greater orienting/regulatory capacity. Additionally, interoceptive attention was negatively related with orienting/regulatory capacity, ρ = -.37, p = .017, indicating caregivers who paid more attention to their interoceptive signals had infants demonstrating lower orienting/regulatory capacity.

Neither depression nor anxiety were associated with the other variables of interest. Interoceptive accuracy (IAS) was negatively correlated with interoceptive attention (IATS). Figure 4.2 displays a scatterplot highlighting the relationship between IAS and IATS.

Figure 4.2
Scatterplot Demonstrating Negative Relationship Between Interoceptive Accuracy and Interoceptive Attention



Bayesian modelling

To explore the relationships between caregiver interoception, their anxiety, and still face duration, Bayesian linear models were produced using the Bayesian Regression Models using Stan (brms) package in R v4.0 (Bürkner, 2017).

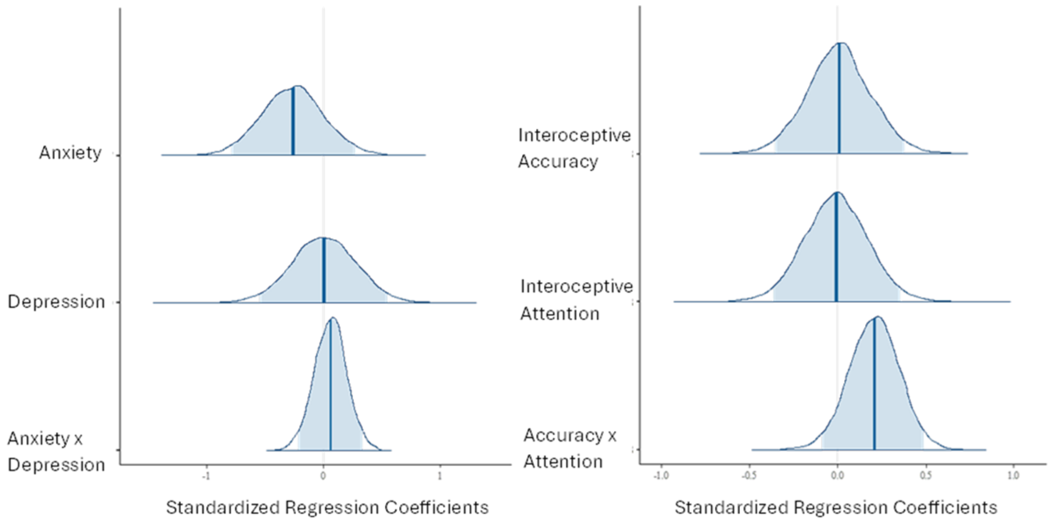
To investigate the first hypothesis, caregiver interoceptive dimensions, IAS and IATS, were examined as predictors of the still face duration. The analysis indicates that neither interoceptive accuracy (95% HPDI [-0.35, 0.38]), interoceptive attention (95% HPDI [-0.37, 0.35]), nor their interaction (95% HPDI [-0.08, 0.49]) demonstrate a clear effect on the still face period held by the caregiver.

The second hypothesis considers caregiver mental health, PHA-9 and GAD-7 scores, as predictors of still face duration. Neither anxiety (95% HPDI [-0.79, 0.27]), depression (95% HPDI [-0.55, 0.55]), nor their interaction (95% HPDI [-0.22, 0.33]) demonstrate a clear effect on the still face period held by the caregiver.

Posterior distributions with medians and 95% confidence intervals are depicted in Figure 4.3.

Figure 4.3

Posterior Distributions of Caregiver Mental Health Scores (Left) and Caregiver Interoception Scores (Right) as Predictors of Still Face Duration



4.3.4 Discussion

In this study, I sought to examine whether differences in caregiver's behaviour in a modified still face paradigm, RSFP, were associated with their own mental health and interoceptive abilities. I hypothesised that (1) higher scores on caregiver mental health screening questionnaires would relate to a shorter duration of the still face period, suggesting greater emotional discomfort to resist interacting with their infant, (2) that caregivers with greater interoceptive accuracy and lower interoceptive attention would feel more comfortable during the still face period and therefore hold the still face longer and (3) that higher surgency and lower negative affect in the infant would relate to longer still face durations.

To consider the first hypothesis, I modelled the relationship between caregivers' mental health measures and their behaviour in the RSFP and found no reliable associations between these variables, nonetheless, anxiety and depression were strongly correlated. This correlation is in line with previous studies of prevalence that have consistently shown high comorbidity between anxiety and depression both in the general population (Grant et al., 2005; Kessler et al., 2008; Noyes, 2001) and among women in the postpartum period (Dennis et al., 2017; Underwood et al., 2016). Influences of caregiver mental health on infant developmental outcomes are well-established in the literature (e.g. Feldman and Eidelman, 2007; Hoffman et al., 2017, see also Chapter 1). Therefore, it was reasonable to expect that caregiver mental health would affect caregiver behaviour towards the infant. However, the non-clinical samples of caregivers in this study were skewed towards the lower scores for anxiety and depression and, as such, it is possible that any effects of mental health were too small to observe. Alternatively, caregiver mental health could have influenced behaviour in a different way from that originally hypothesised. For example, some anxiety regarding correct interpretation of the instructions could have been present. In this case, more anxious caregivers could have been concerned about their own 'performance' in the task, perhaps trying to second-guess whether they had held the still face for either 'long enough' or 'too long.' Indeed, research has shown that both anxiety and depression are associated with rumination (Nolen-Hoeksema, 2000) and, in parenthood, rumination has been associated with child emotion regulation abilities (Wu et al., 2020). This issue has the potential to influence the still face duration in either direction. To fully explore the influence of mental health in a task such as the RSFP, future studies should focus on clinical samples of anxiety, depression and comorbid presentations, to enable meaningful comparison between the influences of anxiety and depressive disorders. Indeed, previous research has related anxiety and depression with caregiver dyadic behaviour in different ways (e.g. Mercuri, Stack, Mantis, et al., 2023; N. Smith et al., 2022; Stepakoff and Beebe, 2024; Murray et al., 2012, also see 1.3.3 for a detailed discussion). For example, depressed caregivers can respond more slowly to their infant (N. Smith et al., 2022) while more anxious caregivers can exaggerate their responses and demonstrate hyper-arousal (Kaitz et al., 2010). In my caregiver sample, however, such distinctions were not observed.

The second hypothesis considered the relationship between caregiver interoception and the still face duration. I found that neither interoceptive accuracy nor interoceptive attention, nor their interaction, demonstrated a consistent association with the duration for which caregivers maintained the still face. There was a non-significant negative association between IAS and IATS scores, consistent with previous studies of the dissociation between interoceptive accuracy and attention (Murphy, Bird, and Catmur, 2019; Gabriele et al., 2022). Caregiver interoceptive abilities have been previously related with their interactive behaviours, both empirically (Abraham et al., 2019; Donaghy et al., 2024) and theoretically (Fotopoulou and Tsakiris, 2017a; Montirosso and McGlone, 2020). Greater interoceptive accuracy, along with a further measure of interoceptive ability not measured in this study, interoceptive sensibility (Garfinkel et al., 2015; Nord and Garfinkel, 2022), could account for a more relaxed attitude of the caregiver, whereby a caregiver who accurately notices their bodily sensations, also feels confident about their interpretation of these sensations, and trusts their own internal state. This could lead the caregiver to trust their ability to infer their infant's state and therefore feel less urgency to jump to their infant's call immediately. Conversely, it is important also to consider the potential effects of low interoceptive accuracy interacting with high interoceptive attention. This describes a potential characteristic of anxiety whereby interoceptive signals are misinterpreted and simultaneously receive excessive attention, such as in panic disorders (Ehlers et al., 1995; Hoehn-Saric and McLeod, 2000). A caregiver who experiences this kind of relationship with their own body might be expected to infer a more immediate need in their infant's behaviour, leading them to respond more urgently, albeit without foundation, as demonstrated by the matching of anxious caregivers' arousal to that of their infant, even in response to small changes in infant arousal (Wass et al., 2019). To address these potential effects, the design of this study could be improved by use of implicit measures of interoceptive processing, as has been recommended recently in a review of the study of interoception and mental health (Nord and Garfinkel, 2022). Studies have revealed mixed associations between self-report and implicit measures of interoception which rely on different cognitive processes (see Desmedt, Luminet, Maurage, and Corneille, 2023 for a recent review and 1.2.2 for a more detailed discussion).

Therefore, these additional measures would enable subconscious influences of interoceptive processing to be examined in relation to caregivers' responses, rather than solely relying on self-report measures of interoception.

To examine the third hypothesis, that infant temperament would be related to the still face duration, several scales from the IBQ were included in the study. These measures were not associated with the duration of the still face held by caregivers. However, interestingly, several dimensions of infant temperament were associated with caregiver interoception, although these associations did not survive correction for multiple comparison and should be treated with caution. Higher caregiver interoceptive accuracy related to greater infant surgency, a measure of behaviours associated with positive affect, suggesting caregivers that believe themselves to be good at noticing and interpreting their bodily sensations had infants demonstrating more positive behaviours. This could suggest that caregivers more in tune with their own interoceptive signals are better at inferring and responding to their infant's needs. One possible explanation for this association is that caregivers' interoceptive abilities influences their behaviour through its impact on emotion recognition and regulation skill (Critchley and Garfinkel, 2017), in turn influencing how they interact with their infants. These skills could shape how caregivers observe and interpret their infant's behaviour, influencing their ability to accurately infer its meaning. Relatedly, the infant's own characteristics (e.g. their temperament) are likely to also shape caregiver's interpretation of the infant's needs (Somers et al., 2021).

The data also showed that higher interoceptive attention in the caregiver was associated with lower orienting/regulatory capacity in the infant. This finding suggests that caregivers who pay more attention to their interoceptive signals have infants demonstrating lower regulatory skills. There could be several explanations for this relationship. Firstly, greater interoceptive attention could indicate mistrust in bodily sensations, or anxiety related to them, such as in some anxiety disorders, e.g. panic disorder (Ehlers et al., 1995). Indeed, increased maternal anxiety has previously been associated with reduced infant self-regulation observed through measures of infant temperament (Lin et al., 2014;Korja et al., 2017) as well as via infant vagal tone (Somers et al., 2021). In these cases, the infant could be receiving incorrect or inconsistent responses from their caregiver, due to the caregiver's mistrust in their own bodily sensations, thus impairing the development of the infant's regulatory abilities. Alternatively, caregivers paying more attention to their bodily sensations could be highly responsive caregivers, perhaps denying the infant the opportunity to self-regulate. To further test these possible interpretations, a larger sample of caregivers demonstrating high interoceptive attention would need to be observed, along with a combination of behavioural observations, as well as explicit (i.e. behavioural) and implicit measures of emotion regulation (such as heart rate variability) in the infant.

It is important to consider the use of self-report questionnaires in this study. Caregivers were reporting on their own interoceptive accuracy and attention, as well as on their perception of their infant's temperament. It is possible that caregiver interoception relates to their attention to and interpretation of their infant's behaviour in the first place, so leading to associations between the responses the caregivers provided about themselves as well as about their infants. Indeed, previously, caregiver mental health has been associated with how caregivers interpret and report on their infant's temperament (Kertz et al., 2008; Mäntymaa, Tamminen, et al., 2006 Morrell and Steele, 2003).

Further exploration is also necessary to better understand whether caregiver interoception influences the development of infant temperament, or vice versa - or whether indeed these relationships are fundamentally bidirectional. Research has suggested that infant temperament begins to emerge in the first months of life and is the product of both genetic and environmental factors (Goldsmith et al., 1999), suggesting that caregiver interoception could play a part directly, through genetics, or indirectly, by influencing the caregiver's behaviour in the infant's early environment. The importance of infant temperament within dyadic interaction therefore requires careful consideration - does a fussy baby create a stressed caregiver, or does a caregiver struggling with their own emotion regulation or poor mental health provide a different early environment leading to different characteristic behaviours in their infant? Studies suggest both are likely to be true. Maternal stress during pregnancy has been associated with negative affect in infancy (Van den Bergh et al., 2020), while maternal depression symptoms in the first two weeks postpartum have been associated with infant temperament at both 4 and 6 months of age (Rigato et al., 2020). While these findings indicate that maternal mental health influences the emergence of infant temperament, studies have also highlighted effects in the opposite direction, i.e. that infant temperament can also influence maternal mental health (J. R. Britton, 2011; Somers et al., 2021).

Consideration of a caregiver-chosen still face duration in the task used here raises a further important question; Is there an optimum response time? If the still face duration is, indeed, representative of caregiver sensitivity and/or contingency in natural settings, responding too soon could prevent the infant from getting to notice and understand their own internal signals fully or learning how to communicate their needs to their caregiver clearly. Responding too slowly, by contrast, could lead to the infant not having their needs met, also denying them the opportunity to learn to trust their bodily sensations through the reinforcement provided by consistent, appropriate care. In very extreme cases, these opposite actions could represent overly attentive parenting, often referred to as *helicopter parenting*, where caregivers are highly responsive to their offspring, potentially limiting the space in which the child can learn to self-regulate (Carone et al., 2022), or neglect, where caregivers fail to notice and attend to the needs of their child. In the case of attentiveness, more anxious parents have demonstrated matching of their arousal state with that of their infant in response to small changes in infant arousal (Wass et al., 2019). Less anxious caregivers, on the other hand, demonstrated this matching ability only during greater peaks of infant arousal. In between these extremes, communication between the infant and caregiver may often become mismatched in daily interactions. Montirosso and McGlone (2020) highlight the importance of repairing these breaks through close proximal contact and touch for the infant's development of a sense of self. This would suggest that an optimum lies somewhere in the middle, where caregivers are responsive, but that inevitable breakdowns in communication provide opportunities for the infant to learn. Indeed, Beebe et al. (2010) proposed previously that an optimal middle level of synchronicity allows space for growth and learning for the infant. However, given the individual differences in personality and temperament, as well as individual differences in interoception, mental health and behavioural styles, the 'optimum' level of responsiveness is likely unique to each caregiver-infant dyad. A suitable response time from caregivers could therefore be considered to be one that enables infants to gradually learn to recognise their own sensations and predict their own needs, in response to their experience and with the close backup of their caregiver to provide reinforcement.

While examining the still face duration in the data collected within the study, it was noticeable that caregivers' decisions to end the still face period were often not driven by any observable infant behaviour, such as fussiness. This suggests that some other trigger, other than the infant's cues, drove the caregiver's decision to end the still face. It would have been interesting to gain further insight into how the caregiver was feeling at this time, and what made them re-engage with their infant at the precise time that they did. In the absence of a clear infant cue, I can only assume that some internal processes for the caregiver, such as feelings of uneasiness, specific cognitive processing regarding what they believed their infant needed, fear of judgement by the experimenter or a simple desire to talk to their infant again was driving their behaviour. Future studies should collect this information immediately following the task, to help clarify the reasons behind caregivers' decision to re-engage with their infant.

The empirical results presented in this study partially support the theoretical foundation of this thesis by highlighting potential relationships between caregiver interoceptive abilities and infant characteristics, such as temperament. While, as discussed above, the data collected here do not fully support the hypotheses set out for this study, they do provide important insight into the interplay between caregiver's and infant's factor within the context of dyadic interactions. However, this study has several limitations. In addition to focusing on a non-clinical sample, another limitation was related to the data collection method. Because the study was conducted during the COVID-19 lockdowns, it had to be run online, which prevented caregivers from asking questions or clarifying instructions in real-time. Although all caregivers appeared to understand the instructions, it remains impossible to know to what extent caregivers followed the instruction to focus on their own feelings during the MSFP. I Study 2c, I sought to address this by using a similar design in a face-to-face study.

In the next study, 2c, below, I looked beyond the caregiver and infant behaviour to examine whether there is evidence that caregiver interoception and mental health are related to physiological arousal and vagal tone in the infant. If such relationships exist, it could offer converging evidence that the development of infant interoceptive processing develops in the context of caregiver interoception, their mental health, and caregiving behaviours.

4.4 Study 2c: Associations between caregiver mental health and interoception, interactive behaviours and infant vagal tone

4.4.1 Introduction

Following on from the behavioural observations of Study 2b, in Study 2c I sought to combine observation of caregiver behaviour in the RSFP with evidence of physiological arousal and interoceptive processing in the infant. As discussed in Chapter 1 and in the introduction to this chapter, interoception plays a fundamental role in the physiological experience of emotion. However, interoceptive attribution, the meaning attributed to bodily sensations (Nord and Garfinkel, 2022), can vary between individuals, and misinterpretations of interoceptive states can characterise panic and anxiety disorders. For example, noticing a pounding heart when anxious could be misinterpreted as a symptom of a heart attack in the case of panic disorder (Ehlers et al., 1995; Hoehn-Saric et al., n.d.). In the case of sub-clinical anxiety, a wide variety of sensations occur commonly, including raised heartbeat, sensations in the stomach, light-headedness, etc. In more severe cases, however, it is the response, such as intolerance or misattribution of these sensations that causes alarm. While older children and adults are able to report such experience, to observe and measure this activity in pre-verbal infants, I must utilise implicit measures of arousal based on the available evidence and infer their meaning. Cardiac activity has been shown to demonstrate autonomic nervous system activity non-intrusively. Infant heart rate variability, HRV, discussed in Chapter 2, is increasingly being used as a measure of infant physical and emotional wellbeing. For example, HRV is an established measure in identifying health complications, such as the risk of sepsis (Javorka et al., 2017; Oliveira et al., 2019), as well as the impact of prenatal stress on fetal brain development (Frasch et al., 2020; Lobmaier et al., 2020). HRV has also been suggested to relate to infant stress and stress-behaviours, with greater heart rate variability being associated with better emotion regulation outcomes (Gardner et al., 2018; Hashiguchi et al., 2020).

One account for the relationship between HRV and emotional wellbeing has been proposed by PolyVagal Theory, PVT, (Porges, 1995a; Porges, 1992; Porges, 1995b Porges, 2001), discussed in detail in Chapter 1. PVT describes the relationship between HRV and respiratory sinus arrhythmia (RSA) as vagal tone, a measure of the performance of the vagus nerve in regulating physiological state in relation to emotion and social connection. When considering physiological arousal associated with feelings of anxiety, the vagal tone has been found to relate to symptom perception (Friedman, 2007). Several methods for measuring vagal tone have been reported previously (Laborde et al., 2017). However, the most simple, involving the least equipment, and therefore the most suitable for use with infants, is to extract the root mean square of successive differences between heartbeats, RMSSD. RMSSD has been found to act as a suitable proxy for vagal tone (Laborde et al., 2017).

Caregiver mental health has previously been associated with infant vagal tone. Specifically, maternal depression has been associated with reduced vagal tone in their infants at six months of age (T. Field et al., 1995). In addition, this study identified different developmental trajectories of vagal tone between 3 and 6 months for infants of depressed versus non-depressed mothers. An alternative view presented by Somers et al. (2021) highlighted the bi-directional nature of this relationship, with infants with lower vagal tone more likely to demonstrate negative behaviours, resulting in greater maternal stress. Infant vagal tone has also been associated with early dyadic interactions, whereby greater synchrony in the dyad has been related to increased infant vagal tone (Porter et al., 1995). The use of infant vagal tone as a proxy measure of interoceptive processing was discussed in more detail in Chapter 1 (1.3.1).

In this study, I repeated the RSFP used online in Study 2b, this time in a laboratory setting. In addition to the measures described in Study 2b relating to caregiver interoception and mental health, Study 2c also examined infant vagal tone, as an indicator of interoceptive processing and emotion regulation, along with infant heart rate, as a measure of emotional arousal, at each stage of the RSFP. Once again, the theoretical rationale for this study is the suggestion that early dyadic relationships facilitate the development of interoceptive processing (Atzil et al., 2018; Filippetti, 2021; Fotopoulou and Tsakiris, 2017a). Based on the PVT's proposition that higher vagal tone is related to better emotion processing and that it develops in relation to early social experience (Porges et al., 1994), I hypothesised that (1) caregiver mental health would be related to infant vagal tone, with higher depression and anxiety being associated with lower infant vagal tone, (2) caregiver interoception would be related to infant vagal tone, with higher interoceptive accuracy and lower interoceptive attention being associated to higher infant vagal tone, (3) caregiver mental health would influence the still face duration, with higher mental health scores predicting reduced duration, (4) caregiver interoception would also influence the still face duration, with higher interoceptive accuracy and lower interoceptive attention predicting longer still face duration, and (5) infant temperament would be associated with infant vagal tone, with higher vagal tone being associated to higher regulatory capacity and surgency.

4.4.2 Method

Caregivers and their infants were recruited via the University of Essex Babylab database. Interested caregivers were provided with information about the study and invited to book a visit to the Babylab. Once this appointment was booked, caregivers were asked to complete their first questionnaire online, before their visit to the lab. This questionnaire comprised the Interoceptive Accuracy Scale, (Murphy, Bird, and Catmur, 2019), the Interoceptive Attention Scale, (Murphy et al., 2020), the Surgency, Negative Affect, and Orienting/Regulatory Capacity scales from the IBQ-R VSF (Putnam et al., 2014) as well as the Distress and Falling reactivity subscales of the IBQ-R(Gartstein and Rothbart, 2003), as used in study 2b above.

Participants

Forty-one primary caregivers (40 female) took part in the study, with their full term, healthy 6- to 8-month-old infants (18 boys, 23 girls, mean age = 7.02 months, *SD* = 25.32 days). Three participants failed to complete the first questionnaire. Once in the lab, ten infants' ECGs were excluded, two due to technical difficulties and eight due to excessive movement. Of these, three dyads failed to complete the questionnaire fully, leaving a final sample of 31 participants. Ethical approval was gained from the University of Essex Ethics Sub-Committee (ETH2122-0534).

Measures

In addition to the measures used in Study 2b, infant heart rate and vagal tone were collected, as follows.

Infant heart rate and vagal tone

ECG data was collected via a Biopac MP160 and examined in AcqKnowledge 5. Three EL512 dry, low-tac, paediatric electrodes were attached to the infant's torso, in a lead-II setup as shown in Figure 2.2. Cardiac data was recorded at a sampling rate of 2000Hz. The electrodes were left in place throughout the baseline and RSFP protocol. R peak identification was performed by Acknowledge software. This was followed by visual inspection with the video recordings for reference, to remove movement artefacts and confirm R-peak identification accuracy. Finally, the root mean square of successive differences (RMSSD) was extracted for the resting baseline period, as a proxy for infant vagal tone. In addition, mean heart rate was extracted for each of the phases of the RSFP, i.e., the interactive baseline, the still face period and the reunion phase. On completion of the task, the infant was returned to their caregiver's lap, electrodes were removed and the skin was cleansed once again.

Infant temperament - IBQ-R-VSF and IBQ-R

As for 2b, above, infant temperament was assessed with the IBQ-R VSF (Putnam et al., 2014) and the IBQ-R (Gartstein and Rothbart, 2003) as described in detail in the previous study. Putnam et al. (2014) reported an average Cronbach's alpha of .75 or above for the three broad IBQ-R VSF scales. In this study, Cronbach's alpha for Surgency was .52, for Negative Affect it was .87 and for Orienting/Regulatory Capacity it was .82. An overview of a number of studies using different versions of the IBQ-R revealed that Cronbach's alpha for Distress and Falling Reactivity ranged between .74 and .79 (M = .76) and between .76 and .84 (M = .80), respectively, when using the short version of the IBQ-R (Putnam et al., 2014). In the current study, Cronbach's alpha for the Distress scale was .54 and for the Falling Reactivity alpha was .84.

Responsive Still Face Paradigm

The modified still face paradigm used and described in detail in Study 2b, was used again here Since this study took place in the Babylab, rather than online, instructions were provided verbally and written consent was provided by participants prior to beginning the tasks. For the RSFP in the Babylab, two video cameras were positioned to capture the infant and the caregiver, who were sat facing each other. Beyond these modifications, the procedure was as described in Study 2b. Still face durations were coded offline by two coders, me and another

PhD candidate, PR, independently. Intraclass correlation coefficients (ICC) were calculated to assess the agreement between raters. A two-way random-effects model was used to compute ICC. The ICC value in this study was 0.979 (95% CI [0.96, 0.989]), $p < .001$, indicating excellent agreement between the coders.

Caregiver mental health

As described in detail in Study 2b, the caregivers were again asked to complete a short questionnaire on Qualtrics. This questionnaire comprised the Patient Health Questionnaire - 9, PHQ-9, (Kroenke et al., 2001) and the Generalised Anxiety Disorder Assessment - 7, or GAD-7, (Spitzer et al., 2006). Kocalevent et al. (2013) reported a Cronbach's alpha of .87 when the PHQ-9 is used as a screening tool in the general population. In this study Cronbach's alpha was .84. Spitzer et al. (2006) reported Cronbach's alpha of .92 for the GAD-7 scale as a measure of generalised anxiety in clinical samples. Subsequently, Lowe et al. (2008) reported a Cronbach's alpha of .89 when the scale is used in the general population. In this study, Cronbach's alpha for the GAD-7 scale was .72.

Caregiver interoception

The Interoceptive Accuracy Scale (Murphy et al., 2020) and the Interoceptive Attention Scale (Gabriele et al., 2022) were used to differentiate between how well someone responds to their bodily sensations, in terms of their accuracy, and how much they focus on their bodily sensations, in terms of their interoceptive attention. These scales are described in detail in Study 2b. For the IAS, Murphy et al. (2020) report a Cronbach's alpha of .88 indicating good internal consistency. In this study, Cronbach's alpha was .87. For the IATS, Gabriele et al. (2022) report a Cronbach's alpha of .91. In this study, Cronbach's alpha was .95.

Procedure

Families were recruited via the University of Essex database of local families. Prior to their visit, caregivers were asked to complete an online questionnaire comprising the Interoceptive Accuracy Scale, the Interoceptive Attention Scale and the Surgency, Negative Affect, Orienting/Regulatory Capacity, Distress and Falling Reactivity subscales of the Infant Behaviour Questionnaire.

Following completion of this first questionnaire, the caregiver and their 6-8-month-old infant were invited to attend the Babylab. During the visit, participants were briefed on the study ad written consent was obtained. First, the ECG was set up. Once ready, the caregiver was then asked to sit in front of a monitor, with their infant on their lap, while electrodes were attached in preparation for recording the ECG. A two-minute baseline ECG was recorded, while the infant watched a soothing animation. Next, the RSFP was explained to caregivers, who were able to ask questions related to the study before commencing. The infant was then moved to a highchair, facing their caregiver and the ECG electrodes were checked for security . Two video cameras were positioned to record both the caregiver and the infant throughout the task and the infant's cardiac data was recorded throughout. The caregiver then carried out the RSFP, as described in Study 2b.

Once the recording of the RSFP was complete, the caregiver was asked to complete a mental health questionnaire, comprising the GAD-7 and PHQ-9 scales, as for Study 2b. Caregivers and infants were then fully debriefed, offered an opportunity to ask questions and thanked for their participation. Participants were presented with a small gift from the Babylab. Given the sensitive nature of the mental health questionnaires completed during the visit, signposting to relevant support services was also provided.

4.4.3 Results

Descriptive statistics

Descriptive statistics of all variables are provided in Table 4.4.

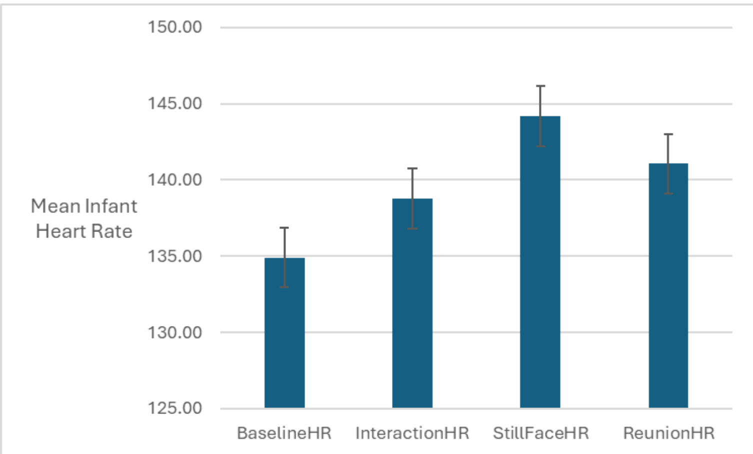
Table 4.4
Study 2c Descriptive Statistics for all Variables

	N	Minimum	Maximum	Mean	Std. Deviation
Baseline RMSSD	30	8.33	57.69	29.47	14.86
Baseline HR	31	111.04	146.88	134.92	7.53
Interaction HR	28	119.72	156.96	138.77	10.19
Still Face HR	28	125.46	163.19	144.20	10.00
Reunion HR	28	123.85	167.68	141.07	9.70
Still Face Duration	40	6.20	389.64	95.25	88.72
PHQ-9 Score	41	0.00	14.00	4.83	3.24
GAD-7 Score	41	0.00	16.00	4.22	3.44
Interoceptive Accuracy Score	38	61.00	101.00	80.26	9.12
Interoceptive Attention Score	38	26.00	90.00	52.63	14.45
IBQ Scale 1: Surgency	38	3.15	5.50	4.38	0.59
IBQ Scale 2: Negative Affect	38	2.17	5.92	3.98	0.85
IBQ Scale 3: Orienting/Regulatory Capacity	38	3.33	6.42	5.10	0.71
IBQ Scale 4: Distress	38	2.17	4.67	3.43	0.62
IBQ Scale 5: Falling Reactivity	38	2.77	6.18	4.64	0.91

Infant heart rate during the RSFP

Mean infant heart rate increased from baseline (M=134.92), during the interaction phase (M=138.77) and increased further during the SF period (M=144.2). During the reunion phase, mean heart rate began to drop (M=141.07). Mauchly's test indicated that the assumption of sphericity had been violated, $\chi^2(5) = 17.77, p = .003$, therefore the Greenhouse-Geisser corrected tests are reported ($\hat{\epsilon} = .79$). The results of a repeated measures ANOVA show that changes to heart rate at each stage of the RSFP were significant, $F(2.36, 63.63) = 12.392$, $p < .001$, $\omega^2 = .073$. Mean infant heart rate before and during the stages of the RSFP are displayed in Figure 4.4.

Figure 4.4
Infant Heart Rate during the RSFP



Caregiver mental health

The GAD-7 screening tool was used as a brief measure of caregiver anxiety (Spitzer et al., 2006). GAD-7 Scores ranged from 0 to 16 (M = 4.22, SD = 3.44). Thirteen caregivers scored above the clinical cut-off for mild anxiety, two caregivers scored above the clinical cut-off for moderate anxiety and one scored in the severe anxiety category. The PHQ-9 screening tool was used alongside the GAD-7 questionnaire, as a brief measure of caregiver depression (Kroenke et al., 2001). PHQ-9 Scores ranged from 0 to 14 (M = 4.83, SD = 3.24). Fifteen caregivers scored above the clinical cut-off for mild depression, four caregivers scored above the clinical cut-off for moderate depression, but no caregivers scored in the severe category. The distribution of GAD-7 and PHQ-9 scores is displayed in Table 4.5.

Caregiver interoception

The Interoceptive Accuracy Scale, IAS (Murphy et al., 2020) provided a self-reported mea-

Table 4.5
Caregiver Mental Health Scores

	None (0 – 4)	Mild (5-9)	Moderate (10-14)	Severe (15+)
Caregiver anxiety (GAD-7)	25	13	2	1
Caregiver depression (PHQ-9)	22	15	4	0

sure of caregiver interoceptive accuracy. This 21-item questionnaire asks participants to assess their own ability to accurately perceive a wide variety of bodily sensations and indicate their agreement on a 5-point Likert scale, from 1, Disagree Strongly, to 5, Strongly Agree. Caregiver interoceptive accuracy (IAS) scores ranged from 61 to 101 (M=89.26, SD=9.12).

The Interoceptive Attention Scale, IATS (Gabriele et al., 2022) was also used, to measure how much attention caregivers paid to their bodily sensations. Like the IAS the IATS asks participants the degree to which they agree with statements about how long their attention is focused on a variety of bodily sensations, again on a 5-point Likert scale. IATS scores ranged from 26 to 90 (M=52.63, SD=14.45). Caregiver interoceptive attention (IATS) scores ranged from 26 to 90 (M=52.63, SD=14.45).

Preliminary exploratory analysis

Bivariate correlations were conducted between the variables of interest, to explore the relationships between them and to inform inferential analyses. Several variables of interest were not normally distributed (Still Face duration, D(40) = .171, p = .005, PHQ-9, D(41) = .162, p = .008, IATS, D(38) = .148, p = .036), so Spearman's ρ correlations were calculated and are displayed in Table 4.6, including Bonferroni-corrected significance level for multiple comparisons ($p < .005$).

Caregiver anxiety (GAD-7) was positively related to caregiver depression (PHQ-9), ($\rho = .62$, $p < .001$). Within the infant temperament data, distress was positively related with negative affect, ($\rho = .58$, $p < .001$) and positively related with falling reactivity ($\rho = .57$, $p < .001$). Falling reactivity was positively related with negative affect ($\rho = .44$, $p = .006$). Surgency and orienting/regulatory capacity were not associated with the other variables of interest as predicted in hypothesis 5. The data did not indicate any significant correlations between still face duration, infant heart rate variability, caregiver mental health or caregiver interoception.

Table 4.6

Correlations between Infant Cardiac Data, Caregiver Interoception, Caregiver Mental Health and Infant Temperament

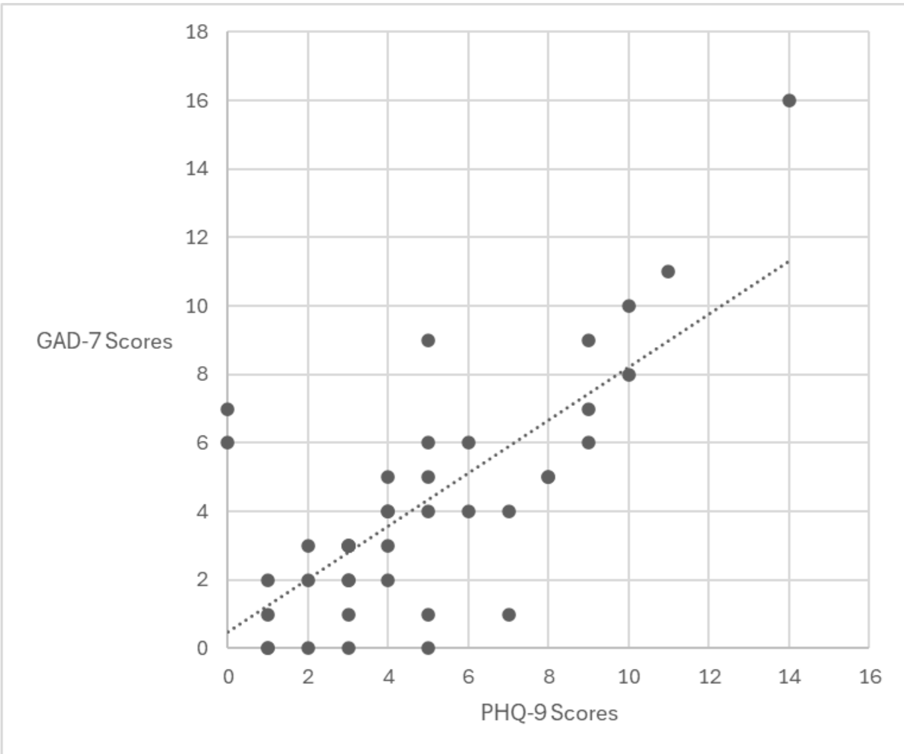
		1	2	3	4	5	6	7	8	9	10
1	Baseline RMSSD										
2	Still Face Duration	.007									
3	PHQ-9 Score	.205	-.051								
4	GAD-7 Score	.342	.171	.615*							
5	Interoceptive Accuracy Score	-.195	.032	.097	.168						
6	Interoceptive Attention Score	.098	-.184	.162	.203	.230					
7	IBQ Scale 1: Surgency	-.159	.058	.093	.074	.074	-.070				
8	IBQ Scale 2: Negative Affect	-.192	.005	.188	.260	.194	-.056	.305			
9	IBQ Scale 3: Orienting/Regulatory Capacity	-.361	.035	.056	-.009	.176	.192	.141	-.012		
10	IBQ Scale 4: Distress	-.208	-.068	.194	.192	-.016	-.026	.292	.579*	-.241	
11	IBQ Scale 5: Falling Reactivity	.101	.190	-.081	-.168	-.318	-.189	-.020	-.440	.061	-.565*

Note * $p < .005$ (Bonferroni-corrected significance level)

Figure 4.5 displays a scatterplot highlighting the relationship between caregiver anxiety and depression.

Figure 4.5

Scatterplot Demonstrating Positive Relationship Between Caregiver Anxiety (GAD-7) and Depression (PHQ-9)



Bayesian modelling

To investigate the relationships between the variables of interest as per the hypotheses, a series of Bayesian linear models were produced using the Bayesian Regression Models using Stan (brms) package in R v4.0 (Bürkner, 2017).

Predictors of infant vagal tone

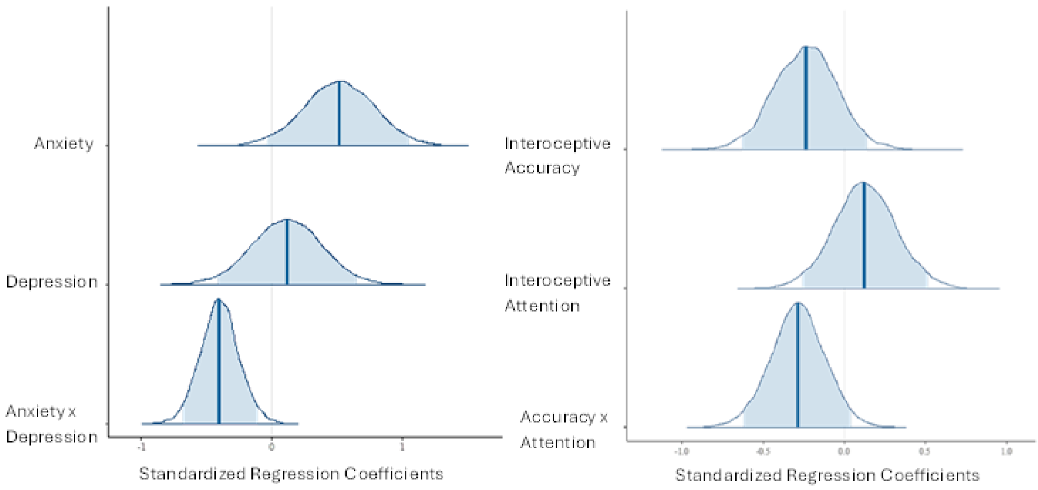
To investigate the first hypothesis, caregiver mental health measures (GAD-7 and PHQ-9 scores) were examined as predictors of infant vagal tone (RMSSD). The analysis indicated that anxiety did not have a clear effect on infant vagal tone individually (95% HPDI [-0.03, 1.05]). Similarly, depression showed no direct effect on infant vagal tone (95% HPDI [-0.42, 0.64]). However, the interaction between anxiety and depression predicted infant vagal tone (95% HPDI [-0.68, -0.11]) with higher anxiety and depression predicting reduced vagal tone.

The second hypothesis considered caregiver interoception as a predictor of infant vagal tone. The analysis indicated that neither interoceptive accuracy (95% HPDI [-0.62, 0.14]) nor interoceptive attention (95% HPDI [-0.26, 0.52]) had a clear direct effect on infant vagal tone individually (95% HPDI [-0.03, 1.05]). The interaction between interoceptive accuracy and interoceptive attention showed a negative relationship with infant vagal tone ((95% HPDI [-0.61, 0.04]), although the estimated model fits were not reliably < 0.

Posterior distributions with medians and 95% confidence intervals are depicted in Figure 4.6.

Figure 4.6

Posterior Distributions of Caregiver Mental Health Scores (Left) and Caregiver Interoception Scores (Right) as Predictors of Infant Vagal Tone



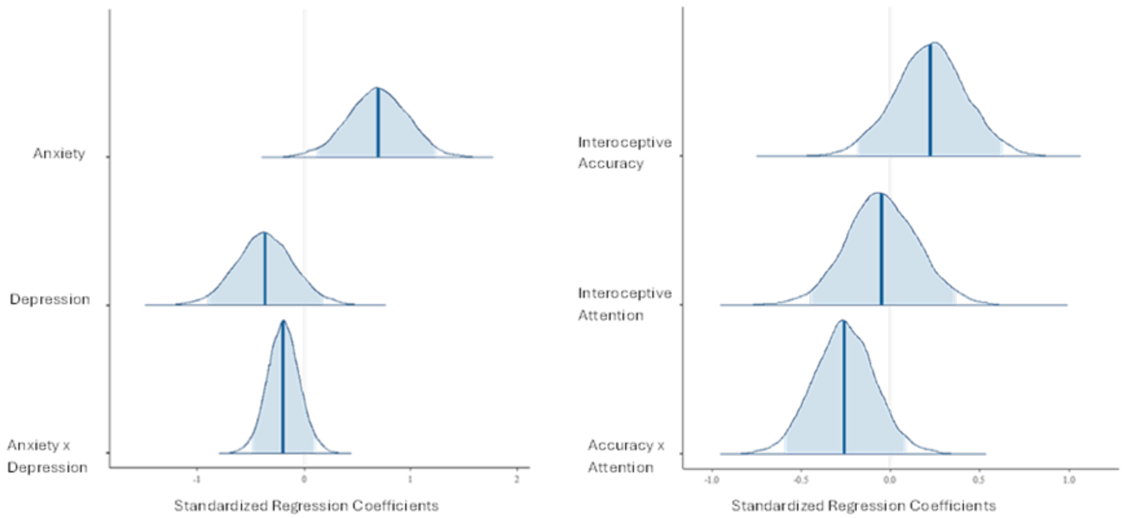
Predictors of the still face duration

The third hypothesis concerned whether caregiver mental health predicts the duration of still face period chosen by the caregiver. The analysis indicated that anxiety had a clearly positive relationship with still face duration (95% HPDI [0.11, 1.25]), while depression did not indicate a clear relationship (95% HPDI [-0.91, 0.18]), and nor did the interaction between anxiety and depression (95% HPDI [-0.50, 0.10]). The distribution of regression coefficients is depicted in Figure 7.

To examine the fourth hypothesis, caregiver interoception scores were considered as predictors of the duration of still face period chosen by the caregiver. In this case, the analysis indicated that neither interoceptive accuracy (95% HPDI [-0.18, 0.25]) nor interoceptive attention (95% HPDI [-0.44, 0.35]) had a clear direct effect on still face duration individually. However, the interaction between interoceptive accuracy and interoceptive attention showed a negative relationship with the still face duration (95% HPDI [-0.60, 0.08]) although the estimated model fits were not reliably < 0.

Posterior distributions with medians and 95% confidence intervals are depicted in Figure 4.7.

Figure 4.7
Posterior Distributions of Caregiver Mental Health Scores (left) and Caregiver Interoception Scores (right) as Predictors of Still Face Duration



4.4.4 Discussion

In this study, I sought to examine the association between caregivers' mental health and interoception, and their infants' arousal and vagal tone in relation to caregiver's behaviour during a dyadic interaction. As I was able to conduct the testing face-to-face in the Babylab, Study 2c included important physiological measures and ensured a more controlled environment compared to Study 2b. I hypothesised that (1) caregiver mental health would be related to infant vagal tone, with higher depression and anxiety being associated to lower infant vagal tone, (2) caregiver interoception would be related to infant vagal tone, with higher interoceptive accuracy and lower interoceptive attention being associated to higher infant vagal tone, (3) caregiver mental health would influence the still face duration, with higher mental health scores predicting reduced duration, (4) caregiver interoception would also influence the still face duration, with higher interoceptive accuracy and lower interoceptive attention predicting longer still face duration and (5) infant temperament would be associated with infant vagal tone, with higher vagal tone relating to higher regulatory capacity and surgency. Hypotheses 3 and 4 were the same as for Study 2b. However, in this study, participants were observed in the Babylab, rather than in their own homes, i.e. in a standard, controlled environment vs different, variable setting. While this allowed for greater experimental control and the addition of measures of infant physiology, the unnatural setting prevents a direct comparison of results between the two studies.

The results of this study suggested that, although anxiety and depression did not reliably relate to infant vagal tone independently, their interaction was related to reduced infant vagal tone, supporting my first hypothesis, with higher anxiety and depression associated with reduced infant vagal tone. This is consistent with previous studies which have related caregiver mental health with infant vagal tone (T. Field et al., 1995; Somers et al., 2021). Field et al. (1995) observed lower vagal tone in infants of depressed mothers. While Somers et al. (2021) observed the same correlation, they further hypothesised that infants with lower vagal tone shaped their own environment, to some extent, by demonstrating more negative behaviours which contributed to poor beliefs of self-efficacy in their mothers. This highlights the bi-directional nature of the influence of caregivers and their infants. Due to the correlational design of this study, no conclusions can be drawn about the direction of the observed associations. Future research should directly investigate this interplay to clarify these relationships.

My results indicating the significant interaction between anxiety and depression in relation to infant vagal tone may also reflect the strong correlation between these two conditions. This is consistent with previous studies that have shown comorbidity between anxiety and depression both in the general population (Grant et al., 2005; Kessler et al., 2008; Noyes, 2001) and among new mothers (Dennis et al., 2017; Underwood et al., 2016). The sample of caregivers in this study was a non-clinical sample, with few caregivers scoring towards the higher end of either scale, so it could be that only when both anxiety and depression scores were very low, any effect too small to be observed. To clarify whether anxiety and depression relate to infant vagal tone in similar or different ways, a large sample of caregivers diagnosed with clinically significant anxiety and depression would need to be studied.

The Bayesian model of interoceptive accuracy and interoceptive attention as predictors of infant vagal tone did not produce a reliable prediction in this study, thus not providing support to the second hypothesis. Caregiver interoceptive accuracy and attention were also unrelated to still face duration in the RSFP, as per the fourth hypothesis. As discussed previously in Study 2b, it is worth noting again here the potential limitations associated with self-reported questionnaires utilised to enable comparison between online (Study 2b) and face-to-face participants (Study 2c). One's beliefs about their accuracy in correctly identifying internal sensations and paying attention to these may greatly differ from their objective abilities in interoceptive accuracy and attention. Thus, it may be possible that other interoceptive tasks, such as a behavioural task, such as the heartbeat detection task (Schandry, 1981), or implicit measures of interoceptive processing in caregivers would produce different results. The use of multiple measures of interoceptive processing to explore the role of different dimensions of interoception, both subconscious and conscious, has been recommended recently (Desmedt, Luminet, Maurage, and Corneille, 2023; Nord and Garfinkel, 2022). This is because different interoceptive tasks rely on different cognitive processes, resulting in inconsistent results across studies (see Desmedt, Luminet, Walentynowicz, and Corneille, 2023 for a review and 1.2.2 for a detailed discussion of the literature).

The Bayesian model examining the third hypothesis, i.e., that caregiver mental health influenced the still face duration, revealed that higher anxiety was related to longer still face duration. While this association did suggest a relationship between mental health and caregiver behaviour, the observation was in the opposite direction to that hypothesized, i.e. that anxiety would relate to a shorter still face duration. Studies of maternal anxiety in dyadic interactions have highlighted a tendency for caregivers to demonstrate increased engagement and exaggerated behaviours (Kaitz and Maytal, 2005; C. G. Smith et al., 2022a). In this light, an extended still face period could be considered as an exaggerated response to the task, so long as the infant was happy (anecdotally, and in line with Study 2b, most caregivers ended the still face period without a behavioural cue indicating any need from their infant). Another important consideration is the assumption that more anxious caregivers would behave as they normally do in the laboratory - this may be unlikely and it is indeed possible that more anxious caregivers felt apprehensive about the RSFP task, and could have been attempting to counter or disguise their own anxiety by trying to act in a more relaxed manner, when being observed in the lab. Indeed, being observed is associated with behavioural alterations. For example, caregivers who know their behaviours are being recorded use a higher frequency of attentive behaviours towards their infant than those who do not (Abels et al., 2017).

The fourth hypothesis considered the relationship between caregiver interoceptive accuracy and attention, and their chosen still face duration. In this sample, the Bayesian model suggested there was no reliable relationship between interoceptive accuracy, attention, or the interaction of the two and still face duration directly. This is inconsistent with previous studies which have linked caregivers' interoception with dyadic interactions (Abraham et al., 2019; Montirosso and McGlone, 2020). Caregivers have demonstrated an ability to match their autonomic state with their infant's state, such that when their infant's arousal increased, so did that of the caregiver (Wass et al., 2019). In addition, in periods where the arousal within the dyad was high, caregivers were able to reduce their own arousal. However, this ability has been observed to differ between anxious and non-anxious caregivers. For example, Smith et al. (2021, 2023) found that parents' anxious symptoms influence co-regulation in mother-infant dyads, with high-anxiety mothers displaying enhanced synchrony and exhibiting greater responsiveness to small-scale fluctuations in their infant's arousal, as compared to low-anxiety mothers who tended to react to peak arousal states. These studies all rely on implicit measures of interoceptive processing or physiological arousal. The null finding in this study could, therefore, relate to use of self-report measures of interoception rather than implicit measures. In Chapter 1 (Section 1.2.2), I discussed the distinction between subconscious and conscious interoceptive processing. As for the second hypothesis, further studies using implicit measures of interoception in caregivers, rather than the self-report questionnaires used here, could reveal different results, as suggested in recent reviews of research in interoception and mental health (Desmedt, Luminet, Maurage, and Corneille, 2023; Nord and Garfinkel, 2022). For example, it may possible that the influence of caregivers' interoceptive processing takes place subconsciously, such as in the physiological and neural synchrony discussed in detail in Chapter 1 (Section 1.3.3) (e.g. Feldman et al., 2011; Nguyen et al., 2020).

My fifth hypothesis predicted a relationship between infant heart rate variability and temperament. Exploratory analyses did not indicate any such relationship, so no further analyses were conducted. However, this contrasts with previous research which has indicated a similar relationship between HRV and emotion regulation in infants as in adults (Huffman et al., 1998).

By conducting this study in a laboratory setting, the instructions for the RSFP were able to be clarified. Caregivers could ask questions if they were unsure and researchers were able to check for understanding and correct any issues with the recording of the task as they occurred. This offered greater confidence in the data relative to that collected online in Study 2b. This study was, however, subject to other limitations. The interpretation of RMSSD requires some caution. Since completion of data collection in this study, Claiborne et al. (2023) have produced a welcome methodological guide to the collection of RMSSD in infants, highlighting its sensitivity and variability between collection methods (Claiborne et al., 2023). While the data collected in this study is suitable for analysis alongside the other variables, comparing RMSSD between studies may potentially be problematic. Specifically, Claiborne et al. (2023) argue in favour of manual (as implemented in the present study), versus automated R-peak detection for maximum accuracy in extraction of RMSSD from ECG recordings and comparability between studies, highlighting variability of RMSSD values extracted by different software. In future, consistent use of a protocol such as that specified by Claiborne et al. (2023), should enable a more consistent interpretation of RMSSD data.

Taken together, the results of this study provide support to the idea that the early caregiver-infant environment influences the development of interoceptive processing by demonstrating that caregiver mental health is associated with infant vagal tone and the duration of still face maintained by caregivers in the RSFP. However, the limited evidence presented here requires more robust testing with a larger, clinical sample of caregivers and infants. Additionally, combining different measures of interoception could provide clearer insights into the role of caregiver interoception in dyadic interactions, and its specific impact on the development of interoceptive processing. A better understanding of this relationship could help clarify the specific mechanism underlying the association between caregiver mental health, early dyadic interactions, and the development of infants' interoceptive processing. Importantly, this evidence may also contribute to further our understanding of familial patterns in psychopathology.

4.5 General discussion

The three studies presented in this chapter all examined the role of caregivers' anxiety and interoception in dyadic interactions with their 6- to 8-month-old infants. The examination of caregiver interoception and mental health along with interactive behaviour, infant arousal, and vagal tone were intended to help shed light on the relationships between these variables and examine whether they provided empirical support for theoretical accounts of the development of interoceptive processing in infants. Overall, these studies offered some support to theoretical accounts of the development of interoceptive processing which provide the backdrop to this thesis (Atzil et al., 2018; Fotopoulou and Tsakiris, 2017a; Filippetti, 2021). However, findings did not directly support the hypothesis and the results between studies were mixed, as I will now summarize.

Firstly, in the pilot study (Study 2a), infants demonstrated greater physiological arousal, via increased heart rate, when processing negative versus positive emotions. This is consistent with previous studies of physiological arousal in infants (e.g. Wass et al., 2018; C. G. Smith et al., 2022b). In addition to increased heart rate, infants have also demonstrated increased amplitude heartbeat-evoked potentials in response to negative emotions (Maister et al., 2017). As well as these differences in magnitude of arousal between negative and positive emotions, the duration of arousal has also been found to differ with different emotions (Wass et al., 2018). Together these findings highlight that infants process negative and positive emotions differently. Importantly, given the role that caregivers play in shaping infants' development of emotional and regulatory skills, the results from previous studies and Study 2a presented in this thesis raise the questions as to whether caregivers' behaviour may influence individual differences in infants' emotion processing, and whether caregiver behaviours influence the processing of positive and negative emotions differently.

The use of affectionate touch in dyadic interactions could provide vital clues to help answer this question. For example, Montirosso and MacGlone (2020) proposed that affectionate touch from the caregiver facilitates interoceptive processing and increases synchrony between the caregiver and infant, helping the infant to develop a sense of bodily-self. Further, they proposed that disruption to attunement and reparation through close proximal interaction enhance this development. The study of affectionate touch has also revealed a soothing effect on infants (McGlone et al., 2014; Olausson et al., 2010) and that infants as young as two months old respond to such touch distinctively (Jönsson et al., 2018). In Study 2a, I had planned to explore the influence of affective touch on infant's emotion processing by collecting data from infants in two conditions - those receiving affectionate touch from their caregiver and those not receiving such touch. Unfortunately, laboratory closure due to the COVID-19 pandemic halted this study, forcing a change in direction and a move to online data collection during this time. It was not possible to extract any meaningful EDA data from the pilot data, due to methodological changes during this pilot phase. Sadly, the abrupt halting of this study due to the COVID-19 pandemic prevented full exploration of the effects of affective touch on physiological evidence of infant emotion processing.

In studies 2b and 2c I explored the role of caregivers' mental health (self-reported anxiety and depression scores (GAD-7, Spitzer et al., 2006; PHQ-9, Kroenke and Spitzer, 2002)) and interoceptive abilities (self-reported interoceptive accuracy and attention (IAS, Murphy et al., 2020; IATS, Gabriele et al., 2022)) in predicting caregivers' behaviour in a structured behavioural task. I used a novel modification to the frequently utilised still face paradigm, (Tronick et al., 1978), in which the caregivers were asked to stop interacting with their infants for *as long as felt comfortable*, rather than a fixed duration, as in the classic paradigm. When looking at the relationship between caregiver mental health and their chosen still face duration, the differences between participants in Studies 2b and 2c was interesting. In Study 2b, no reliable relationship was observed between mental health and still face duration. However, in Study 2c, higher anxiety was related with longer still face duration, with no effect for depression or the interaction of the two. Study 2b took place online, with caregivers recording their RSFP task in their own homes, with no researcher present, and were almost entirely based in the USA. Study 2c participants visited the Essex Babylab and were, therefore, in an unfamiliar environment. While methodological differences could have accounted for the differing results between the studies in this instance, the findings are somewhat consistent with existing research on maternal mental health. Although, maternal depression has been associated with slower responses to their infant (C. G. Smith et al., 2022a) and reduced use of affectionate touch (Mercuri, Stack, Mantis, et al., 2023; Stepakoff and Beebe, 2024), maternal anxiety has been associated with greater engagement and exaggerated behaviours in dyadic interaction (Kaitz and Maytal, 2005), more intense vocalisations and increased physiological arousal (C. G. Smith et al., 2022a), but reduced engagement when carrying out a stressful task (Nicol-harper et al., 2007). My finding relating higher anxiety with longer still face duration could be considered consistent with this enhanced engagement or exaggerated behaviour described by these studies, as discussed in Study 2c, above.

Previous studies have also related caregiver interoception with dyadic interaction (Abraham et al., 2019; Donaghy et al., 2024; MacCormack et al., 2020). However, these studies consider different dimensions of interoception and rely on different measures of interoception. For example, Abraham et al. (2019) used fMRI data focused on the anterior insula as a measurement of interoceptive sensitivity, Donaghy et al. (2024) compared scores on the self-report MAIA-2 questionnaire of interoceptive awareness (Mehling et al., 2018) with self-reported stroking behaviours, while MacCormack et al. (2020) explored caregivers knowledge of emotions and bodily sensations with a novel questionnaire. It would appear, on the one hand, that these studies all measured different things. However, on the other hand, they all reported a relationship between caregiver interoception and dyadic interaction. In Studies 2b and 2c, I relied on self-reported measures of interoceptive accuracy and attention, the IAS and IATS (Gabriele et al., 2022; Murphy, Bird, and Catmur, 2019). The models of interoceptive accuracy and attention as predictors of still face duration did not indicate a reliable association between caregivers' interoception and their behaviour, in either study 2a or 2b. This could relate to the choice of measures of interoception, but could also reflect the nature of the RSFP, in which caregivers were asked to rely on how they were feeling to decide when to end the still face period. The experimental procedure could be improved in future, by asking caregivers how they decided to end the still face period and whether any other factors influenced their decision. For example, they could have been concerned about judgement by the researcher. I did not find a significant association between interoceptive accuracy and attention, consistent with literature demonstrating the dissociation between these dimensions of interoception (Gabriele et al., 2022; Murphy, Bird, and Catmur, 2019).

In study 2c, the focus shifted to evidence of interoceptive processing in the infant, through the observation of the infants' baseline heart rate variability (RMSSD), a measure of vagal tone associated with emotion regulation) and changes in their heart rate during the different stages of the RSFP. The data suggested that caregiver mental health was a reliable predictor of infant vagal tone, with higher mental health scores relating to reduced infant vagal tone. This is in line with my hypothesis, based on previous literature relating caregiver mental health with behavioural outcomes relating to emotion regulation in infancy and childhood (Feldman and Eidelman, 2007; Rattaz et al., 2023). In addition, this result provides empirical support for the importance of early caregiver-infant relationships in the development of interoceptive processing.

Taken together, the studies in this chapter offer some support to the theoretical arguments suggesting that early environmental factors play a facilitating role in the development of interoceptive processing. I have demonstrated evidence of relationships between both caregivers' interoception and their mental health and their behaviour in the caregiver-infant dyad. In addition, I have demonstrated that caregiver mental health is association with early evidence of interoceptive processing in their infant. The studies I presented so far in this thesis have focused on infants and their early environment to explore the influence of caregiver interoception and mental health on the development of interoceptive processing. However, there is still scarce evidence regarding subsequent developmental stages. Do such early influences continue to shape the development of interoceptive processing as the child grows? Does early development of interoceptive processing directly influence a child's risk for mental health difficulties? Strong family trends exist in mental health, and the relationship between caregiver behaviour and developmental outcomes in childhood are long-established. Building on the overarching hypothesis that early caregiver-infant dyadic interactions play a critical role in shaping the infant's interoceptive processing - and considering evidence linking interoceptive abilities to mental health later in life - an important question arises: Do the caregiver's interoceptive abilities and mental health continue to influence their child's interoceptive abilities and mental health as they develop through childhood? To address some of these questions, in the next chapter I examine the relationship between caregiver factors (interoceptive accuracy, interoceptive sensibility, and mental health) and the interoceptive accuracy and threat sensitivity of their children.

Chapter 5

Study 3: Associations Between Caregiver's and Child's Factors in the Development of Interoceptive Processing and Anxiety Risk

5.1 Introduction

This chapter is based on the paper *The association between caregiver's and child's factors in the development of interoceptive processing and anxiety risk*, submitted to *Psychophysiology* on 12 September 2024.

The studies presented in Chapters 3 and 4 focused on exploring factors influencing caregiver behaviour in dyadic interactions with their 6- to 8-month-old infants. With Study 3, I sought to explore the relationship between caregiver, and child interoception and anxiety in older children, aged 5 - 14 years.

Studies 1, 2b and 2c presented in the previous chapters, revealed several associations between caregivers' interoception, mental health, dyadic interaction and infants' emotion processing. Study 1 (Chapter 3) demonstrated that caregivers' interoceptive accuracy and contingency in dyadic behaviours were associated with their use of instrumental touch. Study 2b (Chapter 4) indicated a relationship between caregivers' interoceptive accuracy and their infant's temperament, with higher interoceptive accuracy associated with more positive infant behaviours (surgency) as reported by the caregivers. In Study 2c (Chapter 4), Bayesian modelling suggested that an interaction between higher anxiety and higher depression in the caregiver predicted reduced vagal tone in the infant.

Although mixed, these results justify further investigation of the relationship between caregiver mental health and interactive behaviour, since they seem to support theoretical proposals suggesting that early caregiver-infant dyadic interactions serve as a foundational framework for the development of infant interoceptive processing (Atzil et al., 2018; Filippetti, 2021; Fotopoulou and Tsakiris, 2017a). If this is the case, it raises the question of whether the influence of these caregiver factors extends beyond infancy, persisting throughout childhood and into adulthood. The present study examined whether caregiver interoceptive accuracy, interoceptive sensibility, and anxiety are related to interoceptive accuracy and interoceptive sensibility in their child. It also considered whether these factors predict children's threat sensitivity, an indicator of susceptibility to anxiety.

Despite the growing research on interoception across the lifespan, how and when the relationship between interoception and psychopathology, such as anxiety, develops remains unclear. This is an urgent and important topic for research, since an NHS report recently demonstrated a large, continuing rise in childhood mental health problems in the UK. In 2022, 18.0% of 7-16-year-olds were identified as having a probable mental health problem, with that statistic having risen consistently from 12.1% in 2017. Anxiety disorders affect over 8% of children and are the most prevalent mental health disorders (Newlove-Delgado, 2023). In parallel, referral waiting times continue to rise (officially 10 months on average), with only 25% of children referred to Child and Adolescent Mental Health Services, CAMHS, being seen at all (England and Mughal, 2019; National Audit Office, 2018; National Audit Office, 2023). Early intervention and treatment of anxiety has been demonstrated beneficial to the patient as well as leading to reduced coast and more efficient use of healthcare resources (Brakoulias et al., 2017; Blakey et al., 2017; Lydiard et al., 1996). However, intervention is often triggered on presentation of symptoms worrying enough to necessitate immediate action by parents and teachers. Against this backdrop, understanding the trajectory of the relationship between interoceptive processing and mental health is of critical importance (Murphy, Brewer, Catmur, and Bird, 2017b).

As extensively reviewed in the previous chapters of this thesis, recent theories have suggested that early caregiver-infant dyadic interactions represent the foundation of interoceptive processing (Atzil et al., 2018; Filippetti, 2021; Fotopoulou and Tsakiris, 2017a). It has been suggested that interoceptive accuracy, once established, remains stable during adulthood (Critchley and Harrison, 2013), and interoceptive awareness declines with age (Khalsa, Rudrauf, and Tranel, 2009). However, these data are based on adult populations, offering little insight into the developmental origins of interoceptive processing. In particular, while theoretical accounts have emphasised the importance of interoception for early development (Atzil et al., 2018; Filippetti, 2021; Fotopoulou and Tsakiris, 2017a), research on the development of interoceptive processing is still at its beginning. This is an important gap in the literature, considering that differences in interoceptive processing among individuals may originate from early life experiences. These topics have all been discussed in Chapter 1 (Section 1.3) and the studies presented in chapters 3 and 4 focused on factors influence the development of interoception during infancy. The present study is specifically concerned with whether interoception in children is associated with caregiver's factors (their own interoceptive abilities and mental health), and whether the relationship between interoception and mental health is already evident during childhood.

Converging evidence shows that caregivers' interoceptive abilities relate directly to children's socio-affective skills. For example, lower caregiver interoceptive sensitivity has been found to predict 6-year-olds' increased somatic symptoms, such as nausea, dizziness, headaches and fatigue (Abraham et al., 2019) and to mediate affective dyadic interaction (Suga et al., 2022). Additionally, there is evidence that caregiver's interoception predicts emotion regulation in their 8-9-year-old child (MacCormack et al., 2020). Oldroyd et al. (2019) found that children whose mothers are less tolerant of negative emotions (consistent with disorganised attachment) demonstrated lower congruence between their physiological arousal and self-reported emotional state (Oldroyd et al., 2019). This indicates a relationship between attachment styles and interoception in older children and adolescents. Interestingly, the authors did not find the reverse to be true, i.e. higher acceptance of negative emotion in mothers did not predict greater congruence in their children. Importantly, this study indicates a relationship between interoceptive abilities in older children and their early social environment. This highlights the potential enduring effects of early environment on the relationship between interoception and mental health later on, supporting the theoretical arguments for interoceptive processing development being rooted in early social interactions (Atzil et al., 2018; Fotopoulou and Tsakiris, 2017a; Filippetti, 2021). While these studies offer some evidence relating interoceptive abilities in parents with outcomes in their children, there is also well-established evidence of the inter-generational transmission of mental health difficulties. Specifically, children of anxious parents display a heightened susceptibility to develop an anxiety disorder (Beidel and Turner, 1997; Micco et al., 2009; Warren et al., 2003). While the mechanisms of this transmission are still unclear, one explanation could be that caregiver's anxiety symptoms may be associated with poor interoceptive abilities, which are then passed on to the child and increase their own susceptibility to anxiety.

These studies indicate an influence of caregivers' interoceptive abilities on outcomes for their children. However, despite the well-established association between interoception and psychopathology in adults, few empirical studies have directly examined how children's own developing interoceptive abilities relate to their susceptibility to mental health issues such as anxiety. For example, interoceptive accuracy in 4- to 6-year-old children has been observed to relate to their emotion regulation abilities, with reduced interoceptive accuracy in the Jumping Jack Paradigm being found to be associated with increased cortisol levels among preschool children (Opdensteinen et al., 2021), while higher socially anxious 10-to-12-year-old children demonstrate lower interoceptive accuracy in a heartbeat counting task (Schmitz et al., 2012). By contrast, children with higher heartbeat detection accuracy have demonstrated increased symptoms of panic (Eley et al., 2004). This is consistent with adult studies of interoception in panic disorders (Ehlers et al., 1995; Hoehn-Saric et al., n.d.) and highlights the potentially important disorder-specific variation in the relationship between interoception and mental health. Self-reported interoceptive accuracy in children of this age is negatively associated with internalising behaviours (a potential marker of depressive symptoms), but not with performance on a heartbeat detection task (Brand et al., 2024). This underscores the need for multiple measures of interception to capture a comprehensive understanding and highlights the importance of specificity when exploring the relationship between interoception and mental health, as different disorders are linked with distinct dimensions of interoception (Khalsa et al., 2018; Nord and Garfinkel, 2022).

Given that emotion (dys-)regulation is considered an important component in the development of anxiety (Porges, 1995b), evidence of an association between children's interoceptive accuracy and emotion regulation abilities suggests a potential mechanism linking interoception and anxiety susceptibility Conradt et al., 2020; Faig et al., 2023; Gross and Muñoz, 1995). In fact, several empirical studies have suggested such a link. For example, a study of 9- to 12- year-old children found that scores on self-reported scales of interoceptive awareness were positively associated with emotion regulation (Cheung et al., 2023). In 13-year-olds, De Witte et al. (2016) found that higher interoceptive accuracy was associated with reduced maladaptive emotion regulation behaviours, such as rumination, while higher HRV was related to greater use of external emotional regulatory behaviours, such as support seeking. In this study, the authors also examined the relationship between these measures and parental psychopathology. They found that increased HRV in children, but decreased interoceptive accuracy, were associated with maternal internalising behaviours and child externalising emotion regulation, suggesting a possible protective role for higher HRV (De Witte et al., 2016). Consistent with the adult literature on vagal tone and emotion regulation presented in Chapter 1 (Section 1.2.3), higher vagal tone among 14-year-olds was associated with better emotion regulation (Braet and Braet, 2024). The studies presented here provide some evidence of a relationship between anxiety and interoception during childhood. However, this evidence is somewhat sparse, highlighting the urgent need to better understand how the relationship between interoception and anxiety develops in childhood.

One previously identified indicator of a susceptibility to anxiety among children is sensitivity to threat (J. C. Britton et al., 2011; Dudeney et al., 2015). Several studies have demonstrated that humans show an attention bias to threatening, versus non-threatening, stimuli (e.g. Heuer et al., 2007; Lipp et al., 2004; Ohman et al., 2001; Tipples, 2019). For example, Ohman et al. (2001) reported that adults found images of snakes among images of flowers more quickly than images of flowers among images of snakes, as well as observing the same pattern with spiders and mushrooms, proposing a threat model based on a bias toward evolutionary relevant threat stimuli (Ohman et al., 2001). Similar findings have also been replicated in 3- to 5-year-old children (Lobue and Deloache, 2008), who were able to identify threatening images more quickly than non-threatening images. This finding was also replicated using social threats based on human faces depicting different emotions (Lobue, 2009). In this task, 5-year-old children and adults were asked to find the target emotion, either happy among angry distractors, or angry among happy distractors, and touch the target on a touchscreen as quickly and accurately as possible. The adult and child groups both found the threatening (angry) images significantly more quickly than the non-threatening (happy) targets. The children's latency also demonstrated an interaction with age, with the adults find the targets faster than the children overall. While humans typically demonstrate an ability to detect threats more quickly than non-threats, individual differences in threat detection ability have been related to susceptibility to anxiety (e.g. Abend et al., 2018; J. C. Britton et al., 2011; Dudeney et al., 2015; Hunt et al., 2006; Mark et al., 1996; Pine et al., 2005). In the present study, I measured children's sensitivity to threat as a way of examining the relationship between child and caregiver's interoceptive abilities in the context of anxiety, with the aim of providing important insights into the mechanisms of this transmission.

However, when examining response times in children, there are some important additional factors to consider. Firstly, response times demonstrated by children typically decrease with age (Nettelbeck and Burns, 2010). This means that age must be taken into account and controlled for in the analysis of data from such tasks. Secondly, information processing biases across childhood is a complex subject, with many factors, such as executive function, cognitive ability and temperament having been proposed to moderate response times (see A. P. Field and Lester, 2010 for an overview). This suggests that caution is necessary when interpreting data based purely on response times, since several contributing factors are likely to be influencing the results.

Sensitivity to heartbeat is a common somatic symptom of anxiety (Ehlers et al., 1995; Hoehn-Saric and McLeod, 2000) and, therefore, cardiac interoception represents a good candidate measure of interoceptive abilities for the purpose of the present study. As described in Chapter 1, measures used in the study of cardiac interoceptive accuracy typically require the participant to detect sensations from the heart, either by counting their own heartbeats (Schandry, 1981), or by comparing their heart rhythm with auditory tones or visual signals (Katkin et al., 1983; Whitehead et al., 1977). Models of interoception have identified dissociations between different dimension of interoception (Garfinkel and Critchley, 2013; Garfinkel et al., 2015; Murphy, Bird, and Catmur, 2019; Murphy et al., 2020). The Three-Dimensional Model of interoception (Garfinkel et al., 2015), distinguishes between *interoceptive accuracy*, i.e., how well an individual performs on a heartbeat detection task, *interoceptive sensibility*, i.e., the extent to which they believe themselves to focus on internal sensation, and *interoceptive awareness*, i.e., a higher-order metacognitive measure of the level of awareness of their own interoceptive abilities. Previous research has found a positive association between interoceptive sensibility and interoceptive accuracy in childhood, with interoceptive sensibility - but not interoceptive accuracy - being also positively related to anxiety (Palser, Fotopoulou, et al., 2018a). In the present study, I included measures of both interoceptive accuracy, and a mean confidence rating (comparable to interoceptive sensibility in Garfinkel's Three-dimensional model and henceforth referred to as interoceptive sensibility), as a way to examine the relationship between anxiety and the differing dimensions of interoception.

To measure interoceptive accuracy in children, the standard cardiac interoceptive tasks have been adapted to account for children's developmental abilities. Several studies have used an adaptation of the heartbeat detection tasks based on the original Schandry's paradigm (Schandry, 1981) in children aged six and over (e.g. Palser, Fotopoulou, et al., 2018a). The Jumping Jack Paradigm is one example of using heartbeat detection abilities in children, in this case by examining their perception of the change in their heart rate after exercising. Children aged 4 to 6 years were asked to indicate the strength of their heartbeat before and after exercise, using four different sized circles. Changes in the circle the child chooses before and after exercise can then be compared with their actual change in heart rate, measured via a pulse oximeter (Schaan et al., 2019). A further adaptation of the Jumping Jack Paradigm with the same age group provided consistent findings (Opdensteinen et al., 2021), suggesting that this measure of cardiac interoception can be successfully used in young populations. In the present study, I adopted the Jumping Jack Paradigm as a way to assess cardiac interoceptive accuracy in children aged 5 to 14 years and their caregivers.

Understanding the development of interoceptive processing is especially important when considering mental health in the developing child (Khalsa et al., 2018, Murphy, Brewer, Catmur, and Bird, 2017b), with impairments to interoception having been proposed as a potential risk factor for childhood psychopathology (Murphy, Brewer, Catmur, and Bird, 2017b). Incidents of mental health diagnoses among children in the United Kingdom have been steadily increasing in recent years, both before and since the COVID-19 pandemic (National Health Service, 2022). In the face of this growing crisis, it is increasingly important to be able to identify predictors of anxiety, with the aim of facilitating early identification, diagnosis, and intervention. With the present study, I thus sought to examine the relationship between caregiver and child interoception in children aged between 5 and 14 years. My aims were to: (1) assess whether child interoceptive accuracy is associated with the caregiver's own interoceptive abilities (accuracy and sensibility) and self-reported anxiety; and (2) whether a child's susceptibility to anxiety is associated with their interoceptive accuracy or sensibility, as well as their caregivers' interoceptive abilities (accuracy and sensibility) and self-reported anxiety. I hypothesised that higher interoceptive accuracy in caregivers would be associated with higher interoceptive accuracy in their child and that higher caregiver anxiety would be associated with lower interoceptive accuracy in their child (hypothesis 1). I also expected higher caregiver anxiety levels and lower caregiver interoceptive accuracy to predict greater threat sensitivity in the child (hypothesis 2). Previous literature suggests interoceptive accuracy is stable across the lifespan once established (Critchley and Harrison, 2013) but that children show a more varied performance at the heartbeat counting task compared to adults (Koch and Pollatos, 2014a; Murphy, Cheesman, et al., 2019). Yet, the developmental trajectories of interoceptive processing remains unknown. Albeit correlational in nature, my study also aimed to explore any change in interoceptive ability during childhood, and therefore I included child age in my analysis.

5.2 Method

5.2.1 Participants

Fifty-six children (25 girls), along with their primary caregiver (45 mothers, 11 fathers), participated in the study during their visit to an annual science fair for families held in Colchester, UK. Children were aged 5 to 14 years (mean age = 8.7 years, SD = 2.19) and were recruited throughout the day. Twenty-three participants' data were excluded from further analysis due to movement artefacts on the ECG signal (N = 13) and wi-fi disconnection whilst completing the anxiety questionnaire or the Jumping Jack Paradigm (N = 10). The study took place on 19 March, 2022 and 18 March, 2023. Ethical approval was gained from the University of Essex Ethics Sub-Committee (ID ETH 2122-0890).

5.2.2 Measures

Heartbeat detection task - Jumping Jack Paradigm

Children and caregivers each completed the same heartbeat detection task, based on the Jumping Jack Paradigm (Schaan et al., 2019). The choice behind using this paradigm was twofold: first, I wanted to utilise a task that could be easily adapted to a setting conducive to a family event (i.e. be engaging) whilst providing a reliable measure of the variable of interest; second, I wanted to ensure that both children and caregivers could be assessed using a comparable measure of cardiac interoception. Participants (children and adults) were fitted with a pulse oximeter, connected to a Nexus10 MkII. They were instructed to stay still and quiet and pay attention to their body for 30 seconds. Noise cancelling headphones were provided to aid concentration. To assess participants' interoceptive accuracy, they were asked to choose from four circles of increasing diameter, on a touchscreen, to represent how quickly they thought their heart was beating. Then, participants were asked 'how sure' they felt about their answer, using a sliding scale from 1, not very sure, to 5, very sure. This provided the Interoceptive Sensibility score. Next, participants were asked to do as many jumping jacks as they could for 10 seconds, timed with a stopwatch. Right after performing the jumping jacks, they were asked to sit and pay attention to their body again, as before, while their heart rate was recorded via the pulse oximeter. Participants then repeated the interoceptive accuracy task by choosing the circle that would best represent how quickly their heart was beating and, again, indicating how sure they felt about their answer. The number of heartbeats in each 30 second recording was extracted. The difference between absolute heart rates and perceived heart rates was z-scored to provide an Interoceptive Accuracy score. Interoceptive Accuracy and Interoceptive Sensibility scores were then used in the analyses.

Threat detection task

Each child took part in a game to measure individual differences in sensitivity to threat-relevant stimuli (Lobue and Deloache, 2008; Ohman et al., 2001). Since this study is concerned with the association between interoception and emotion processing, my stimuli of choice were social threats, i.e. angry faces were used as threats, whereas happy faces were used as the non-threats. Faces were taken from the NimStim Facial Expression Set (Tottenham et al., 2009). Each trial required the child to spot a threat among 8 non-threatening distractors, or a non-threat among 8 threatening distractors. Each child completed 48 trials, 24 each of finding either a happy or angry face in a grid of 9 faces, counterbalanced for order, with either happy or angry first. Children were asked to place their hands on the table in front of them within a marked area, and they were instructed to touch either the happy or angry face on the touchscreen as quickly as they could. The instruction to find the correct face as quickly as they could was repeated before each trial. The original task (Lobue and Deloache, 2008), was tested on 3-, 4- and 5-year-olds. This study was open to children from 5 years upwards, so this threat detection game was deemed a suitable task for the youngest children. From the threat detection task, I extracted Threat and Non-Threat accuracy and response times.

Caregiver anxiety rating

Caregivers completed the Generalised Anxiety Disorder Assessment - 7 (GAD-7, Spitzer et al., 2006) on a tablet, while their child was completing the threat detection task. The GAD-7 is widely used as an initial screening of anxiety levels in clinical settings. The participant is asked to think about how they have felt over the previous two weeks, then rate the frequency of seven items using a Likert-scale questionnaire, with each item scored from 0 (not at all) up to 3 (nearly every day). The scale combines questions on physiological, cognitive and emotional aspects of anxiety to produce a GAD-7 score out of 21. Clinical cut-offs are 5, 10 and 15 for mild, moderate and severe anxiety, respectively. Spitzer et al. (2006) reported Cronbach's alpha of .92 for the GAD-7 scale as a measure of generalised anxiety in clinical samples. Subsequently, Lowe et al. (2008) reported a Cronbach's alpha of .89 when the scale is used in the general population. In this study, Cronbach's alpha for the GAD-7 scale was .84.

5.2.3 Procedure

The study was explained to families visiting the Essex Babylab stand and participant information was provided to interested families, who were then invited to take part. Parents were provided with the information sheet of the study and consent forms to be signed for their and their child's participation. Next, the child completed the jumping jack task to assess cardiac interoceptive accuracy, followed by the caregiver who completed the task once the child finished. After that, the child completed the threat detection task, while the caregiver filled out the GAD-7 questionnaire. At the end of the study, caregiver and child were debriefed from the study and the experimenter answered any question the participants might have had in relation to the research.

5.3 Results

5.3.1 Descriptive statistics

Means and standard deviations for all variables are reported in Table 5.1. I first analysed each measure separately to explore the distribution of the data within each variable and ensure that the tasks and questionnaires accurately measured what they intended to measure. In the next sub-sections, I report these results.

Table 5.1
Study 3 Descriptive Statistics for all Variables

	M *(SD)*
Caregiver GAD-7 Score	4.92 (3.40)
Caregiver Interoceptive Accuracy	0.91 (0.80)
Caregiver Interoceptive Confidence	3.53 (1.21)
Child Age	8.75 (2.21)
Child Interoceptive Accuracy	0.92 (0.74)
Child Interoceptive Confidence	3.27 (0.91)
Child Threat Response Time	3.61 (1.51)

GAD-7 = Generalised Anxiety Disorder Assessment-7

Jumping Jack Paradigm

Both children and caregivers demonstrated large, significant changes in heartbeat recorded via the pulse-oximeter after completing the Jumping Jack Paradigm, compared to before the game

(Caregiver M_{change} = 12.42s, $t(51) = 9.84$, $p < 0.001$, d= 1.45; Child M_{change} = 12.38s, $t(41)$ = 10.01, $p < 0.001$, $d = 0.82$). Both groups also reported perceiving a significant change in their heart rate after completing the jumping jacks (Caregiver M = 1.33, $t(51) = 10.37$, $p < 0.001$, d=2.10; Child M = 0.86, $t(41) = 0.86$, $p < 0.001$, $d = 1.06$), suggesting that the paradigm I selected was successful in eliciting a physiological perturbation. Interoceptive accuracy was calculated for both caregivers and children in terms of the difference in z-scores between their perceived and actual changes in heart rate. There was no significant difference in accuracy between caregivers and children (Caregiver M = .92, Child M = .90, $t(38) = 0.168$, $p < 0.868$, $d = 0.03$). Mean heart rates and interoceptive accuracy are reported in Table 5.2.

Table 5.2
Mean Heart Rates in Beats per Minute for Caregivers and Children, pre- and post- Jumping Jacks

	Mean Heart Rate, Resting	Mean Heart Rate, post Jumping Jacks	Mean Change	Mean Interoceptive Accuracy
Caregiver	70.15	82.58	12.42	0.91
Child	83.67	96.00	12.38	0.92

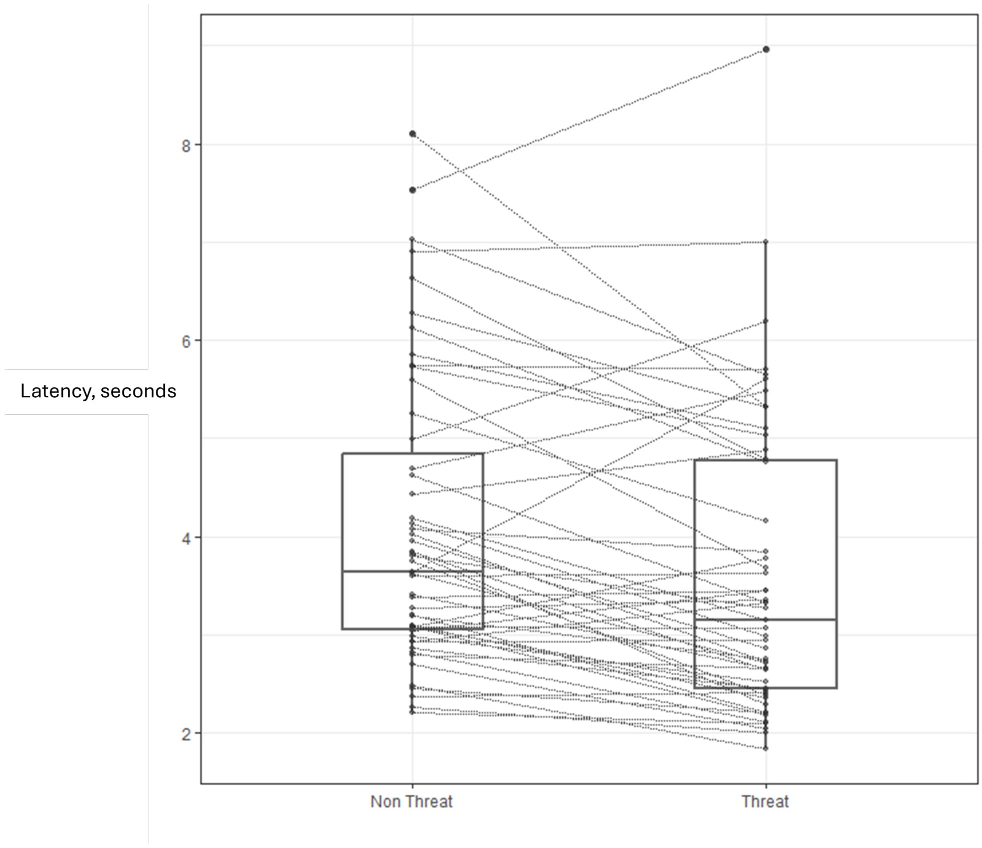
Threat detection task

The Threat Detection task elicited a significant difference in response times between threatening versus non-threatening images, consistent with the original task. A paired samples t-test indicated that children were quicker to find angry (threatening) faces among happy (non-threatening) faces (M_{threat} =3.61s, SE = 0.21), than happy faces among angry faces ($M_{non-threat}$ = 4.09s, SE = 0.21). The difference in response time, 0.49s, BCa 95% CI [0.72, 0.25], was significant $t(51)$ = -4.009, $p < 0.001$, $d = 0.32$. The children were equally accurate at finding threatening images and non-threatening images (M_{threat} = .96, $M_{non-threat}$ = .94, $t(51) = 0.918$, $p < 0.363$, $d = 0.15$). Paired response times per child are displayed in Figure 5.1.

Caregiver anxiety - GAD-7

GAD-7 scores ranged from 0 to 13 (M = 4.95, SD = 3.49). Five caregivers scored above the clinical cut-off for moderate anxiety and 11 caregivers scored above the clinical cut-off for mild anxiety. No caregiver scored above the clinical cut-off for severe anxiety. The distribution of

Figure 5.1
Paired Response Times for Finding Non-Threatening (Happy) Versus Threatening (Angry) Images



GAD-7 scores is displayed in Figure 5.3.

Table 5.3
Distribution of Primary Caregiver GAD-7 Scores

Caregiver GAD-7 Score	0 – 4 (No anxiety)	5 – 9 (Mild anxiety)	10 – 14 (Moderate anxiety)	15 – 21 (Severe anxiety)
N	24	11	5	0

5.3.2 Preliminary analyses

Exploratory analyses were conducted using Spearman's r_s correlations between variables. These are reported in Table 5.4, along with Bonferroni-corrected significance level ($p < 0.007$). Significant positive correlations were found between caregiver interoceptive accuracy and child interoceptive accuracy, $r_s = .543$, $p = .001$, and between caregiver interoceptive sensibility and child threat response times, $r_s = .370$, $p = .006$. This latter association suggests that higher caregivers' confidence judgements on accuracy after heartbeat detection trials were related to their children's slower responses to angry faces in the Threat Detection Task, indicating reduced threat sensitivity. Child threat response time was also negatively associated to child age, $r_s =$ -.596, $p < .001$, suggesting that the younger children in my sample were slower at identifying the threatening faces amongst the non-threatening faces. Caregiver interoceptive accuracy was positively associated with caregiver interoceptive sensibility, $r_s = .314$, $p = .024$, however this correlation did not survive Bonferroni correction. The same association (between interoceptive accuracy and sensibility) was not observed in the children. Finally, I did not find associations between caregiver anxiety (GAD-7) scores and any other variables. The distribution of caregiver versus child interoceptive accuracy is displayed in Figure 5.2, the relationship between caregiver interoceptive sensibility and child threat sensitivity is displayed in Figure 5.3 and the relationship between child age and child threat sensitivity is displayed in Figure 5.4

Table 5.4
Correlation Matrix for All Variables

		1	2	3	4	5	6	7
1	Caregiver GAD-7 Score							
2	Caregiver Interoceptive Accuracy	-.085						
3	Caregiver Interoceptive Sensibility	.051	.314*					
4	Child Age	.045	.135	-.180				
5	Child Interoceptive Accuracy	-.083	.543**	.048	-.112			
6	Child Interoceptive Sensibility	.150	-.028	.125	-.015	-.019		
7	Child Threat Response Time	.049	.221	.370**	-.590**	.235	-.060	
8	Child Response Difference (Threat – Non-threat)	.040	-.206	-.080	-.038	-.175	.121	-.221

Note Caregiver GAD-7 = Generalised Anxiety Disorder Assessment-7
* $p < 0.05$
** $p < 0.007$ (Bonferroni-corrected significance level)

5.3.3 Child interoceptive accuracy

To examine my first hypothesis, I conducted a hierarchical regression to examine whether caregiver interoceptive accuracy, interoceptive sensibility, and anxiety predicted child interoceptive accuracy. Tests for multicollinearity indicated that a very low level of multicollinearity was present (VIF = 1.132, Tolerance = .884 for Caregiver Interoceptive Accuracy, VIF = 1.013, Tolerance = .987 for Caregiver GAD-7 Score; VIF = 1.118, Tolerance = .895 for Caregiver Interoceptive Sensibility). Caregiver Interoceptive Accuracy was entered first, followed by Interoceptive Sensibility and GAD-7 score. Results showed that caregiver Interoceptive accuracy

Figure 5.2
Scatter Plot Representing the Significant Positive Relationship between Caregiver and Child Interoceptive Accuracy

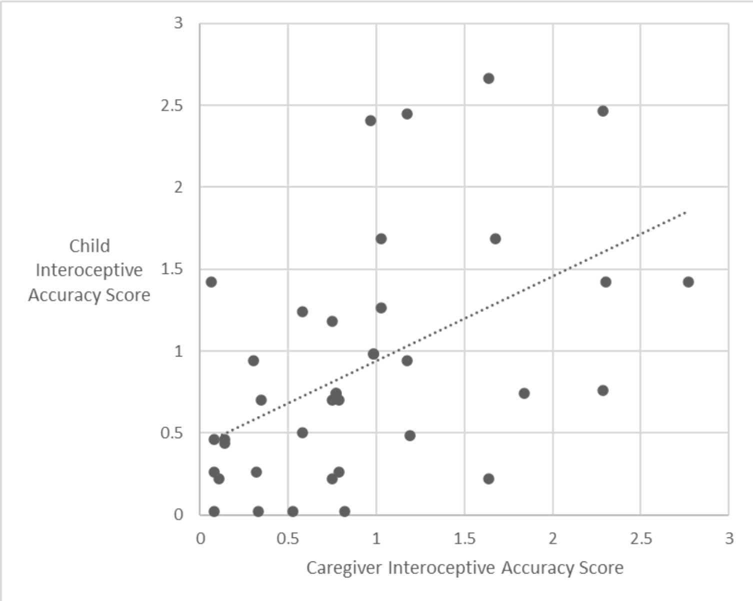


Figure 5.3
Scatter Plot Representing the Significant Positive Relationship between Caregiver Interoceptive Sensibility and Child Threat Sensitivity

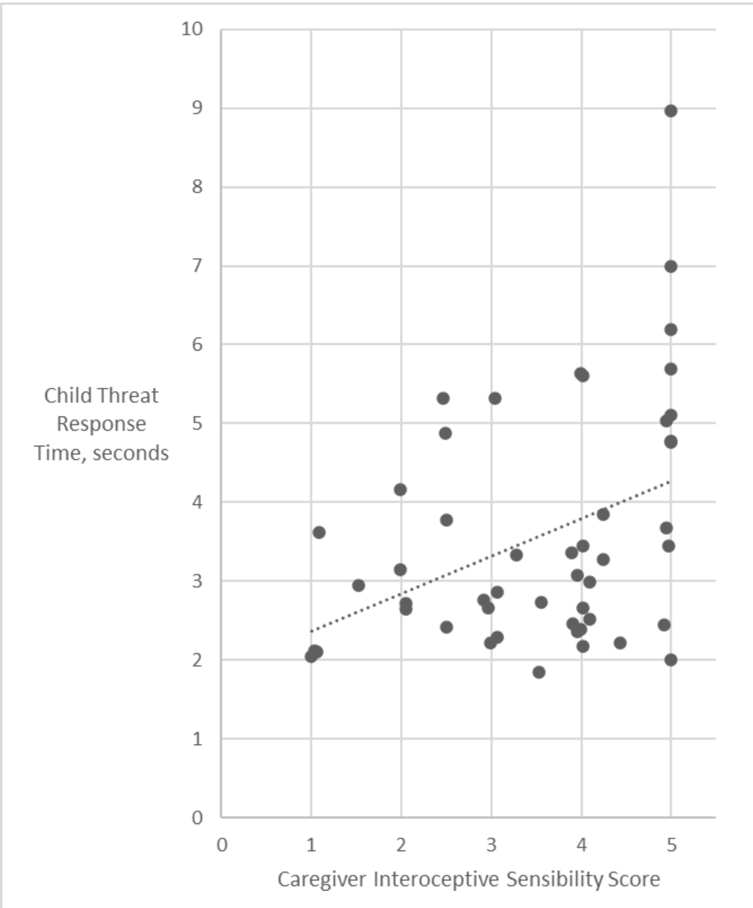
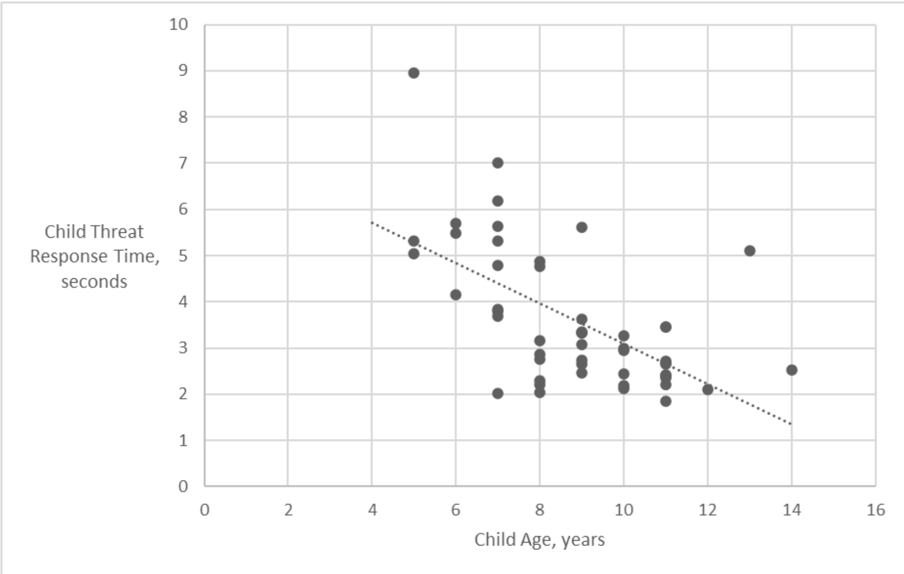


Figure 5.4
Scatter Plot Representing the Significant Positive Relationship between Child Age and Child Threat Sensitivity



was the only significant predictor of child Interoceptive accuracy (R = .486, R^2 = .236, F(1,34) = 10.182, p = .003, see Table 5.5 for beta coefficients). The inclusion of neither caregiver Interoceptive Sensibility nor caregiver GAD-7 score resulted in a significant improvement to the regression model.

5.3.4 Child threat sensitivity

To examine my second hypothesis, a second hierarchical regression was conducted to examine whether caregiver interoceptive accuracy, interoceptive sensibility and anxiety predicted child threat sensitivity. Once again, tests for multicollinearity indicated that a very low level of multicollinearity was present (VIF = 1.071, Tolerance = .934 for Child Age; VIF = 1.207, Tolerance = .828 for Caregiver Interoceptive Accuracy; VIF = 1.159, Tolerance = .863 for Caregiver Interoceptive Sensibility; VIF = 1.098, Tolerance = .911 for Caregiver GAD-7 Score). In the first block I entered child's age, since the preliminary analysis indicated a significant negative correlation between child age and threat sensitivity. This was followed by caregiver interoceptive sensibility and caregiver interoceptive accuracy, and finally by caregiver GAD-7 scores. Results of the hierarchical regression showed that both child age and caregiver interoceptive sensibility were significant predictors of child threat sensitivity. However, the best fitting model also included caregiver interoceptive accuracy. The model did not significantly improve when caregivers' GAD-7 scores were included (R = .624, R^2 = .346, F(3,42) = 8.947, p = .001, see Table 5.5 for beta coefficients).

Table 5.5
Results of Hierarchical Regression on Child Interoceptive Accuracy and Child Threat Sensitivity

	B	SE B	β	p
Dependent variable: Child interoceptive accuracy				
Step 1				
(Constant)	.413	.161		.015
Caregiver interoceptive accuracy	.450	.141	.486	.003
Step 2				
(Constant)	.948	.314		.005
Caregiver interoceptive accuracy	.515	.146	.556	.001
Caregiver interoceptive sensibility	-.142	.084	-.266	.099
Caregiver anxiety	-.027	0.28	-.141	.350
Dependent variable: Child threat sensitivity				
Step 1				
(Constant)	6.491	.755		<.001
Child age	-.339	.082	-.528	<.001
Step 2				
(Constant)	5.249	.892		<.001
Child age	-.330	.080	-.519	<.001
Caregiver interoceptive sensibility	.285	.137	.265	.043
Caregiver interoceptive accuracy	.259	.229	.145	.264
Step 3				
(Constant)	5.221	.909		<.001
Child age	-.336	.081	-.523	<.001
Caregiver interoceptive sensibility	.277	.141	.257	.057
Caregiver interoceptive accuracy	.276	.240	.154	.257
Caregiver anxiety	.014	.049	.034	.793

Note: Unstandardised coefficient, B, standard error of B and standardised coefficient Beta are reported for each step.

5.4 Discussion

In this study, I set out to test whether caregiver anxiety and dimensions of caregiver interoception (accuracy and sensibility), were related to their children's own developing interoceptive abilities and susceptibility to anxiety. I asked caregivers and their children to complete a modified heartbeat detection task (the Jumping Jack Paradigm) to measure interoceptive accuracy and interoceptive sensibility. Child's susceptibility to anxiety was measured using a threat-sensitivity task, while their caregiver completed an anxiety screening questionnaire (GAD-7 Spitzer et al., 2006). I hypothesised that higher interoceptive accuracy in caregivers would be associated with higher interoceptive accuracy in their child. In addition, I predicted that higher caregiver anxiety would be associated with lower interoceptive accuracy in their child. I also expected higher caregiver anxiety levels and lower caregiver interoceptive accuracy to predict lower interoceptive accuracy and greater threat sensitivity in the child. My data partially supported these hypotheses.

Caregiver interoceptive accuracy was positively associated with child interoceptive accuracy as measured via the Jumping Jack Paradigm. This is in line with my hypothesis and provides direct evidence to support the suggestion that the development of interoception in the child is related to the caregiver's own interoceptive abilities. Although I did not longitudinally examine this association from infancy to childhood, my findings provide converging evidence that caregiver-infant interactions may help explain the association between child and caregiver interoceptive accuracy. Emerging theories of interoceptive processing development place great importance on early dyadic interactions (Atzil et al., 2018; Ciaunica et al., 2021; Ciaunica and Crucianelli, 2019; Filippetti, 2021; Fotopoulou and Tsakiris, 2017a; Fotopoulou et al., 2022; Montirosso and McGlone, 2020). These theories suggest that infants learn to interpret and respond to internal bodily sensations through proximity and early dyadic exchanges with their caregivers. This study demonstrates that the role the caregiver plays in this interaction is also likely influenced by their own interoceptive abilities (Montirosso and McGlone, 2020; Tylka et al., 2015). These findings have implications for early developmental processes and caregiving practices. For example, heightened attention to internal sensations in the caregiver may lead them to favour their own perception of the infant's needs and act upon these before the infant is given the opportunity to sense their own internal bodily cues. Therefore, individual differences in a caregiver's capacity to identify and address their own visceral and autonomic states might impact early dyadic interactions, as the infant's dependency requires the caregiver to infer the infant's needs. My data suggest that these associations (that are most likely established early in life) are still evident during childhood.

The results also showed that caregiver interoceptive sensibility was associated with child threat sensitivity in the threat detection task, whereby caregivers with higher confidence in their own interoceptive aptitude had children with longer threat response times. This could indicate lower sensitivity to threats. Caregivers' interoceptive sensibility was not significantly related to the difference between their children's threat and non-threat response times, however. While adults and children, generally, demonstrate an attention bias to threat (Lipp et al., 2004, Lobue and Deloache, 2008, Lobue, 2009, Keogh et al., 2001, Ohman et al., 2001, Tipples, 2019), individual variation in this ability is an established marker of potential anxiety difficulties, with higher threat detection abilities potentially indicating greater sensitivity to threat resulting in higher anxious arousal (e.g. J. C. Britton et al., 2011, Hunt et al., 2006, Mark et al., 1996, Pine et al., 2005). While I did not see a direct relationship between child interoceptive sensibility and their threat detection abilities, the relationship between caregiver interoceptive sensibility and child threat response times in my data does suggest a relationship between interoception and anxiety across the generations. This provides further support for the idea that caregivers' interoceptive abilities may provide the framework for the child's ability to detect, appraise, and act upon their internal sensations, as well as highlighting a potential mechanism for the transfer of anxiety between caregivers and their children. Interoceptive sensibility is considered a dispositional measure of self-focus on internal bodily signals (Garfinkel et al., 2015). Several anxiety disorders are characterised by a misinterpretation of, or discomfort with, bodily sensations associated with anxious arousal, such as panic disorder or generalised anxiety disorder, respectively. Converging evidence show that such disorders are associated with atypically high interoceptive accuracy (Domschke et al., 2010). Regarding interoceptive sensibility, however, the relationship is less clear. I speculate that caregivers who believe themselves to be interoceptively cognisant, i.e. with higher interoceptive sensibility, may be more effective in communicating changes in bodily sensations to their child (e.g. "your heart races when you run"), thereby promoting child's interoceptive learning. Similarly, caregiver's interoceptive sensibility may also foster their ability to tune into the child's own states, thus aiding the child's ability to identify, appraise, and attach value onto their own bodily sensations (MacCormack et al., 2020; Meins et al., 2013; Fogel, 2011). Converging evidence demonstrated that caregiver interoceptive knowledge is associated with children's socio-affective development (MacCormack et al., 2020). Future studies should directly examine the processes that may be directly involved in this relationship, particularly focusing on the mechanisms through which caregiver interoception influences child development.

The extent to which lower threat sensitivity can directly translate into lower anxiety susceptibility could be questioned. While hypersensitivity to threat could indicate clinical risk for anxiety difficulties, too low a response to threat could also be unhelpful when considering that healthy levels of anxious arousal are a necessary survival mechanism prompting action to ensure safety. The finding of an association between child threat sensitivity and caregiver interoceptive abilities should, therefore, be interpreted with caution. While lower threat sensitivity appears to suggest lower anxiety, I do not know whether this may be driven by greater confidence with bodily sensations leading to lower likelihood of a negative attribution bias, or whether slower threat detection could indicate differential information processing for the child, such as higher internal focus and/or reduced attention to external stimuli.

The associations between interoceptive measures in my data were irrespective of child age (with the youngest children being 5 years old). The absence of a relationship between child age and child interoceptive accuracy in the data suggests that interoceptive accuracy is established and stable by the time children reach 5 years of age. It has previously been suggested that interoceptive sensitivity remains stable across the lifespan (Critchley and Harrison, 2013), while interoceptive awareness is thought to decline with age (Khalsa, Rudrauf, and Tranel, 2009). Additionally, children demonstrate lower long-term stability of the heartbeat counting measure compared to adults (Bornemann and Singer, 2017) across 1-year and 2-year periods (Koch and Pollatos, 2014a). Future longitudinal research will be essential to understand the developmental trajectories of interoceptive processing across different dimensions.

Contrary to my hypothesis, I did not observe a direct relationship between caregiver anxiety and the other variables of interest. In this regard and in line with the other studies presented in this thesis, it is important to note that I tested a non-clinical sample, with anxiety levels skewed towards the lower level of the GAD-7 scale. Many studies of caregiver mental health based on clinical samples with higher levels of anxiety have found relationships between caregiver anxiety and several aspects of child development (e.g. Brouwers et al., 2001, Glasheen et al., 2010, Polte et al., 2019, Rees et al., 2019). It is also widely accepted that anxious caregivers are more likely to have anxious children (Beidel and Turner, 1997; Warren et al., 2003). The GAD-7 scale is a short, rapid assessment that combines questions on physiological, cognitive and emotional aspects of anxiety. The relatively small, non-clinical sample of caregivers in the present study did not allow for a meaningful examination of these different aspects of anxiety individually and this could be worthy of further examination. However, the null finding regarding GAD-

7 scores could highlight an important distinction in the variability of functional impairment alongside anxiety symptoms. Anxiety scores have been found to only moderately correlate with functional impairment due to symptoms (McKnight et al., 2016). This suggests that while some individuals may cope well despite their anxiety, others suffer much greater impairment due to the severity of the symptoms. To what extent primary caregivers can conceal their anxiety for the sake of their child, or continue to fulfil their caregiving duties despite experiencing anxiety symptoms, and whether this "resilience" effectively acts as a buffer, remains an area of limited research. To fully explore these complex dynamics, future studies should incorporate measures of coping strategies in a sample of caregivers with clinical levels of anxiety.

There are some limitations to the present study that primarily pertain to the data collection method. The experiment was conducted in a public event, which limited my ability to collect more well-established measures of interoceptive accuracy (such as the heartbeat detection task; Schandry, 1981) and include a more thorough assessment of anxiety, including a historical assessment, which would have enabled a more detailed exploration of the relationship between interoception and anxiety symptoms. Therefore, future studies should seek to replicate the present findings in a laboratory-controlled setting.

The relationship between interoception and anxiety continues to attract research attention, with potential implications for clinical practice. Interoceptive exposure has been used within cognitive behavioural therapeutic treatment of anxiety for many years with the goal of improving a patient's tolerance for physiological symptoms. Yet, more recent developments (e.g., bio-feedback, breathing exercises and mindfulness) are the subject of ongoing research. For example, mindfulness-based interventions for children have undergone rapid development, but their effectiveness is yet to be supported by consistent evidence from randomised controlled trials (RCTs) (see Dunning et al., 2022 for a systematic review of sixty-six RCTs). With regard to anxiety, specifically, a systematic review of twenty RCTs found overall effects of mindfulness-based interventions in the treatment of anxiety to be both small and short lived (Odgers et al., 2020). If these new approaches to the clinical treatment of anxiety are found to be effective, perhaps there is an educational potential for even young children to learn to tolerate and manage unwanted or disliked bodily sensations. This idea is supported by previous research which has indicated that confidence in the ability to detect cardiac sensations can be improved with intervention (Parkin et al., 2014). Widespread education regarding emotion regulation and its relationship with bodily sensation could also aid to mitigate the risk of anxiety for both caregiver and child. Clearly, on an individual level, this is a potentially sensitive subject and any increase in pressure on an already struggling caregiver concerned about 'passing on' their own anxiety is likely to be counterproductive. Therefore, a wider societal focus on self-care and greater education among new caregivers and those responsible for caring for them is likely to be more effective. Longer term, with further exploration of early development of interoceptive processing and anxiety, I could one day identify those children at greatest risk before they present in clinic with very severe symptoms, to minimise the overall impact on their lives and help reduce the growing clinical burden on healthcare resources.

In conclusion, this study demonstrated a close family relationship between caregiver and child interoceptive accuracy in 5-to-14-year-old children, providing empirical support to previous theories suggesting that the development of interoception is related to early caregiver-infant dyadic interaction and that interoceptive accuracy remains stable across childhood. The studies presented in Chapters 3 and 4 shed light on the role of caregiver interoception and mental health in early dyadic interactions and how differences in caregiver interoception and mental health could influence the development of interoceptive processing in infancy and childhood. The results from this study seem to suggest that the effects of a caregiver's influence on the development of interoceptive processing can still be observed during childhood, albeit in a different manner. This finding warrants further investigation, as it illuminates the role of interoception as a potential key mechanism underlying the trans-generational transmission of anxiety.

Chapter 6

General Discussion and Conclusions

6.1 Introduction

To understand how we are feeling, both physically and emotionally, we rely on a constant stream of information about the internal state of our body, or interoception (Brewer et al., 2021). Some of this information reaches our conscious attention, such as when we are hungry, thirsty, or tired, prompting us to take actions to maintain our bodily state. However, much of this information is relayed subconsciously, prompting physiological changes such as to heart rate and blood pressure. In addition to its role in homeostatic maintenance, interoceptive information also informs our emotional state, since emotions are often characterized by internal physiological sensations. Examples of this include a pounding heart when we are scared, or butterflies in the stomach when we are nervous. Several theories of emotion, such as the Theory of Constructed Emotion (L. F. Barrett, 2017), have acknowledged the fundamental role of internal sensations for emotion processing. In adulthood, interoception is understood to inform both how emotions are processed as well as how they are regulated (Critchley and Garfinkel, 2017; Porges et al., 1994). The nervous system plays an important role in the communication and modulation of interoceptive information, with the vagus nerve, in particular, being involved in the regulation of emotions. Considering the tight link between interoception, emotion processing and emotion regulation, it is not surprising that interoception has been implicated in mental health. Indeed, a considerable body of literature suggests that impairments in interoception contribute to psychopathology risk (Khalsa et al., 2018; Nord and Garfinkel, 2022). Developmental research has highlighted a link between children's interoceptive abilities and both emotion regulation (e.g., Braet and Braet, 2024; De Witte et al., 2016), and caregiver's characteristics (e.g., Oldroyd et al., 2019). While these findings converge with adult research on interoception, little is still known about the developmental origins of interoception and its relationship with mental health (Murphy, Brewer, Catmur, and Bird, 2017a).

While the body of research on interoception continues to grow, a worsening landscape of child mental health is unfolding in the UK, with anxiety disorders being the most prevalent difficulties (Newlove-Delgado, 2023). Given the evidence from adult studies highlighting the importance of interoception in mental health, understanding the developmental trajectories of interoceptive processing and the origins of its relationship with mental health seems both critical and urgent.

The overarching goal of this thesis was to examine factors influencing the development of interoceptive processing in infancy and to explore the developmental origins of its relationship with mental health, as demonstrated in adult studies (Khalsa et al., 2018; Nord and Garfinkel, 2022). Theoretical accounts proposed that the early social environment, specifically contingent caregiver behaviour, facilitates interoceptive processing development (Atzil et al., 2018; Fotopoulou and Tsakiris, 2017a; Filippetti, 2021). In light of these theoretical accounts, I chose to focus my research on dyadic interactions. Based on the literature review presented in Chapter 1, I identified a set of key research questions that I sought to answer in this PhD thesis:

1. How do caregiver mental health and interoception relate to caregiver behaviour in naturalistic caregiver-infant dyadic interactions? (Study 1)

2. How does touch influence physiological evidence of emotion processing in infants? (Study 2a)

3. Do caregiver mental health and/or interoception relate to caregiver behaviour in a structured interaction task? (Study 2b and 2c)

4. Do caregiver mental health and/or interoception relate to infant vagal tone? (Study 2c)

5. Do caregiver interoception and/or mental health relate to child interoception and anxiety risk? (Study 3)

To answer the questions outlined above, I conducted five studies, presented in Chapters 3 (Study 1), 4 (Studies 2a, 2b and 2c), and 5 (Study 3). A summary of the key findings from each of the studies can be found in Table 6.1. The relevant chapters for each study include detailed discussions of the results in response to my specific research questions.

Table 6.1
Summary of Findings by Study

	Study	Participants	Methods	Findings
Chapter 3	**Study 1**			
	How do caregiver mental health and/or interoception relate to caregiver behaviour in naturalistic caregiver-infant dyadic interactions?	Infants aged 6 - 8 months and their primary caregiver	Behavioural observation of caregivers' use of touch and caregiver contingency Self-reported measures of caregiver interoceptive accuracy, interoceptive attention and anxiety	Higher caregiver contingency was associated with reduced instrumental touch Higher caregiver interoceptive accuracy was associated with reduced instrumental touch
Chapter 4	**Study 2a**			
	How does affective touch from the caregiver influence physiological evidence of emotion processing in infants?	Infants aged 6 - 8 months and their primary caregiver	ECG and EDA responses to processing of different emotions, with and without affective touch	Mean infant heart rate increased while processing negative emotions Study was halted due to COVID-19 lockdown, preventing further data collection
	Study 2b			
	Do caregiver mental health and/or interoception relate to caregivers' behaviour in a structured interaction task?	Infants aged 6 - 8 months and their primary caregiver	Self-reported measures of caregiver interoceptive accuracy, interoceptive attention and anxiety Caregiver-reported infant behaviour Caregiver behaviour in a modified Still Face Paradigm	No associations were observed between caregiver interoception, caregiver anxiety or caregiver behaviour in the modified Still Face Paradigm. Higher caregiver interoceptive accuracy was associated with higher infant surgency and orienting/regulatory capacity. Lower interoceptive attention was also associated with higher orienting/regulatory capacity.
	Study 2c			
	Do caregiver mental health and/or interoception relate to caregivers' behaviour in a structured interaction task? Do caregiver mental health and/or interoception relate to infant vagal tone?	Infants aged 6 - 8 months and their primary caregiver	Self-reported measures of caregiver interoceptive accuracy, interoceptive attention and anxiety Caregiver behaviour in a modified Still Face Paradigm Infant heart rate and heart rate variability during the modified Still Face Paradigm	Infant heart rate variability was negatively associated with an interaction between caregiver anxiety and depression Anxiety, but not depression, predicted a longer duration in the Responsive Still Face Paradigm
Chapter 5	**Study 3**			
	Do caregiver interoception and mental health relate to interoception and anxiety risk in older children?	Children aged 5 - 14 and their primary caregiver	Caregiver and child interoceptive accuracy in a heartbeat detection task (Jumping Jack Paradigm) Caregiver self-reported anxiety Child threat sensitivity in a computer game	Child interoceptive accuracy is associated with caregiver interoceptive accuracy Child threat sensitivity is associated with caregiver interoceptive sensibility

6.2 General discussion

In this section, I will examine what the findings of my studies collectively reveal, discussing how they contribute to the broader understanding of interoception in relation to previous research. First, I discuss whether and how caregivers' interoceptive abilities and mental health may influence the development of interoceptive processing in infancy. I then consider whether these factors have an enduring association with interoception and mental health throughout childhood. Finally, I reflect on how my findings add to the literature on the developmental trajectories of interoceptive processing.

6.2.1 The role of caregivers' interoceptive abilities

Caregiver behaviour in dyadic interactions

Previous studies have related caregiver interoceptive abilities with caregiver behaviour in dyadic interactions (Donaghy et al., 2024; Wigley et al., 2024). For example, caregivers reporting greater awareness of their interoceptive signals also show more stroking and rocking behaviours with their infants (Donaghy et al., 2024), while caregivers with higher interoceptive sensibility make greater use of stroking (Wigley et al., 2024). Touch is particularly interesting when considering interoceptive processing, due to the activation of C-T fibres (which also convey interoceptive information) in response to affective touch (Björnsdotter et al., 2010). Touch could, therefore, be hypothesized to facilitate interoceptive processing development, given this shared pathway and the role that proximity and touch play in infancy, as discussed in Chapters 1 and 4.

Caregivers' interoceptive abilities have also been suggested to facilitate simultaneous monitoring of their own bodily signals and their infant's arousal state to enable sensitive caregiving (Abraham et al., 2019; Montirosso and McGlone, 2020). To investigate the relationship between caregiver interoception, mental health and interactive behaviours, in Study 1 I examined caregivers' use of touch and the contingency of their behaviours in dyadic interactions with their infants in two naturalistic tasks (free play and story time). I also used self-reported measures of caregivers' state and trait anxiety and interoceptive accuracy and attention. While I did not observe a significant direct relationship between caregiver contingency and caregiver interoception, both of these variables were significantly associated with reduced instrumental touch in behavioural observations, suggesting they both influence the caregivers' behaviour. Anecdotally, in many cases instrumental touch involved restrictive touch, for example to prevent the infant from moving when the caregiver was trying to read a story. In this example, a more contingent response could have been to pause and acknowledge the infant's desire to move. While instrumental touch includes this kind of restrictive touch, it also covered more contingent touch behaviours, such as moving the infant towards an object in which they had shown interest. Further investigation of this specific behaviour is necessary, since instrumental touch can be interpreted in different ways. Notably, difficulties in interpreting contingency and instrumental touch behaviours were evidenced by the low inter-rater agreement in the study. More broadly, further research examining the relationship between caregiver contingency and caregiver interoception should include examination of different dimensions of interoception, to take account of the different underlying processes involved in different dimensions of interoception. One could have expected caregivers' interoceptive abilities to relate to how well they are able to infer their infant's needs and thus provide a contingent response. This is because empathy and emotional inference abilities have been associated with interoception previously (Critchley et al., 2004; Fukushima et al., 2011).

Beyond Study 1, I observed no other relationships between caregiver interoception and their behaviour in dyadic interaction. In studies 2b and 2c, I examined whether caregiver behaviour in a structured task, the Responsive Still Face Paradigm, RSFP, was associated with their interoceptive accuracy and attention as well as their anxiety levels. In these studies, the caregiver was asked to maintain a still face, without interacting with their infant, for as long as felt comfortable for them. I found that the duration of still face adopted by caregivers in either study was not associated with caregiver interoceptive accuracy nor interoceptive attention as measured by self-reported questionnaires. This raises the question of what factors may have driven caregivers' still face durations. It would be valuable to gain deeper insights into the thoughts and feelings that motivated caregivers to re-engage with their infants, particularly in instances where this behaviour was not prompted by a clear behavioural cue from the infant. For example, future studies could add a simple follow up question to elicit this information. The RSFP also requires further testing to establish whether it provides a reliable measure of caregiver behaviour, to ensure that caregivers are relying on their own thoughts and feelings to decide when to re-engage with their infant and are not, for example, trying to guess when a good time would be or fearing judgement by the researcher.

Infant vagal tone

The association between caregiver interoceptive abilities and infant vagal tone is of particular interest in the study of interoceptive processing development, as vagal tone depends on interoceptive information, represents parasympathetic nervous system activity, and is related to emotion regulation (Porges et al., 1994; Laborde et al., 2017). In Study 2c, I examined infant vagal tone in relation to caregiver interoceptive accuracy and attention, but did not observe a reliable relationship between caregiver interoception and infant baseline vagal tone. This is inconsistent with previous literature on emotion, which provides indirect evidence of a link between caregiver interoceptive abilities and infant vagal tone. For example, caregiver interoceptive knowledge has been positively related with their child's emotion regulation abilities at age 8-9 years (MacCormack et al., 2020). Previous research has also related increased caregiver interoceptive processing in the first few months of parenthood with reduced somatic symptoms in their children aged 6 (Abraham et al., 2019), suggesting that caregiver's interoceptive processing when caring for their infant could relate to their child's interoceptive processing abilities several years later. The authors suggested that this association is related to the quality of early dyadic interactions, particularly the extent of neural and behavioural synchrony within the dyad. In addition, they highlighted two different cross-generational pathways for this association: one relating to evolutionary threat response in the amygdala and dependent on social cues, and the other relying on higher-order caregiver empathy and sensitivity. Although focused on emotion regulation in older children, these studies suggest a potential developmental influence of caregivers' interoceptive abilities, since caregivers' interoceptive processing was observed in the first few months of parenthood. Consistent with this idea, a study on infant vagal tone has also found an association with early dyadic interaction, with greater synchrony associated with higher vagal tone in 3-4-month-old infants (Puglisi et al., 2023). However, this study did not specifically examine caregiver interoceptive abilities. Alternatively, the relationship between caregiver interoception and infant vagal tone could be indirect, i.e. caregiver interoception underpinning caregiver interactive behaviour, which, in turn, influences interoceptive processing development in the infant. If this is the case, a more robust sample and statistical analysis might be required, to detect any moderation/mediation effects.

Infant behaviour and temperament

In Study 2b, I investigated the relationship between caregiver interoception, their behaviour in a structured task, and their infant's temperament. The data suggested a relationship between caregiver interoception and the infant's behaviour, with higher caregiver interoceptive accuracy being associated with higher surgency and orienting/regulatory capacity. Lower interoceptive attention in the caregiver was also associated with higher orienting/regulatory capacity. In other words, higher interoceptive accuracy and lower interoceptive attention were associated with more positive infant behaviours. The findings from Study 2b could be interpreted to suggest that higher accuracy and lower attention relate to better emotion regulation in the infant. Indeed, maternal interoceptive knowledge has been positively associated with emotion regulation abilities and social skills in older children (MacCormack et al., 2020). However, these results were not replicated in Study 2c, where I did not find such relationships between caregiver interoception and infant temperament. It is worth noting that Studies 2b and 2c differed in several ways (See Discussion section in Chapter 4), and therefore discrepancies in the results could be explained by variations in methodology and sample characteristics. Future research is necessary to shed light on the interplay between infant temperament and caregiver's factors in influencing early dyadic interactions.

Children's interoceptive abilities and susceptibility to anxiety

In Study 3, I explored the relationship between caregivers' factors (interoception and anxiety) and interoception and threat sensitivity, a risk factor for anxiety susceptibility, in their children (Bar-Haim et al., 2007). Caregivers' interoceptive accuracy was positively associated with their children's interoceptive accuracy, directly supporting the idea that caregivers influence the development of interoceptive processing in their children. In addition, greater caregiver interoceptive sensibility was associated with reduced threat sensitivity in the child. Heightened threat sensitivity is considered a risk factor for anxiety difficulties (e.g. Bar-Haim et al., 2007J. C. Britton et al., 2011, Hunt et al., 2006, Mark et al., 1996, Pine et al., 2005). Therefore, the findings from Study 3 suggest a relationship between caregiver interoceptive abilities and child mental health risk. This is consistent with previous fMRI data relating higher maternal interoceptive processing activity, observed through activity in the anterior insula and amygdala, with fewer somatic problems in their children at age 6, moderated by greater sensitivity towards the child at age 4 (Abraham et al., 2019). Together, these findings are consistent with two separate bodies of research, both discussed in Chapter 1, suggesting that 1) interoceptive abilities are associated with psychopathology (Khalsa et al., 2018; Nord and Garfinkel, 2022) and 2) anxious parents are more likely to have anxious children (Beidel and Turner, 1997; Warren et al., 2003). One interpretation for these relationships could be that interoceptive abilities underpin emotion regulation and, hence, susceptibility to anxiety difficulties. Therefore, since interoceptive abilities appear to follow familial patterns, this association could provide insight into the mechanisms behind heritability of psychopathology. One could expect some degree of correlation between interoceptive accuracy in parents and their children, since interoceptive abilities inform parasympathetic-regulated cardiac activity (see Chapter 1), and cardiac regulation is considered to have a high degree of heritability (Neijts et al., 2014). Nonetheless, the finding relating interoceptive sensibility with threat sensitivity suggests environmental factors may still play a key role. Interoceptive sensibility is a measure of how confidently one trusts bodily sensations, which could be modelled to the child through their caregiver's behaviour (Giallo et al., 2014). An educational intervention to encourage caregivers to trust their bodily sensations in a healthy, adaptive way (as opposed to any potential hypervigilance or maladaptive focus) could reveal whether interoceptive sensibility can be specifically encouraged in early childhood.

Study 3 demonstrated no relationship between interoceptive accuracy and age, suggesting that interoceptive accuracy is already established by 5 years of age. This is supported by fMRI data, which has highlighted activity in similar brain regions in children aged 6 to 11 years old to those activated in adults during heartbeat detection tasks (Klabunde et al., 2019). Previously, it was suggested that, once established, interoceptive accuracy remains stable across the lifespan (Critchley and Harrison, 2013), suggesting that the development of interoceptive processing much earlier in life influences interoceptive accuracy across the lifespan. The strong positive relationship between caregiver and child interoceptive abilities demonstrated in Study

5, regardless of child age, suggests that caregivers influence the development of interoceptive processing very early in their child's life and that this influence is enduring throughout childhood. The importance of early environment is highlighted by studies of twins. Monozygotic twins have been observed to differ in their interoceptive abilities by eight years old, indicating that interoceptive processing is not a purely genetic phenomenon. In addition, the relationship between caregivers' interoceptive sensibility and children's threat sensitivity shines some light on a potential mechanism behind the established family relationships in psychopathology (Beidel and Turner, 1997; Warren et al., 2003).

Summary

In summary, the findings discussed so far support the idea that caregiver interoceptive abilities influence dyadic interactive behaviour and, thus, are in line with theoretical accounts of interoceptive processing development in infancy (Atzil et al., 2018; Fotopoulou and Tsakiris, 2017a; Filippetti, 2021). I observed a specific relationship between caregivers' interoceptive accuracy and how they use touch when interacting with their infants. I also observed relationships between caregiver interoception and behavioural evidence of emerging emotion regulation abilities in the infant as reported by their caregivers. The influence of caregiver interoception observed in these studies appears to be enduring, evidenced by a very strong relationship between caregiver interoceptive accuracy and that of their older children. In addition, I found caregiver interoceptive sensibility to relate to threat sensitivity in children, a risk factor for anxiety difficulties, a result that can inform clinical practise by potentially shedding light on the relationship between caregiver and child mental health.

6.2.2 The role of caregivers' mental health

Caregiver behaviour in dyadic interactions

A vast body of research has shown the influence of caregiver's mental health in their behaviour within the dyad. For example, higher caregiver anxiety has been associated with exaggerated and more intense behaviours towards their infants, with some speculation that this relates to higher physiological arousal in both caregivers and infants (Kaitz et al., 2010; C. G. Smith et al., 2022a). Caregiver depression, on the other hand, has been associated with reduced affectionate touch (Mercuri, Stack, Mantis, et al., 2023; Stepakoff and Beebe, 2024) and slower speech responses (N. Smith et al., 2022). In Studies 1 and 2b, I observed no association between anxiety or depression and caregiver behaviour in caregiver-infant interactions. One possible explanation for the discrepancy in results between my studies and the previous research is that my studies relied on non-clinical samples of caregivers, with anxiety data being skewed towards lower levels of anxiety. It is therefore possible that any behaviour associated with significant mental health difficulties was simply not present. It is important for future studies to focus not only on clinical samples, but also to consider both a disorder-specific and a trans-diagnostic assessment of individual differences in cognitive, somatic, emotional and behavioural characteristics. This approach could help determine whether specific characteristics of mental health problems, such as rumination, sensory intolerance, or behavioural avoidance of threat, for example, may be key drivers of the relationship between caregiver's mental health and the development of interoceptive processing in their infant. Limited research has explored specific behaviours related to maternal mental health, such as rumination (Wu et al., 2020) and avoidance (Morelen et al., 2014), with these behaviours both being associated with parenting behaviours and child emotion regulation. However, these studies involve older children and do not examine the effects of these behaviours during infancy, which would appear to be a critical period for the development of interoceptive processing and emotion regulation.

Infant vagal tone

In Study 2c, I investigated the relationship between caregivers' factors (mental health and interoception) and infant vagal tone. Bayesian modelling of the data suggested a relationship between caregiver mental health and infant vagal tone, with reduced infant vagal tone predicted in infants whose caregivers self-reported mental health difficulties (higher depression and anxiety). Since lower vagal tone is associated with poorer emotion regulation (Porges et al., 1994), this result is consistent with previous findings associating lower infant vagal tone with poorer maternal mental health (T. Field et al., 1995; Rattaz et al., 2022). This also offers some explanation for familial patterns in mental health, since reduced vagal tone is related to emotion regulation (Porges et al., 1994) and poor emotion regulation characterises several mental health difficulties (Pinna and Edwards, 2020; Sahar et al., 2001). Rattaz et al. (2023) proposed that the quality of interactive behaviour, measured by maternal sensitivity. may explain the association between maternal mental health with infant vagal tone. This suggests a potential role for education and behavioural interventions to mitigate the risk of reduced infant vagal tone in dyads, especially in situations where the primary caregiver is experiencing poor mental health.

Infant behaviour and temperament

I observed no direct relationship between caregiver mental health and infant behaviour and temperament, in contrast with existing research. Neither anxiety nor depression scores were associated with infant behaviour scores reported by their caregivers. Once again, this could relate to the caregivers taking part in these studies being drawn from a non-clinical sample, typically demonstrating low anxiety and depression scores. Examining caregivers with more significant mental health difficulties could reveal stronger evidence of a direct relationship with infant behaviour, as demonstrated in clinical studies (Warren et al., 2003).

Children's interoceptive abilities and susceptibility to anxiety

Caregiver mental health has long been considered a risk factor for child psychopathology (Vostanis et al., 2006), but the precise mechanism behind this transfer is unclear. In Study 3, conducted with children aged 5-14 years old, I did not observe any direct association between caregivers' anxiety and child threat sensitivity or interoceptive accuracy. This is in contrast to well-established family patterns in anxiety (Beidel and Turner, 1997; Warren et al., 2003). However, the finding discussed above, that child threat sensitivity was associated negatively with caregivers' interoceptive sensibility, does suggest a potential link between the mental health of the caregiver and the child, since those caregivers more confident about their interoceptive accuracy had children who were less sensitive to threat. I suggest that caregiver interoceptive sensibility is a likely mediator of this relationship, whereby a caregiver's confidence of their own interoceptive abilities allows a child to attend to internal sensations, which in turn allows for adaptive sensitivity to threatening cues. The limited sample of my studies did not allow for such analysis, and further research on family patterns of interoceptive ability are necessary to understand whether interoceptive sensibility mediates psychopathology risk.

Summary

Overall, in these studies, I observed some evidence of a potential direct influence of caregiver mental health on interoceptive processing development. Specifically, caregiver mental health appeared to predict infant vagal tone. Despite these modest findings, previous research in psychology and psychiatry consistently relates caregiver mental health with developmental outcomes in children, highlighting the importance of this avenue of research. Below I make recommendations for greater specificity in the examination of caregiver mental health involving clinical samples, which I was unable to follow within the confines of this thesis. By looking more in depth into these important factors, such as the different characteristics within mental health diagnoses, it is hoped that further light can be shed on the influence of caregiver mental health on interoceptive processing development.

6.2.3 Infant emotion processing

Studies of infant emotion processing have previously indicated differences in physiological arousal in relation to the processing of different emotions (Wass et al., 2018; Wass, 2021). I found significant changes in absolute heart rate in different emotional states across Studies 2a and 2c. In 2a, these differences were associated with the infant observing different emotional states. Infants' heart rates increased while observing negative emotions, relative to positive and neutral emotions. In 2b, changes to infant heart rate were associated with phases of the RSFP. After a baseline recording during playful interaction between the caregiver and infant, the caregiver adopted the still face and became temporarily unavailable to their infant. At this stage, infants heart rates increased, suggesting increasing arousal. Once caregivers re-engaged with their infants, the infants' heart rates began to drop, but did not fully recover during the period of recording. This is consistent with previous studies of infant physiology in the still face paradigm, in which infants' arousal increases, alongside increasing negative affect in the infant (Moore and Calkins, 2004). Some residual effects, the still face effect, continue during the reunion phase. These findings are also consistent with previous studies that indicate increased arousal with negative emotions relative to positive emotions (Wass, 2021) and provide physiological evidence of emotion processing in response to stimuli in 6-8-month-old infants. This suggests that, by this age, infants are experiencing different emotions in different ways. In addition to heart rate, heartbeat-evoked potentials in 5-month-old infants show larger amplitudes in response to negative emotions than positive emotions (Maister et al., 2017), further indicating differences in how negative and positive emotions are being processed. Vagal tone provides a marker of regulation of the parasympathetic nervous system in response to emotional arousal (Porges et al., 1994) and, as discussed in 6.2.2 above, my data suggested that caregiver mental health influences infant vagal tone. Taken together, my findings indicate that caregiver mental health could be influencing infants' emotion processing in this age group. This supports the theoretical accounts providing the backdrop to this research (Atzil et al., 2018; Fotopoulou and Tsakiris, 2017a; Filippetti, 2021) which all propose that the early social environment facilitates the development of interoceptive processing.

6.3 Limitations

Participation in my studies was open to all caregivers of healthy infants and children, i.e. they were not drawn from any clinical groups. While some caregivers did meet clinical thresholds for anxiety and/or depression, the sample sizes did not allow for meaningful between-groups comparisons, nor to examine the variables of interest within a clinical group. As argued in previous studies relating interoception with mental health, the specificity of interoceptive dimension as well as of mental health condition, or even the cognitive, behavioural, emotional or somatic symptoms within diagnoses, may be necessary in order to observe consistent trends (Nord and Garfinkel, 2022). Mental health is heavily influenced by individual differences, after all.

The COVID-19 pandemic and associated lockdowns forced a change in direction and the use of online studies, with a return to face-to-face activities once the lockdown had been lifted (September 2021 for the Essex Babylab). This meant that experimental conditions between studies varied, preventing a direct comparison of results. For example, Study 2b was conducted online with participants based in the USA, while Study 2c, which used the same measures, was conducted at Essex Babylab, in the UK. Despite these difficulties, the different experiments revealed some interesting results, prompting further questions. For example, data collected from the Babylab, with a researcher present, indicated a relationship between still face duration in the RSFP and anxiety, whereas the data collected online, recorded in participants' homes, did not. This raises questions about how caregivers behave towards their infants in different circumstances. Despite the lockdowns, I managed to continue researching the topic of dyadic influences on interoceptive processing, albeit in a different way from that initially planned. Original plans had included the use of implicit measures of interoception in both infant and caregiver, along with a longitudinal follow-up to highlight any developmental change over time. While I was no longer able to do this, I managed to investigate further along the developmental trajectory of interoception and anxiety, by looking at the relationship between caregiver and child interoceptive accuracy and threat sensitivity in older children. This study revealed strong family associations in interoceptive accuracy and highlighted a relationship between interoceptive sensibility in the caregiver and anxiety susceptibility in the child.

In Chapter 1, I highlighted the importance of acknowledging differences in the data collection methods when examining different dimensions of interoception and so it is important to highlight those differences again here. While in Study 3 I observed cardiac interoceptive accuracy through an objective heartbeat detection task, in Studies 1, 2b and 2c, I refer to cardiac interoceptive accuracy as scored on a self-report questionnaire. As discussed in Chapter 2, each task has its own strengths and weaknesses, and they involve different cognitive processing, so caution is required when comparing the results across studies.

As discussed at length in Chapter 1, many studies, including those I have presented here, focus on cardiac interoception. In the study of anxiety, this is justified, since a racing heart often characterises the somatic symptoms of anxiety. However, the same could be said of, for example, gastric sensations. It is important to highlight once again, that cardiac interoception does not necessarily translate to interoceptive abilities in other channels. It is equally as important to consider applying similar research attention to the other interoceptive channels.

Sample sizes were conservative throughout the thesis, due to time and resource limitations, recruitment challenges, and data quality. Studies 1, 2b and 2c relied on Bayesian modelling where it can be argued that sample sizes are less critical due to posterior sampling. Nevertheless, frequentist analysis, as in Study 3, would require a minimum sample of 107 to provide statistical power, based on a linear regression with two predictors detecting a medium-sized effect. Further studies based on similar methods would ideally be based on suitable sample sizes to ensure statistical power.

6.4 Recommendations for future research

While the studies conducted and presented in this thesis provide some support to the theoretical accounts for the development of interoceptive processing, they do not provide a longitudinal picture of its developmental trajectory. Many gaps remain in our understanding of how interoceptive processing develops and how this is influenced by caregivers' interoceptive abilities and their mental health, both early in infancy and throughout childhood. Future research needs to address these important gaps. This would be essential, not only to improve our understanding of interoception in itself, but also to explore in more depth the relationship between the development of interoceptive processing and child mental health. In light of the findings I have summarised and discussed above, together with other recent studies regarding interoceptive processing development (e.g. Imafuku et al., 2023; Maister et al., 2017; Tünte et al., 2024), and the current state of the adult research on interoception (Desmedt, Luminet, Maurage, and Corneille, 2023; Murphy, 2023; Nord and Garfinkel, 2022), I propose that further research should focus both on greater specificity of interoceptive dimensions and mental health conditions, as well as focusing on developmental trajectories, such as:

1. Taking a longitudinal approach from infancy to childhood to identify age-related changes and build a model of the developmental trajectories of interoceptive processing development

2. Examining implicit and explicit measures of interoceptive ability across different dimensions of interoception in caregivers to identify specific relationships between caregivers' and children's interoceptive abilities

3. Taking disorder-specific account of caregiver mental health and its relationship with caregiver dyadic behaviour, based on clinical samples

4. Examining trans-diagnostic components of psychopathology to explore whether, for example, cognitive factors (e.g. rumination, distorted beliefs), behavioural factors (e.g. avoidance, reassurance seeking) or emotional factors (emotion dysregulation difficulties, individual differences in physiological arousal) are associated with the unfolding interoceptive abilities and emotional wellbeing in the infant/child.

First, a longitudinal approach is necessary to provide a clear picture of the developmental trajectories of interoceptive processing. While this was part of the original research plan for my thesis, the COVID-19 pandemic rendered this research not possible. Examining a variety of measures relating to interceptive processing, such as heartbeat evoked potential, vagal tone, and physiological measures such as heart rate and electrodermal activity at multiple time points from infancy would allow any age-related trends to be observed. Drawing on previous research as well as my findings, this longitudinal picture is necessary across the first five years of life, with a focus on changes in the first weeks and months of life. This is because emotional arousal is evident in the first six months of life, both in my results and in the wider research (e.g. Wass, 2021), while Study 3 demonstrated that interoceptive accuracy appears to be established and stable in children over 5 years old. Indeed, interoceptive accuracy has previously been suggested to be stable across the lifespan once established (Critchley, 2002).

Once explicit measures of interoceptive abilities become feasible, i.e. in children with the appropriate cognitive, verbal, and motor skills necessary to take part in validated tasks, studies of interoceptive ability should examine various measures, i.e. both implicit, such as HEPs and vagal tone, as well as explicit measures, such as heartbeat detection tasks. This would facilitate a more thorough understanding of the different dimensions of interoception in childhood. In addition, once children are able to take part in such tasks, the data, when considered in relation to self-reported interpretations of bodily sensations and child mental health screening, would enable us to build a more thorough understanding of the emerging relationship between interoceptive abilities and child mental health. With this information, it could be possible for therapeutic developments to target specific issues, such as misattribution, or sensory intolerance of bodily sensations.

To assess the relationship between caregiver mental health and interoceptive processing development, studies should involve clinical samples of caregivers with a variety of mental health presentations. Across those diagnoses, studies should also examine trans-diagnostic components of psychopathology, i.e. cognitive, (e.g. rumination, distorted beliefs), behavioural (e.g. avoidance, reassurance seeking), somatic (e.g. physiological arousal, self-reported somatic symptoms) or emotional (e.g. emotion dysregulation difficulties, vagal tone) aspects of clinical presentations, in order to clarify the specific nature of any influence between caregivers' mental health and the development of interoceptive processing in their infant. Studies have also highlighted the potential clinical importance of interoceptive awareness (e.g. Garfinkel and Critchley, 2016; Murphy, Bird, and Catmur, 2019). While it is not straightforward to assess this meta-cognitive dimension of interoception in pre-verbal infants, it would be possible to examine interoceptive awareness in older children and caregivers to explore whether there is any direct influence from the caregiver in this respect, and whether a clinical relationship exists between interoceptive awareness and mental health difficulties in children.

6.5 Implications of this work

It is hoped that this thesis contributes to a deeper understanding of the factors influencing the development of interoceptive processing early in life, as well as the role caregivers play in shaping this process. As this understanding continues to unfold through ongoing research, it could facilitate important psychoeducation for new parents and wider society. This subject is potentially sensitive however, since new parents often face significant pressure to be 'good parents', and additional concerns about unintentionally passing on mental health difficulties to their children could add to this burden. Perhaps the current trend for increased openness, reduced stigma surrounding mental health difficulties, and calls for greater mental health support for new parents could provide a supportive cushion to this important topic, since, despite its sensitivity, the caregivers' mental health is extremely important in the provision of optimal care for infants.

From a clinical perspective, the unfolding relationship between interoceptive processing development and psychopathology risk for children could open avenues for therapeutic development. It is widely recognised in clinical practice that early intervention and treatment of anxiety is beneficial to the patient and the efficient use of resources (Brakoulias et al., 2017; Blakey et al., 2017; Lydiard et al., 1996). This is now of critical importance against the backdrop of a growing child mental health crisis in the UK (England and Mughal, 2019; National Audit Office, 2018; National Audit Office, 2023). Studies of clinical applications of interoception are under way in adulthood (e.g. Quadt et al., 2021; Suksasilp et al., 2024). Meanwhile, it is hoped that better understanding of the early developmental trajectories of interoceptive processing can aid in identifying any associated risk of childhood psychopathology. Further into childhood, assessment of interoceptive abilities could become the subject of routine assessment, just as we routinely test children's other senses, such as sight and hearing. This could potentially highlight risk of psychopathology, neurodevelopmental disorder and other health issues before the mental health of the child, as well as their family, is severely impacted. At the very least, assessment of interoceptive abilities should become routine within initial clinical assessments once children are referred for mental health consultations. Earlier in life, behavioural interventions and psychoeducation for new parents could help prevent the development of systemic family patterns that may predispose infants to anxiety difficulties.

6.6 Concluding remarks

The studies I conducted examined the influence of caregivers' interoception and mental health, on their own behaviour when interacting with their infants. In addition, I investigated the relationship between these factors and aspects of infant physiology and interoceptive processing development. I also examined these factors in relation to interoception and threat sensitivity in older children. Overall, some of the findings from this thesis provide support for theoretical approaches of interoceptive processing development (Atzil et al., 2018; Fotopoulou and Tsakiris, 2017a; Filippetti, 2021) and add to the limited empirical evidence of interoceptive processing published to date. The results demonstrate associations between caregivers' interoception and mental health, and behavioural mechanisms that may facilitate interoceptive processing development, such as dyadic interactions and the use of touch, specifically. However, inconsistent findings in my data, as in the previous research, highlights the need for consistent research methods and replication in future studies. I have suggested several avenues for future research. I hope that continued investigation into the development of interoceptive processing within the context of early social experience will further clarify the role of interoception in emotional development and its impact on psychopathology risk across the lifespan. Importantly, this work must continue in the midst of a worsening landscape of childhood psychopathology, since understanding the development of interoceptive processing early in life will add to the opportunities for therapeutic development that studies with adults have begun to highlight. While the studies I conducted focused primarily on the caregivers' behaviour, Study 1 demonstrated that caregivers' contingency in response to infants' behavioural cues depends quite heavily on the infant's ability to communicate their needs, in other words, the development of dyadic interaction is bi-directional. Somers et al. (2021) considered the impact of the infant's temperament on the caregiver, rather than the other way around, arguing that infants shape their own environment, at least to some extent, through their temperament. Montirosso and McGlone (2020) highlighted the importance of reparation in periods of misattunement in dyadic synchrony for infant development, similar to a sentiment first ventured by Beebe et al. (2010), who proposed an optimum middle ground for caregiver-infant synchrony. Together, these different perspectives provide a useful reminder that while a responsive caregiver can provide an environment in which the infant can discover their sense of self and learn to recognise their own bodily sensations, there is no need for perfection. In fact, optimum caregiving, with respect to interoceptive and emotional development, would appear to depend on imperfection.

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