

Citation:

Pfeifer, G and Cawkwell, S (2025) Interoceptive ageing and the impact on psychophysiological processes: A systematic review. International Journal of Psychophysiology, 207. pp. 1-17. ISSN 0167-8760 DOI: https://doi.org/10.1016/j.ijpsycho.2024.112483

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Document Version: Article (Published Version)

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Contents lists available at ScienceDirect

International Journal of Psychophysiology

journal homepage: www.elsevier.com/locate/ijpsycho

Interoceptive ageing and the impact on psychophysiological processes: A systematic review

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ARTICLE INFO

Keywords Ageing Old adults Interoception Emotion Cognition Body representation

ABSTRACT

Interoception, the perception and response to internal bodily states, significantly influences physical and mental wellbeing. While ageing is associated with interoceptive decline, research has primarily examined selective dimensions of interoception. Understanding these changes is vital as the global population ages, addressing age-related health issues and sustaining psychological wellbeing. This systematic review synthesised findings from 22 studies on age-related interoceptive changes and their impact on psychophysiological processes. Results showed age-related declines (48.4 %), no age differences (32.3 %), an age-related increase (16.13 %), and an inverted U-shaped curvilinear relationship (3.23 %) in interoceptive sensitivity across age groups and interoceptive dimensions. Three patterns emerged regarding psychophysiological processes in older adults: altered mind-body connections with age were associated with reduced high-arousal and increased positive emotional experiences, cognitive protective effects, and improved body representation that correlated with better interoceptive sensitivity. These patterns indicate the complex relationships between interoceptive ageing and psychophysiological processes, showing both, aspects of decline and compensatory mechanisms. We propose future research avenues to elucidate the functional significance of different interoceptive dimensions across the lifespan for optimised psychological wellbeing and health behaviours in older adults.

1. Introduction

Interoception refers to the representation of internal bodily states at conscious and preconscious levels (Desmedt et al., 2022; Suksasilp and Garfinkel, 2022). It plays a critical role in physiological and psychological wellbeing, influencing homeostasis, emotions, decision-making, body representation, and self-awareness (Monti et al., 2022); Tsakiris and Critchley (2016). Despite growing interest in interoception (Brener and Ring, 2016; Khalsa et al., 2018), the study of its lifespan changes, particularly in ageing, are only beginning to emerge. Given the global increase in life expectancy (WHO, 2024, October 01, understanding how interoception affects ageing populations is crucial for mitigating health problems and maintaining wellbeing (Scott, 2021).

1.1. Dimensions of interoception

Interoception encompasses multiple dimensions, including the

sensation, integration, interpretation, and regulation of internal bodily signals, operating both unconsciously and consciously (Chen et al., 2021; Suksasilp and Garfinkel, 2022). Unconscious interoception refers to peripheral autonomic signals that influence emotional states (Garfinkel and Critchley, 2016), while conscious interoception includes accuracy, self-reported beliefs, metacognitive insight, and attention to interoceptive sensations (Suksasilp and Garfinkel, 2022). In this review, we adopt Suksasilp and Garfinkel's (2022) dimensional framework of interoception to define specific dimensions and integrate the respective measurements from the studies reviewed: The Interoceptive accuracy (IAcc) dimension refers to the accurate detection of interoceptive sensations that correspond to physiological measures, as validated by behavioural tests (e.g., the heartbeat counting task (Schandry, 1981) and heartbeat detection task (Brener and Kluvitse, 1988; Katkin et al., 1983)). Interoceptive belief (IB) is assessed through self-report tools such as interoception questionnaires, confidence ratings, and beliefs about one's interoceptive sensations and experiences. Interoceptive insight, also

Abbreviations: BMI, Body Mass Index; BP, Blood pressure; HCT, Heartbeat Counting Task; HDT, Heartbeat Detection Task; HR, Heartrate; HRV, Heartrate variability; IAcc, Interoceptive Accuracy; IA, Interoceptive Attention; IB, Interoceptive Belief; SST, Socioemotional Selectivity Theory.

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https://doi.org/10.1016/j.ijpsycho.2024.112483

Received 2 May 2024; Received in revised form 2 December 2024; Accepted 5 December 2024

Available online 9 December 2024

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Review



NTERNATIONAL JOURNAL O PSYCHOPHYSIOLOGY known as *metacognitive insight*, measures the correspondence between participants' confidence ratings and their actual accuracy in perceiving internal sensations, as assessed by behavioural tasks. *Interoceptive attention (IA)* encompasses both the ability to focus on interoceptive sensations when instructed, and the habitual attention to these sensations. For example, the commonly used Awareness subscale of the Body Perception Questionnaire (BPQ; Cabrera et al., 2018), is a self-report measure of IA, specifically assessing habitual attention by asking participants about their 'awareness' of bodily sensations during most situations. Throughout this review, we use the term *interoceptive sensitivity* as an umbrella term to capture all interoceptive dimensions, including those assessed through subjective and performance-based measures.

Advancements in understanding interoception promise insights into its changes across the lifespan and their psychophysiological impacts. Before presenting the methods and results of our review, we provide a brief overview of age-related interoceptive changes, and how they affect physical and psychological wellbeing.

1.2. Interoceptive ageing and physical health risks

Interoceptive signals are transmitted via various sensors (e.g., mechanoreceptors, chemoreceptors) connecting the peripheral and central nervous systems along multiple biological axes, including cardiac, respiratory, gastric, genitourinary, and skeletal systems (Berntson and Khalsa, 2021; Lv et al., 2022). Ageing impairs multiple sensory systems, including the interoceptive system, starting as early as age 20 and becoming prevalent by age 60 (Volter et al., 2021). This decline includes reduced sensitivity to gastrointestinal symptoms (Beckers et al., 2021) and cardiac signals (Khalsa et al., 2009). Poorer visceral pain perception is linked to impaired nerve conduction and decreased connectivity in key brain regions (González-Roldán et al., 2020), raising the risk of injury (Gibson and Farrell, 2004). Altered chemoreceptor senses can lead to malnutrition (Rayner et al., 2000; Schiffman, 1997), while reduced baroreceptor and osmoreceptor sensitivity increases the risk of dehydration (Cowen et al., 2023). These findings suggest interoceptive ageing impairs homeostatic functions and allostatic control, complicating older adults' ability to detect and respond to internal bodily changes. Moreover, as physical discomfort becomes normative with age, seeking medical help may be delayed, posing additional health risks for older adults.

1.3. Interoceptive ageing and emotional wellbeing

Individuals with higher interoceptive sensitivity tend to show greater emotional reactivity (Hantas et al., 1982; Pollatos et al., 2007; Wiens et al., 2000) and regulation (Füstös et al., 2013; Price and Hooven, 2018), which not only facilitate greater responsiveness to illness and infection, but also improve coping strategies after they occurred. However, ageing is linked to reduced emotional reactivity (MacCormack et al., 2022; Mendes, 2010), potentially increasing dependency on external guidance (Loeb et al., 2001). Research also shows a relationship between ageing and alexithymia, hindering older adults' emotional communication (Mattila et al., 2006; Onor et al., 2010).

Despite physical and cognitive challenges, older adults often experience greater emotional wellbeing and improved emotion regulation compared to younger adults (Carstensen et al., 2011; Kunzmann et al., 2000). The Socioemotional Selectivity Theory (SST) explains this positivity effect by suggesting that older adults prioritise emotionally meaningful experiences as they perceive their time as limited (Carstensen, 2006; Carstensen et al., 1999). However, SST does not integrate sensory decline and physiological changes with emotional experiences. Synthesising recent findings on interoceptive ageing and emotions will provide a more nuanced understanding of emotional wellbeing in older adulthood by integrating the underlying physiological changes with age.

1.4. Relationships between age-related physiological changes and arousal

In addition to sensory decline, ageing is associated with a range of physiological changes that impact the interoceptive system. Examples include cardiovascular changes such as reduced cardiac output, arteriosclerosis, heightened blood pressure and hypertension; changes in the gastrointestinal system and altered metabolism; as well as respiratory changes such as reduced lung vital capacity (Boss and Seegmiller, 1981). These physiological changes affect the function of visceral afferents and their neural representation, triggering a cascade of preconscious and conscious influences on emotion and cognition. According to arousal theories of emotion (James, 1884; Lange, 1885), physiological responses to environmental challenges precede emotional experiences. While high-arousal states are marked by feelings of energy, excitement, and tension, low-arousal states are characterised by calmness, relaxation, and depression (Niven and Miles, 2013). Consequently, the age-related physiological changes described above modulate emotional intensity and arousal, thus impacting affective arousal states (Barrett and Russell, 1999) (Russell, 2003). A body of research has reported a higher frequency of experienced low-arousal states in older individuals, irrespective of the valence (pleasantness) of the emotion (Bialkebring et al., 2015; English and Carstensen, 2014; Scheibe et al., 2013; Wang et al., 2020). Some have shown faster recovery from high negative to low negative affect states in older adults (Hay and Diehl, 2011), as well as less variability in the experience of high-arousal emotions, including frustration, excitement, and happiness, relative to young adults (Wang et al., 2020). Neural explanations attribute the experience of lowarousal affective states to altered amygdala functioning in the ageing brain (Cacioppo et al., 2011). Specifically, decreased amygdala activation in response to negative stimuli leads to selectively lower arousal responses, contributing to the reduced negativity frequently reported by older adults (Hess et al., 2017; Mather et al., 2004; Petro et al., 2021). While reduced negativity benefits mental health, it may also lead to inaccurate health self-assessment and increased risk-taking (Herman et al., 2018; Mata et al., 2011; Nolte and Hanoch, 2023). This review examines findings on age-related physiological changes and arousal to explore their impact on positive and negative emotional experiences, aiming to provide a deeper understanding of these interconnected processes in older adulthood.

1.5. Physiological theories of ageing

Physiological theories acknowledge the causal relationship between senescent sensory, physiological, and interoceptive changes, and their influence on emotional experiences and behaviour (Kuehn et al., 2018; Costello and Bloesch, 2017; MacCormack et al., 2022; Mendes, 2010). *Maturational Dualism* posits that weakened mind-body connections due to sensory decline and reduced physiological reactivity result in blunted emotions (Mendes, 2010). Enhanced emotional wellbeing with age is thus seen as a reduction in negative emotions due to physiological decline, rather than an increase in positive emotions – unless older adults actively seek positive emotional experiences as proposed by SST (Carstensen, 2006; Carstensen et al., 1999).

The Physiological Hypothesis of Emotional Ageing (PHEA; MacCormack et al. (2022)) suggests that age-related physiological changes and their neural representations impact emotional experiences and social behaviour. As physiological functioning and interoceptive sensitivity decline with age, older adults increasingly rely on their accumulated knowledge and expertise to interpret emotional situations, which enhance emotional wellbeing and facilitate more effective emotion regulation. The process is supported by the cognitive construction of emotions (Barrett, 2017), where individuals actively interpret and reframe emotional experiences based on their past knowledge. In addition to this, older adults, in line with SST (Carstensen, 2006; Carstensen et al., 1999), employ goal-directed strategies that prioritise positive emotional experiences. Together, these mechanisms enhance emotional resilience and contribute to a greater sense of wellbeing. Thus, the PHEA differs from maturational dualism in its explicit integration, rather than separation, of physiological, cognitive, and socio-emotional theories in explaining age-related changes in emotional experiences and communication.

Embodied cognition models of ageing suggest that physiological changes and sensory decline disrupt the integration of exteroceptive and interoceptive sensations, impacting body representation and sense of self (Costello and Bloesch, 2017; Kuehn et al., 2018). Research shows that interoceptive accuracy correlates with body ownership and agency (Kirsch and Kunde, 2023; Suzuki et al., 2013; Tsakiris et al., 2011). However, age-related changes likely affect these aspects, altering the sense of body ownership and self (Monti et al., 2022).

The above theories shape our understanding of interoceptive ageing and its impact on psychophysiological processes. They are crucial for interpreting our review findings and enhancing insights into mind-body connections (Mendes, 2010), emotional experiences (MacCormack et al., 2022), and body representation (Costello and Bloesch, 2017; Kuehn et al., 2018).

1.6. Review aims

To advance our understanding of interoceptive ageing, we conducted a systematic review addressing the following research questions:

1. What are the age-related changes across various interoceptive dimensions?

2. How do age-related changes in interoception impact psychophysiological processes, including emotional processing, physiological regulation, and cognitive functioning?

Addressing these research questions will provide deeper insights into the complex interplay between interoceptive changes and ageing, offering a more comprehensive understanding of how these changes impact physical health, emotional and cognitive wellbeing in older adults.

2. Method

2.1. Search strategy

This review adhered to the Preferred Reporting Items for Systematic Reviews and Meta-Analysis (PRISMA) guidelines (Moher et al., 2009) and was registered on PROSPERO (CRD42023474563). Eligible articles were initially identified by one researcher (GP), conducting searches using the electronic databases PsycARTICLES, PsycINFO, and PubMed. The databases were accessed via the University of Southampton's EBSCO online system in June 2023, with an updated search completed in July 2024. Two sets of keywords relating to ageing and interoception were combined using the Boolean operator "AND". Search terms related to ageing were varied to capture different English spellings (e.g., ageing; ageing), and were truncated to include derivatives (e.g., age*, agi*, old* (e.g, older); life* (e.g., lifespan); development* (e.g., developmental), as well as adulthood). All search terms related to ageing were searched in the articles title, while the truncated term interocept* was searched using the All Text function in EBSCO. The rationale for this was that studies examining age-related changes in interoception would focus their title on the ageing concept. The truncated search term combinations were: Age* AND Interocept*; Agi* AND Interocept*; Life* AND Interocept*; Development* AND Interocept*; Old* AND Interocept*; Adulthood AND Interocept*. No restriction was set concerning publication dates, and non-peer reviewed articles were included in the search. The following inclusion and exclusion criteria were set:

Inclusion:

a) Studies were included if there was either a systematic age comparison in interoceptive sensitivity, or a correlational design examining age-related changes in interoceptive sensitivity.

- b) Although our review considered studies that included children and young adults, studies were excluded if they focused on examining age groups below the age of 40 (i.e., examining children and young adults only).
- c) Non-clinical and sub-clinical populations. Papers that examined populations with a developmental condition (Autism Spectrum Disorder) and a control group were retained with a focus on reviewing control group performance.
- d) Studies using an interoceptive measure that systematically investigated participants' interoception at one of the dimensions described in (Suksasilp and Garfinkel, 2022), e.g.
 - o Interoceptive Accuracy (IAcc): Heartbeat counting, detection, or both; alternative measures that assess the alignment between the subjective detection and actual physiological signals, as evaluated by behavioural measures.
 - o Interoceptive Belief (IB): Including commonly used questionnaires; e.g. the Multidimensional Assessment of Interoceptive Awareness (MAIA; (Mehling et al., 2018); Mehling et al. (2012)), the Self-Awareness Questionnaire (SAQ; Longarzo et al. (2015)).
 - o Interoceptive Attention (IA): Including the Body Perception Questionnaire (BPQ; Cabrera et al. (2018)).
 - o Interoceptive Insight: Confidence ratings in response to IAcc measures.
 - o Studies investigating the preconscious impact of afferent signals on emotion and cognition (Suksasilp and Garfinkel, 2022): e.g., cardiac signals, heartbeat evoked potentials.

Exclusion

- a) Populations with a physical or mental health condition (e.g. frailty, irritable bowel syndrome, diabetes, dementia, eating disorders, and participants with a psychiatric and neurological condition).
- b) Indirect measures of interoception (e.g. inferences made from activation of brain areas involved in interoception without probing participants' interoception).
- c) Unspecific measures of interoception (e.g. the 10-item interoceptive-subscale of EDI-2; Garner et al. (1983)).
- d) Review articles
- e) Non-English language
- f) Non-human participants

2.2. Data extraction

All identified papers were uploaded into EndNote (The EndNote Team, 2013) and duplicates were removed. Two reviewers (GP and SC) independently screened the article titles and abstracts to retain those meeting the defined inclusion criteria. Inconsistencies were discussed and consensus was reached between researchers. Full-text articles were then reviewed and discussed again (GP and SC) against the inclusion / exclusion criteria before extracting information of key features of each included article. The selection process is shown in Fig. 1.

2.3. Data analysis and synthesis

The data extraction from the 22 included studies was guided by our two research questions, focusing on (1) age-related changes in interoception, and (2) the impact of age-related changes on psychophysiological processes, including emotional processing, physiological regulation, and cognitive functioning. All relevant methodological details and results were extracted and documented in a spreadsheet. A synthesis of the key findings, summarised in Table 1, was conducted using the systematic narrative review approach outlined by Siddaway et al. (2019). This involved:

a) Grouping studies based to shared research aims and topics.

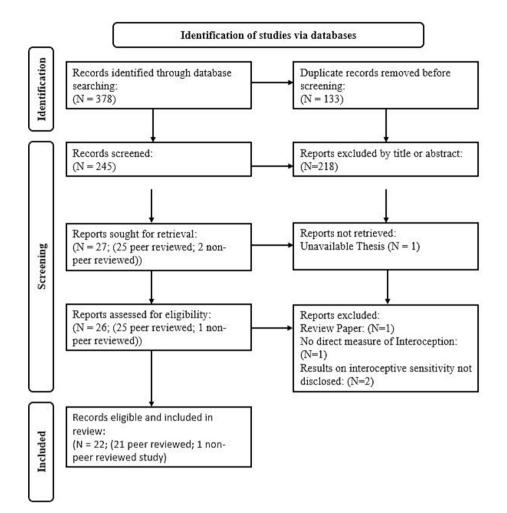


Fig. 1. PRISMA flowchart describing the number of studies identified, screened, excluded and included in the systematic review process.

- b) Categorising findings according to the methodological approaches used to measure different dimensions of interoception and their relationship with age (research question 1).
- c) Organising findings based on the relationships between interoception and the various psychophysiological processes examined in the studies (research question 2).
- d) Examining variations in results and identifying potential reasons for these discrepancies, such as differences in sample characteristics or task paradigms.
- e) Evaluating the strength of the evidence supporting key themes and conclusions.

By synthesising the data in this manner, we identified three consistent result patterns related to age-related changes in interoception and their impact on psychophysiological processes.

3. Results and discussion

Our systematic review of 22 studies on the topic of ageing and interoception revealed findings from three disparate research aims and topics, which are reported accordingly in Table 1: 1) Age-related changes in interoception, 2) Ageing, Interoception and the relationship with emotion and cognition, 3) Ageing, Interoception and the effects on body representation.

To address our first research question concerning age-related changes across various interoceptive dimensions, the 22 studies yielded 31 findings. These findings encompass changes in IAcc, insight, beliefs, preconscious afferent signals, and alternative measures of

interoception (see breakdown of findings in Fig. 2). The results were heterogenous: Studies using the HCT indicated a significant age-related decline in IAcc in 3 out of 9 findings (Murphy et al., 2018; Murphy et al., 2019; Nusser et al., 2020), although one of these findings became nonsignificant after controlling for confounding factors such as time perception, systolic BP, HRV, resting HR, BMI, and beliefs of average HR (Murphy et al., 2019). Five of the nine findings showed no age-related differences (Failla et al., 2020; Haustein et al., 2023; Mash et al., 2017; Mikkelsen et al., 2019; Ueno et al., 2020). Notably, however, except for Mikkelsen et al. (2019), who compared young and older adults, the other four studies focused on narrower age ranges, from childhood (aged 4-8) to middle age (up to 54 years) (Failla et al., 2020; Mash et al., 2017), or from old to very old adults (Haustein et al., 2023; Ueno et al., 2020), potentially obscuring transitional differences in IAcc that might occur between middle-age and older adulthood. One study, comparing young and older adults on the HCT, demonstrated an agerelated increase in IAcc (Cioffi et al., 2017).

Of the 4 findings from the HDT task, 3 suggested an age-related decline in IAcc (Dobrushina et al., 2024; Khalsa et al., 2009; Lohani, 2014), and one found no age-related differences (Dobrushina et al., 2020). However, Dobrushina et al.'s (2020) study of middle-aged to older adults (aged 42–62) may have overlooked age-related changes seen in the other three studies, which included participants spanning a broader age range from young to old. Concerning metacognitive insight, 1 study reported a significant age-related increase in HCT confidence (Nusser et al., 2020). Among the 12 findings related to interoceptive attention (IA) and interoceptive belief (IB), 3 studies using the BPQ showed an age-related decline (Elliott and Pfeifer, 2022; Murphy et al.,

Study	Study aim(s)	Participant Characteristics	Methods	Key Findings	Key Implication	Interoceptive Dimension
Ageing and inte	eroception					
Khalsa et al., 2009	Relationship between age and IAcc	<i>N</i> = 59 (ages 22–63)	Heartbeat Detection Task (HDT)	Significant decrease in heartbeat detection accuracy with age.	IAcc declines with age	Accuracy
Murphy et al., 2018	Relationship between age, IA, and IAcc	Study 1: <i>N</i> = 345 Study 2: <i>N</i> = 136) ages 18–89)	Study 1: Body Perception Questionnaire-Very Short Form (BPQ-VSF) Study 2: Heartbeat Counting Task (HCT); Controlled for BMI, gender, HR, HRV, beliefs about HR, time perception, systolic BP.	-Study 1: Negative relationship between age and IA -Study 2: Negative relationship between age and IAcc	Age-related interoceptive decline persists even after adjusting for confounding variables	Attention Accuracy
Nusser et al.,	Age-related changes in	N=137 (ages	-HCT,	- Significant decline in IAcc	IAcc declines with age,	Accuracy
2020	IAcc, metacognitive insight, and IB.	19–81)	-Heartbeat counting confidence -MAIA subscales (Noticing, Attention Regulation, and Body-Listening).	with age. - Significant improvement in metacognitive insight with age. - No significant age-related change in IB, based on the composite scores of the three MAIA subscales.	interoceptive insight improves, suggesting greater reliance on external	Insight
					cues to assess interoceptive states and regulate homeostatic needs.	Belief
	eption and the effects on	-		** .1 . 11	• • • • • • • • • • • • • • • • • • •	
Dobrushina et al., 2020	Relationships between interoception, brain activation, and emotional intelligence (EI).	N = 30 females (age 42–62).	 Brain activation measured in fMRI during performance on the HDT. White matter integrity assessed using diffusion- weighted MRI. EI assessed using the Mayer-Salovey-Caruso Emotional Intelligence Test (MSCEIT). 	 Heartbeat detection yielded significant activation in interoception-related brain structures such as the right anterior insula. Age showed no significant correlation with IAcc or insula activation. Age was related to significantly lower scores on the 'Understanding Emotions' subscale of the MSCEIT. Higher scores on the 'Understanding Emotions' subscale associated with increased activation in the right anterior insula and enhanced white matter integrity. 	 Age-related decline in EI linked to reduced coherence in brain regions supporting interoception. 	Accuracy Neural representation
Dobrushina et al., 2024	Age-related changes in interoceptive brain networks and relationships with alexithymia.	N = 258 (ages 18–73), including N = 62 who underwent fMRI.	 Brain activation measured in fMRI during performance on the HDT. MAIA-2 Toronto Alexithymia Scale (TAS-20) 	 Age was negatively correlated with IAcc and the Trusting subscale of the MAIA-2. Positive relationship between age and the 'Externally Oriented Thinking' subscale of the TAS-20, but higher IAcc associated to lower 'Externally Oriented Thinking'. Decreased activation in interoceptive brain regions with age. 	 Weakened interoceptive network coherence in older adults suggests compensatory mechanisms in brain connectivity. 	Accuracy Neural representation
Elliott and Pfeifer, 2022	Relationship between IA, IB, age, and Covid- 19 anxiety during the first lockdown in the UK.	<i>N</i> = 232 (ages 18–76), categorised in four groups: ages 18–24, ages 25–34, ages 35–54, ages 55–76.	 Body Perception Questionnaire-Short Form (BPQ-SF), MAIA-2 State-Trait Anxiety Inventory (STAI). State anxiety measured by asking participants to focus on the COVID-19 pandemic. 	 Age associated with significantly lower BPQ- SF, MAIA-2 Body- Listening scores, and lower COVID-19 State anxiety after controlling for Trait anxiety. Higher COVID-19 State anxiety correlated with higher scores on BPQ-SF and the MAIA-2 subscales Noticing, Emotion Awareness, and Body- Listening. 	- Lower IA and IB in older age associated with reduced state anxiety.	Attention Belief

(continued on next page)

Study	Study aim(s)	Participant Characteristics	Methods	Key Findings	Key Implication	Interoceptive Dimension
Haustein et al., 2023	Relationship between IAcc and affective / cognitive measures in older adults.	<i>N</i> = 91 (ages 60–91)	 HCT and the time estimation control task, Positive and negative affect schedule (PANAS), Big Five Personality Inventory, delayed verbal memory, Wechsler Full Scale IQ. 	 No significant decline in IAcc after controlling for time estimation. IAcc significantly negatively related with positive affect and extraversion. IAcc significantly positively related to cognitive performance (delayed verbal memory). 	 IAcc might plateau from old to very old age. Higher IAcc linked to less positive affect and lower extraversion in older adults. Cognitive ability might mitigate interoceptive decline in older adults. 	Accuracy
Kamp et al., 2021	Age-differences in preconscious processing of cardiac signals in the brain (heartbeat evoked potentials, HEP) and relationships with everyday metacognition.	N = 49 older adults (ages 63–82) N = 28 young adults (ages 20–36)	 ECG, EEG, cardiac measures. HEP amplitudes across midline electrodes (Fz, Cz, Pz). Self-report questionnaires assessed daily metacognitive experiences related to memory. 	 Older adults had significantly higher HEP amplitudes and wider scalp distributions than younger adults. Lower HEP amplitudes in older adults associated with more favourable self- perceived memory abilities. No relationship between HEP amplitudes and metacognition found in young adults. 	- HEP might be a biomarker for preconscious interoceptive signals that influence metacognitive performance.	Preconscious afferent signal:
Lohani, 2014	Age-differences in IAcc, coherence between subjective emotional experiences behavioural, and physiological states.	N = 60 young adults (ages 18–23) N = 60 older adults (ages 60–87)	 HDT Emotional experiences, facial expressions, and physiological responses during sadness-inducing videos. 	 Young adults had significantly higher IAcc than older adults. In young adults, IAcc significantly predicted coherence between: Subjective emotional experience and facial expression. Facial expression and physiological reactivity. Older adults showed significantly greater coherence between subjective experience and physiological reactivity, but this was unrelated to IAcc. 	- Older adults show a disconnect between IAcc and emotional reactivity, aligning with Mendes' (2010) concept of an age- related mind-body disconnect.	Accuracy
MacCormack et al., 2021	Mental associations between emotions and subjective interoceptive sensations, behaviours, and situations.	Experiment 1: <i>N</i> = 143 participants (ages 18–75) Experiment 2: <i>N</i> = 198 participants (ages 18–67)	Experiment 1: Property- association task: associating emotion words (high/low arousal negative) with word properties (interoceptive sensations, behaviours, situations). Experiment 2: Day Reconstruction Method (DRM): recalling and rating daily experiences of interoceptive sensations, behaviours, situations, and subjective states (emotional, physical, cognitive).	 Experiment 1: No significant age differences in emotion- property associations. Significant curvilinear relationship: emotion- interoceptive associations peaked at age 45, then declined. Older adults performed significantly poorer in associating high arousal emotions with interoceptive properties (e.g., ANGER – HOT), but retained associations between low arousal emotions and interoceptive properties (e.g., SADNESS – WEAK). Experiment 2: No significant age differences in interoceptive experiences. 	 Disconnect between subjective interoceptive sensations and emotions from middle to old age. Ageing is associated with fewer high arousal sensations and emotions. 	Belief
				 Age predicted fewer high arousal interoceptive sensations and emotions, but more intense low arousal emotions. 		

Table 1 (continued)

(continued on next page)

N = 623 (ages Age-differences in - MAIA-2 subscales - Significant negative Belief - Mindfulness approaches Windsor. mindfulness, IB, goal 18-84) (Noticing, Emotional relationship between age focusing on interoceptive 2021 setting, and wellbeing. and IB (using composite bodily states may be less Awareness), mindfulness components, scores of the two MAIA-2 effective in older adults goal-setting, and wellsubscales) than external presentbeing measures. Significant positive moment and nonjudgrelationship between age ment practices, which and mindfulness measures enhance positive emotions, aligning with (present-moment attention, non-judgment, Socio-Emotionalacceptance, nonattach Selectivity (Carstensen et al., 1999). ment, decentring). Mikkelsen - HCT No significant age Disconnect between IAcc Age-differences in IAcc N = 65 younger Accuracy et al., 2019 adults (ages 19-46) - Emotional reactivity differences in IAcc, and emotional reactivity and emotional reactivity N = 32 older adults measured by rating emotional reactivity, or in older adults, aligning (ages 50-77) negative affect-inducing change in affect. with Mendes' (2010) A significant negative concept of weakened images. relationship between IAcc mind-body connections - Affective states assessed and emotional reactivity with age. before and after viewing was moderated by age, images using the PANAS. indicating that this relationship weakens as age increases High IAcc significantly related to lower negative image ratings in young, but not in older adults. Higher IAcc significantly correlated with lower negative affect (PANAS) across age-groups. Murphy et al., Relationship between N = 134 (ages - HCT (controlling for Significant age-related - Findings are indicative of Accuracy 2019 age and emotion 20-90) confounds time decline in IAcc, but this a mitigating effect of perception, systolic BP, fluid intelligence on IAcc, relationship disappeared recognition. HRV, resting HR, BMI, irrespective of the wellafter controlling for and beliefs about average confounders. known age-related HR) Fluid intelligence decline in fluid Emotion recognition significantly positively intelligence. tasks, fluid intelligence, related to IAcc but The disappearing processing speed, and negatively to age. significant relationship affective traits Fluid intelligence-IAcc between age and IAcc, (depression, alexithymia, relationship disappeared and between fluid after adjusting for time intelligence and IAcc anxiety). perception and cardiac emphasise the measures. importance of controlling Emotion recognition for confounding factors (anger, disgust) predicted while performing the by processing speed and HCT. fluid intelligence. Depression negatively affected emotion recognition. No significant effect of age, IAcc (controlled), alexithymia, crystallised intelligence, and anxiety on emotion recognition. Ulus and Interoception and its Experiment 1: N =Experiment 1: Experiment 1: Poorer IAcc and IA in Accuracy Aisenbergrelationship with 18 young adults older adults linked to Attention (ages 20-34) - Compared subjective Young adults showed Shafran, emotional experiences reduced emotional 2022 across different age N = 20 older adults arousal ratings with higher IA and a significant experience. (ages 73-87) physiological changes positive correlation Age-related disconnect groups. Experiment 2: N =(BP, HR) during between self-reported and between perceived and emotional image viewing. 27 older adults actual physiological actual physiological (ages 70-86) BPQ-SF arousal. arousal. Experiment 2: Older adults showed no significant correlation - Emotional valence and between perceived and arousal ratings during actual arousal. image viewing and Older adults reported concurrent physiological greater subjective measures (BP, HR). physiological changes - BPQ-SF during emotional image

Study aim(s)

Participant

Characteristics

Methods

Key Findings

Table 1 (continued)

Study

Mahlo and

Key Implication

Interoceptive

Dimension

viewing despite similar

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Table 1 (continued)

Study	Study aim(s)	Participant Characteristics	Methods	Key Findings	Key Implication	Interoceptive Dimension
				actual physiological changes to young adults. Experiment 2:		
Jeno et al., 2020	IAcc and functional brain connectivity in older adults.	N = 27 (ages 61–87)	 Resting state fMRI scans. HCT performed outside the scanner. Time perception task included as a control 	 Older adults' IA was significantly negatively related to emotional valence, with lower IA linked to more pleasant experiences and less negative emotional experiences. Higher IA in old adults linked to reduced physiological changes (HR, BP) during emotional image viewing. Higher subjective arousal in older adults linked to greater reduction in HR and systolic BP. No significant relationship between IAcc and age from old to very old age. Time perception not significantly related to IAcc. 	 IAcc linked to increased connectivity in regions related to conflict/error monitoring, indicating higher regulatory effort. 	Accuracy Neural representation
			measure.	- Significant positive correlations between IAcc and functional connectivity of the rostral prefrontal cortex (rPFC) with the insular cortex, anterior cingulate cortex (ACC), and orbitofrontal cortex.	 The negative insula- visual cortex connectiv- ity indicates a compen- satory anterior shift in brain activity to offset sensory decline. 	
				- Significant negative correlation between IAcc and connectivity between the left anterior insula and posterior visual regions.		
ailla et al., 2020	Relationship between IAcc and age in ASD and typically developing (TD) individuals.	 Total N = 100 ASD group: N = 46 (ages 8-54) TD group: N = 54 (ages 8-53) 	Whole brain activation measured in fMRI during HCT performance.IQ measures (WASI-II)	 IQ was a significant predictor of IAcc in both ASD and TD groups, even after controlling for age. Significant positive relationship between age and activation in regions of the interoceptive network, including insular and anterior cingulate cortices. Peak interoceptive 	 Cognitive ability influences interoception more than diagnostic status. The positive relationship between age and activation in interoceptive regions, peaking in early adulthood, indicates a developmental trajectory for interoceptive 	Accuracy Neural representatio
				 activation observed in early adulthood, with curvilinear age effects in the insula, independent of diagnostic group. No significant group differences in brain activation during heartbeat counting. 	processing.	
Aash et al., 2017	Relationship between age, ASD, IQ, and IAcc.	Total <i>N</i> = 104 - ASD group: <i>N</i> = 46 (ages 8–54) - TD group: <i>N</i> = 58 (ages 8–54)	- HCT - IQ measures (WASI-II)	 In TD individuals with lower IQ (<115), age positively correlated with IAcc, suggesting improved interoception from childhood to middle adulthood. In ASD individuals with lower IQ, age negatively correlated with IAcc, indicating a decline in interoception with age. Higher IQ (>115) 	 Age impacts interoception differently based on IQ, with lower IQ individuals showing distinct age-related tra- jectories in TD versus ASD groups. Higher IQ may protect against age-related de- clines in IAcc, suggesting cognitive factors play a significant role in intero- ceptive processing. 	Accuracy

Table 1 (continued)

Study	Study aim(s)	Participant Characteristics	Methods	Key Findings	Key Implication	Interoceptiv Dimension
				had better IAcc overall and showed no significant age-related changes in IAcc.		
'ang et al., 2022	Relationship between age, autistic traits, and IAcc in a non-clinical sample.	Total $N = 266$ Age groups: $N = 52$ children (ages 4–6) N = 50 adolescents (ages 12–16) N = 114 emerging adults (ages 19–22) N = 50 young to middle-aged adults (ages 23–54)	 Eye-tracking Interoceptive Accuracy Task (EIAT) HCT used in a subgroup of (<i>N</i> = 78) adolescents (ages 12–16) and adults (ages 23–54) MAIA administered to a subsample of <i>N</i> = 35 adolescents (ages 12–16) and <i>N</i> = 21 adults (ages 23–54). Autism-Spectrum Quotient (AQ). 	 Significant positive correlation between age and EIAT performance. No significant relationship between autistic traits and IAcc (AQ score and EIAT. Significant positive correlation between EIAT and IAcc measured with the classic HCT. Young to middle-aged adults scored significantly higher on the MAIA Body Listening subscale compared to adolescents. 	 IAcc significantly increased from childhood to middle adulthood. Using multiple interoceptive measures (EIAT, HCT, MAIA) reveals a developmental peak in interoceptive sensitivity during emerging and young adulthood, with age showing a stronger association with IAcc than autistic traits. 	Accuracy
Ageing, interoc Cioffi et al., 2017	Age and the effect of internal and external cues on the sense of agency (SoAg) and sense of body	Experiment 1: $N =$ 14 younger adults (ages 17–34) and 14 older adults (ages 54–72).	Experiments 1 + 2: Vicarious Agency Paradigm. Experiment 2:	 Older adults reported significantly lower SoAg and SoO ratings overall compared to younger adults. 	 Older adults may rely more on internal bodily cues, leading to decreased sensitivity to external cues in agency 	Accuracy
	ownership (SoO).	Experiment 2: $N =$ 18 younger adults (ages 18–35) and 17 older adults (ages 62–92).	 HCT. Proprioceptive accuracy. 	- Significant interaction between age and condition, with older adults showing a weaker response to agency manipulation, perceiving similar SoAg and SoO in both congruent and incongruent vicarious actions.	 processing. This reliance might stem from the increased reliability of internal sensations over a lifetime, potentially reducing the distinction between self-generated and external actions. 	
				 Older adults performed significantly better than younger adults on IAcc and proprioceptive accuracy tasks, indicating a stronger reliance on internal cues. 		
araindas and Cooney, 2023	Relationship between Body Image Disturbance (BID), IB, and body schema across age groups.	Total <i>N</i> = 1214 female participants Age groups: - Young adults (ages 18–24) - Adults (ages 25–39)	 BID: Questionnaires assessing body objectification, state and trait body dissatisfaction. MAIA-2 Body Schema: Own Body Transformation (OBT) task involving mental rotations to assess 	 Older adults (ages 60–75) scored significantly lower on composite MAIA-2 score than adults (ages 25–39). Older adults had significantly lower BID compared to younger age groups. 	 Older adults have lower IB and BID compared to younger groups, but BID, not IB, is a stronger predictor of body schema across all ages. 	Belief
		 Middle-aged adults (ages 40–59) Older adults (ages 60–75) 	changes in body position.	 No significant age differences in body schema. Higher IB significantly correlated with lower BID across all age groups. BID, not IB, predicted body schema across age groups, suggesting BID's greater influence on body schema than IB. 		
Raimo et al., 2021a	Effects of IB on body representation (BR) across age groups.	Total <i>N</i> = 239 Age Groups: - Young children:	 Self Awareness Questionnaire (SAQ) BR tasks: Action-Oriented Task: 	 IB: No significant main effect of age on SAQ scores. Descriptive statistics 	- IB affects body representation differently across the lifespan, indicating that IB can contribute to	Belief
		 Young Children: N = 65 (ages 7–8) Older children: N = 37 (ages 9–10) Young adults: N = 50 (ages 18–40) 	 Action-Oriented Task: Hand laterality task assessing motor imagery and body schema. Non-Action Oriented Task: Frontal Body Evocation (FBE) task 	Descriptive statistics showed U-shaped performance with youngest children and older adults scoring highest on SAQ. BR:	IB can contribute to declines in action- oriented body schema, but might improve body structural representa- tion/ownership with age.	

(continued on next page)

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Table 1 (continued)

Study	Study aim(s)	Participant Characteristics	Methods	Key Findings	Key Implication	Interoceptive Dimension
		 Middle-aged adults: N = 50 (ages 41–60) Older adults: N = 37 (ages 60+) 	assessing body structure and ownership.	 Significant inverted U- shaped relationship: poorest performance in children and older adults on action- and non-action oriented BR. IB moderated the relationship between age and BR: 		
Raimo et al., 2021b	Effects of IB on body representation (BR) across age groups.	 Data derived from the same sample as Raimo et al. (2021a) excluding the two groups of children. Total N = 137 Age groups: Young adults: N = 50 (ages 18–40) Middle-aged adults: N = 50 (ages 41–60) Older adults: N = 	- SAQ BR tasks: - Hand laterality - FBE. - Additional BR measure to Raimo et al. (2021a): Object-body part associa- tion task (e.g., hat with head) assessing body semantics.	 Higher IB significantly correlated with poorer performance on the hand laterality task, with this effect increasing with age. Higher IB significantly correlated with better performance on the FBE task, with this effect increasing with age. Findings from the BR tasks (hand laterality and FBE) and moderating effects of IB comparable to Raimo, Di Vita, et al. (2021a). No significant differences in IB across age groups. No significant age differences in object-body part association performance. IB did not moderate the relationship between age and body semantics. 	 Higher IB in older adults reduces body schema measured by the action- oriented hand laterality task (decisions whether a visual hand stimulus is a left or right hand). Higher IB in older adults increases non-action- oriented BR (body ownership), improving their ability to assemble body parts into a com- plete body. 	Belief

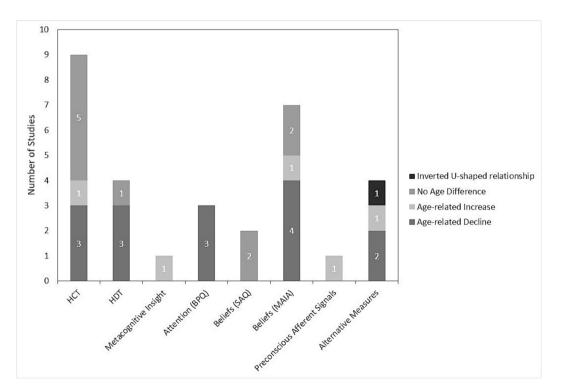


Fig. 2. Breakdown of age-differences for each interoceptive measure.

2018; Ulus and Aisenberg-Shafran, 2022), 6 studies using selective subscales or composite scores of the MAIA indicated 4 significant age related declines (Dobrushina et al., 2024; Elliott and Pfeifer, 2022; Mahlo and Windsor, 2021; Naraindas and Cooney, 2023), 2 showed no significant age difference (Dobrushina et al., 2024; Nusser et al., 2020), and 1 reported a significant increase in IB from adolescence to middle age (Yang et al., 2022). The 2 findings using the SAQ did not reveal any significant age differences in IB (Raimo, Boccia, et al., 2021; Raimo, Di Vita, et al., 2021).

One study on preconscious afferent signals reported a significant agerelated increase in heartbeat evoked potential (HEP) amplitude and broader cortical amplitude distribution in older adults (Kamp et al., 2021), suggesting an age-related decline and compensation in cardiac signal processing. Additionally, studies using alternative behavioural measures of interoception produced four key findings: one study showed an age-related increase in IAcc from childhood to middle age (Yang et al., 2022), while 2 studies indicated an age-related decline in interoceptive sensitivity—1 related to detecting physiological changes (Ulus and Aisenberg-Shafran, 2022) and the other to word associations with interoceptive properties and high-arousal emotions (MacCormack et al., 2021). One study found a significant inverted U-shaped relationship regarding mental associations (MacCormack et al., 2021).

Concerning the second research question on how age-related interoceptive changes affect psychophysiological processes, three distinct patterns emerged from our review:

- 1) Age is associated with altered mind-body connections, which are linked to reduced high-arousal emotional experiences and an increase in positive emotional experiences.
- 2) There is a relationship between cognitive measures / intelligence and interoceptive sensitivity in older age.
- 3) Interoception in old age enhances body ownership, reduces body schema and agency, and moderates body image disturbances.

We report the details from these patterns below:

3.1. Pattern 1

3.1.1. Altered mind-body connections with age are related to reduced higharousal and increased positive emotional experiences

Several of the reviewed studies pointed to an age-related disconnect between interoceptive sensitivity and emotional experiences, consistent with maturational dualism (Mendes, 2010) and other physiological theories of ageing (Costello and Bloesch, 2017; Kuehn et al., 2018; MacCormack et al., 2022). The age-related mind-body disconnect was seen across studies using experimental and behavioural measures of interoception, with the expression of this disconnect varying between studies (Lohani, 2014; MacCormack et al., 2021; Mikkelsen et al., 2019; Ulus and Aisenberg-Shafran, 2022): One study found that while IAcc (HCT) did not significantly differ between young and older adults, only young adults showed a significant relationship between IAcc and emotional reactivity, whereas no such relationship was found in older adults (Mikkelsen et al., 2019). This suggests a disconnect between bodily states and emotional experiences in older adults. By contrast, Lohani (2014) found that older adults had significantly poorer IAcc (HDT) than young adults. Additionally, only in young adults did IAcc significantly predict coherence between subjective emotional experience, facial expression, and physiological reactivity to sadness. While older adults exhibited more coherence between subjective experience and physiological reactivity, this was unrelated to IAcc, further suggesting a reduced mind-body connection in this age group.

Taking a lifespan approach, MacCormack et al. (2021) found a curvilinear relationship with age for associating emotion with interoception words, with the strongest associations at middle-age and impoverished associations in childhood and old age, suggesting a disconnect between subjective interoceptive states and emotional experiences. This disconnect was particularly evident in how older adults perceived and responded to arousal, showing significantly poorer associations between high-arousal emotions and interoceptive words (e. g., ANGER-HOT) but maintaining associations with low-arousal emotions (e.g., SADNESS-FATIGUED). The study also noted that with age, people tended to experience more intense positive emotions and less intense negative emotions, aligning with the well-known positivity effect observed in older adults (Carstensen, 2006; Carstensen et al., 2011).

Similarly, Ulus and Aisenberg-Shafran (2022) found that young adults were significantly better at detecting physiological arousal changes in response to emotional stimuli than older adults, indicating an age-related decline in IAcc. Despite this decline, older adults reported higher subjective physiological arousal to emotional images compared to younger adults, although objective physiological measures (HR and BP) showed no significant age differences. This suggests that older adults increasingly rely on cognitive interpretations of their interoceptive signals, which may lead to an exaggerated perception of arousal. This lowered threshold for subjective arousal might explain older adults' preference for low arousal emotions and positive affect relative to young adults (Sands and Isaacowitz, 2017; Scheibe et al., 2013).

Research using subjective measures of interoception similarly uncovered a recurrent theme, whereby poorer IB and IA in older adults were associated with more positive and less negative emotional experiences, traits, and behaviours. For example, Ulus and Aisenberg-Shafran (2022) found that older adults scored lower for IA (BPQ) than younger adults. Lower IA was associated with more pleasant emotional experiences across positive and negative images and significantly fewer negative responses to negative images, suggesting reduced negative emotional experiences in older adults. Similarly, Elliott and Pfeifer (2022) found that older adults scored lower on IA and IB (the BPQ-SF and the MAIA-2 subscale Body-Listening, respectively) and experienced less state anxiety during the COVID-19 pandemic after controlling for trait anxiety. Mahlo and Windsor (2021) further showed that age was negatively related with IB (2 MAIA subscales, Noticing and Emotional Awareness), while showing positive relationships with adaptive mindfulness components such as present moment attention, nonjudgment, acceptance of thoughts and emotions, and nonattachment to transient pleasant experiences, suggesting greater emotional wellbeing in older adults. Note, however, neither study examined whether age moderated the significant direct relationships between IB and mindfulness (Mahlo and Windsor, 2021) or IA/IB and state anxiety (Elliott and Pfeifer, 2022). As such, while lower IB in older adults was associated with greater mindfulness and reduced anxiety, these traits may still operate independently and will need to be addressed in future research.

Interestingly, (Haustein et al., 2023) found an inverted relationship between interoception and positive affect using a behavioural measure of interoception, the HCT. They only examined older adults between the ages of 60–91 years and found that within their older sample, lower IAcc was related to higher extraversion and a greater experience of positive affect (PANAS). This suggested that poorer IAcc might increase a positive outlook in older adults, while potentially contributing to higher emotional volatility. Similarly, Dobrushina et al. (2024) showed that as age increased, IAcc decreased (measured by the HDT), while alexithymia, particularly in the Externally Oriented Thinking component of the Toronto Alexithymia Scale (TAS-20), increased. However, heartbeat detection accuracy was negatively related to Externally Oriented Thinking, indicating that individuals with better integration of interoceptive and exteroceptive signals are more oriented toward their internal feelings.

In summary, across the reviewed studies, age-related changes in interoception were evident across both subjective and behavioural measures. Both types of interoceptive measures yielded a predominant decline with age, accompanied by weakened connections between interoceptive signals and emotional reactivity. Poorer age-related interoception was associated with enhanced emotional wellbeing, reduced anxiety, greater mindfulness, higher extraversion, and increased positive affect. This may be explained by the fact that positive emotions, unlike high-arousal negative emotions (e.g., anger, fear, disgust), are generally lower in arousal and less influenced by interoceptive signals or acute physiological changes. As a result, older adults might rely more on cognitive appraisal and less on interoceptive sensitivity to experience positivity. Consequently, older adults appear to maintain a (negative) relationship between interoception and positive emotional experiences, while showing weakened connections, particularly with high-arousal emotions. These altered mind-body connections reflect a shift in emotional priorities with age, favouring low-arousal and positive affect over high-arousal states.

3.2. Pattern 2

3.2.1. The relationship between cognitive measures / intelligence and interoceptive sensitivity in old age

Four studies have highlighted the importance of IQ and other cognitive measures as potentially protective functions against agerelated changes of interoceptive accuracy (Failla et al., 2020; Haustein et al., 2023; Mash et al., 2017; Murphy et al., 2019). Note that in Mash et al. (2017) and Failla et al. (2020) the relationship between IQ and IAcc was observed in younger samples ranging from childhood to middle age. However, Haustein et al. (2023) showed that verbal memory predicted IAcc in their sample of 60–91 year olds, and Murphy et al. (2019) showed that fluid intelligence was positively related with IAcc in their sample of 20-90 year olds, suggesting that the relationship between cognitive functioning and interoception might extend into older age. However, it is possible that intelligence correlates with improved time perception and knowledge of heartrate that drive IAcc (Murphy et al., 2019), and these factors would need to be controlled for. Moreover, a causal relationship between intelligence and interoception cannot be implied, and relationships with intelligence might vary across different interoceptive dimensions. As shown in one of our reviewed studies (Kamp et al., 2021), lower HEP amplitudes in older adults were associated with better subjective metacognitive memory, suggesting a potential influence of afferent signal strength on cognition (although note that this study was correlational).

3.3. Pattern 3

3.3.1. Interoception in old age enhances body ownership, reduces body schema and agency, and moderates body image disturbances

Four of the reviewed studies have explored how body representation (BR) changes with age (Table 1). Body representation refers to the mental processes and perceptions of one's body and includes two key components. First, body schema, an action-oriented component of BR, which can be assessed through tasks that evaluate motor imagery. These tasks require individuals to determine whether body parts displayed at varying angles correspond to the left or right side of the body (Naraindas and Cooney, 2023; Raimo, Boccia, et al., 2021; Raimo, Di Vita, et al., 2021). Second, BR involves a non-action oriented, perceptual representation of body structure, evaluated through tasks requiring participants to assemble body parts into a complete body, reflecting perceived ownership. Findings indicated that good interoception in old age increased body ownership (Raimo, Boccia, et al., 2021; Raimo, Di Vita, et al., 2021), reduced body schema (Raimo, Boccia, et al., 2021; Raimo, Di Vita, et al., 2021) and impaired the processing of external cues indicating poorer sense of agency (Cioffi et al., 2017). Specifically, increased reliance on internal bodily sensations in old age, as observed by Cioffi et al. (2017), may blur the distinction between real and artificial body parts, which can enhance body ownership while disrupting body schema and agency.

Interestingly, Naraindas and Cooney (2023) showed that older adults scored lower than younger age groups on body image disturbance, suggesting that older adults are generally more content with their body image than younger age groups. This is counterintuitive to the experience of common age-related bodily changes (e.g. reduced skin elasticity, greying of hair, etc.), the awareness of which can profoundly affect older people's identity (Clarke and Korotchenko, 2011), and be expected to contribute to poorer body image than in young adults. Indeed, Naraindas and Cooney (2023) found a positive relationship between age and state body dissatisfaction, suggesting less satisfaction with transient bodily changes. However, a negative relationship between age and trait body dissatisfaction indicated that older adults might have become more acceptant of their physical body compared to current young adults. An open question is whether older adults with good interoceptive sensitivity (Cioffi et al., 2017; Raimo, Di Vita, et al., 2021) are better able to manage concerns about age-related changes in body image. Preliminary findings by Naraindas and Cooney (2023) suggest that good IB, indexed by composite MAIA-2 scores, predicted lower body image disturbance across age groups. The MAIA-2 assesses adaptive interoceptive sensations, such as "Trusting" and "Not Worrying" about bodily sensations (Mehling et al., 2018; Mehling et al., 2012)), suggesting that older adults scoring high for adaptive interoceptive sensations might demonstrate a more positive body image experience. Recent qualitative research by Ross and Gillett (2019) supports the notion that older adults develop a deep subjective understanding of their internal bodily states through a lifetime of experiencing embodied feedback sensations. This suggests that as individuals age, higher-order subjective dimensions such as IB might take precedence over lower-order bodily sensations (e.g., IAcc). An important consequence of this is that high IB, in the absence of good IAcc, might negatively affect older adults' decision-making abilities in medical contexts, such as potentially leading them to alter prescribed medication dosages against their physician's recommendations (Ross and Gillett, 2019).

4. General discussion

4.1. Summary of main findings

This paper systematically reviewed 22 studies examining age-related changes in interoception and the impact of these changes on different psychophysiological processes. Our review enabled us to address the two research questions set out in the introduction. Firstly, what are the age-related changes across various interoceptive dimensions? Secondly, what are the effects of age-related interoceptive changes on psychophysiological processes, including emotional processing, physiological regulation, and cognitive functioning?

Regarding the first research question, we observed that age-related changes in interoceptive dimensions generally followed a predominant pattern of decline (48.4 % of the findings). This was followed by studies showing no age-related differences (32.3 %), an age-related increase (16.13%), and an inverted U-shaped curvilinear relationship (3.23%) in interoceptive sensitivity, across different dimensions. The extent of these effects was influenced by the age ranges of the samples: studies comparing participants across a broad age range, from young to very old, often found more pronounced declines in interoceptive sensitivity. This is consistent with the marked decline in sensory perception observed in older age (Cavazzana et al., 2018; Volter et al., 2021), which modulates the quality of perceived interoceptive changes, such as gastric functions (Rayner et al., 2000), thirst (Kenney and Chiu, 2001; Phillips et al., 1991), and pain tolerance thresholds (Lautenbacher et al., 2017). Conversely, studies comparing young to middle-aged or old to very old adults generally reported non-significant differences in interoceptive sensitivity.

Three patterns emerged concerning the second research question, which examined the effects of age-related interoceptive changes on psychophysiological processes.

The first pattern, observed in studies investigating the hypothesis of weakened mind-body connections in older adults, is supported by physiological theories of ageing (Costello and Bloesch, 2017; Kuehn et al., 2018; Mendes, 2010). Indeed, some of our reviewed studies have

shown an age-related disconnect between interoception and emotional experiences (Lohani, 2014; MacCormack et al., 2021; Mikkelsen et al., 2019; Ulus and Aisenberg-Shafran, 2022). However, several studies using subjective measures of interoception (Elliott and Pfeifer, 2022; MacCormack et al., 2021; Mahlo and Windsor, 2021; Ulus and Aisenberg-Shafran, 2022), and two using the HCT (Haustein et al., 2023) and HDT (Dobrushina et al., 2024), suggested an age-related change rather than a disconnect, such that interoceptive ageing was associated with increased positivity and reduced high-arousal negative emotions. Regarding the various methods for assessing interoception, IB measures might enable older adults to rely on cognitive faculties to construct subjective interoceptive sensations (Barrett, 2017). Specifically, these subjective measures allow older adults to draw on bodily knowledge gained through experience (i.e., memory). This might help restore the connection with emotional experiences which appears weakened when using experimental and behavioural measures of interoception (Lohani, 2014; MacCormack et al., 2021; Mikkelsen et al., 2019; Ulus and Aisenberg-Shafran, 2022). Conversely, using behavioural measures of interoception coupled with questionnaires relating to personality (Haustein et al., 2023) and emotional processing (Dobrushina et al., 2024; Mahlo and Windsor, 2021) could reveal older adult's capacity to integrate internal bodily states with their emotional experiences, potentially leading to deeper introspective thought. In this context, individual differences in interoception may shed light on trait characteristic behaviours and embodied experiences of positive emotions in later adulthood. While enhanced interoceptive sensitivity in later life might not guarantee strong positive feelings and high-arousal emotions, it could evoke introverted tendencies such as introspection and less externally oriented thought. This could account for the greater sense of equanimity in approaching the remaining years of life, and preparing for death (Busch, 2023). Better interoceptive sensitivity in late adulthood might potentially serve as a means to offset a lack of future time perception and goal-setting behaviour as the typical drivers for positivity (Carstensen, 2006; Carstensen et al., 1999), while fostering lowarousal, peaceful life experiences that are valued by some older adults (Sands and Isaacowitz, 2017; Scheibe et al., 2013).

The second pattern emerged from findings pointing to a positive relationship between cognitive measures / intelligence and interoception across age groups. Based on initial evidence reviewed above, higher IQ might be protective of interoceptive sensitivity in young and middle-aged adults (Failla et al., 2020; Mash et al., 2017) as well in older adults (Haustein et al., 2023; Kamp et al., 2021)). However, a causal relationship has yet to be established. For example, rather than cognitive faculties preserving interoceptive sensitivity, evidence suggests that low-level visceral signals can influence cognition and aid decision making (Bechara et al., 1997; Dunn et al., 2010). Several reports have shown that interoceptive cardiac signals shape cognitive processing and improve memory during diastole (Fiacconi et al., 2016; Garfinkel et al., 2013; Pfeifer et al., 2017). This relationship was strengthened in individuals with high IAcc, indicating the impact on cognitive performance across interoceptive dimensions. With current evidence pointing to an age-related decline in IAcc alongside older adults' well-established decline in fluid intelligence and other cognitive abilities (Horn and Donaldson, 1980), future studies would benefit from including IQ measures when investigating lifespan changes in interoception.

The third pattern of results showed that body representation (BR) related to body schema and ownership tended to decline with age, while BR related to body image improved with age. This might stem from older adults relying more on interoceptive versus exteroceptive cues, or from diminished interoceptive-exteroceptive integration in BR tasks (Cioffi et al., 2017). However, an important caveat is that existing geriatric research on BR primarily relies on cross-sectional data, which fails to capture nuanced developmental changes that longitudinal studies could reveal. For example, Body Dysmorphic Disorder (BDD), a condition that severely impacts body image, has a weighted prevalence of 3.3 % among young adults and adolescents (Veale et al., 2016). Those with severe

BDD often face early mortality, including from suicide, or self-select out of body image studies, potentially leading to a sample of older adults less likely to have experienced debilitating BDD (Naraindas and Cooney, 2023). This selective survival may skew findings toward improved body image in older adults. Additionally, BDD is closely linked to interoceptive disturbances (Jenkinson and Rossell, 2024), complicating interpretations of body dissatisfaction across age groups. In summary, while older adults may seem to show greater body acceptance, this could result from the survival of individuals without severe BDD, rather than a true developmental shift. Further research is needed to examine the interplay between interoceptive sensitivity, body image, and age, accounting for biases introduced by BDD.

4.2. Limitations and future directions

A key limitation of the 22 reviewed studies is their reliance on crosssectional data, which prevents an understanding of interoceptive changes over time. None of the studies employed a longitudinal design, making them vulnerable to cohort effects. For example, older generations, such as the Veterans and Baby Boomers, were raised with a "mindover-matter" mentality, prioritising mental resilience and self-efficacy over physical and mental wellbeing (Rowe and Kahn, 1997). This approach emphasised determination and perseverance, which shaped their lifestyle choices and professional environments (Cvenkel, 2020). By contrast, younger generations such as Millennials and Gen Z have experienced a greater focus on mind-body connections through yoga practices and meditation (Sharma and Sharma, 2018), and view psychological wellbeing as essential for successfully transitioning into adulthood (Baggio et al., 2016). Often labelled "snowflakes," Gen Z prioritises mental health and safety while grappling with high levels of anxiety, depression, and loneliness (Twenge, 2017). These generational differences may account for some of the observed age-related trends in interoception, rather than reflecting true developmental changes. Critically, longitudinal research could address these cohort effects by revealing the actual trajectory of interoceptive sensitivity across different dimensions.

However, such studies may also introduce challenges. Repeated assessments of interoception, particularly through heartbeat perception tasks, could lead to improvements in IAcc and other interoceptive dimensions, as a result of learning effects (Schillings et al., 2022; Sugawara et al., 2024; Sugawara et al., 2020). To mitigate this, alternative measures of IAcc, such as those focusing on physiological responses to external stimuli (e.g., Ulus and Aisenberg-Shafran (2022)), may reduce learning biases. Furthermore, exploring subconscious processing of interoceptive signals could uncover lifespan changes in how interoceptive signals influence psychophysiological processes, offering a deeper understanding of interoceptive ageing.

Additional caution is needed when interpreting the three identified patterns from this review, as the findings come from a range of measures, sometimes even within the same dimension of interoception. For example, several reviewed studies examined age differences in IAcc using the two mainstay cardiac perception tasks, HCT and HDT, with divergent results. Although both tasks require participants to perceive cardiac signals, the HCT asks participants to attend to their heartbeat sensations, while the HDT requires the integration of cardiac signals with an external stimulus (Garfinkel et al., 2015). Thus, due to the underlying cognitive differences inherent in the two heartbeat perception tasks, conclusions concerning older adults' IAcc should be interpreted within the context of the measurements used. The HCT has received substantial critique as a valid measure of IAcc in recent years. Notably, it has been suggested that successful performance on this task can be achieved via non-interoceptive strategies, such as participants' beliefs about their resting heart rate and time estimation abilities (see Murphy (2023) for overview). By contrast, the HDT has been criticised for differences in the time delay at which participants perceive an external stimulus to coincide with their internal heartbeat (Brener and Ring,

2016). Critiques of the HCT and HDT, primarily grounded in data from younger individuals, might hold even greater relevance for older adults. Older adults, with their accumulated life experiences, might possess greater familiarity with their heartrate and time perception. Thus, while younger adults might be able to sense their internal bodily signals more accurately than older adults in the HCT, older adults could capitalise on knowledge concerning heartrate and time perception and achieve comparable performance to young adults (as in Dobrushina et al., 2020; Failla et al., 2020; Haustein et al., 2023; Mash et al., 2017; Mikkelsen et al., 2019; Ueno et al., 2020). By contrast, older adults might be disadvantaged relative to younger adults in the performance of the HDT (as in Dobrushina et al., 2024; Khalsa et al., 2009; Lohani, 2014). Firstly, none of the reviewed studies using the HDT pre-screened participants for hearing deficits, which could introduce a potential confound, as the HDT demands a high level of auditory acuity. Future research involving ageing populations should implement participant pre-screening for hearing impairments and consider adjusting tone volume to accommodate individual hearing thresholds to enhance the validity of the findings. Secondly, cardiovascular changes such as reduced elasticity of blood vessels (Lakatta, 2003), reduced tactile sensation (Stevens, 1992; Stevens and Cruz, 1996), slower nerve conduction velocity (Palve and Palve, 2018), and cognitive decline in processing speed (Eckert et al., 2010) might contribute to an age-related increase in the delay perception between the internal heartbeat and the sound of an external stimulus. Thus, the tone delivery timings of a HDT used with young adults might be too fast to accurately discriminate from heartbeats by older adults, resulting in poor performance (Dobrushina et al., 2024; Khalsa et al., 2009; Lohani, 2014), which might be erroneously interpreted as age-related interoceptive inaccuracy.

Concerning questionnaire measures, the BPQ consistently showed an age-related decline in interoceptive attention (IA) across three studies, while the SAQ showed no significant age differences in IB in two studies. One explanation is that the BPQ assesses attention to neutral and uncomfortable bodily sensations (Cabrera et al., 2018), which may decrease in older adults for two reasons: first, reduced bodily sensitivity with age, and second, declines in selective attention and the ability to sustain attention over time (Zanto and Gazzaley, 2014). By contrast, the SAQ captures the frequency of 'feeling' adverse, painful, and symptomatic sensations (Longarzo et al., 2015). As older adults experience more pain with age, they may become more attuned to these sensations, resulting in performance comparable to younger adults. However, studies using selective subscales or composite measures of the MAIA/ MAIA-2 displayed considerable variation, with findings ranging from age-related increases and decreases to no significant age differences in IB. This variability may stem from the fact that self-report measures of interoception do not always assess the same construct (Desmedt et al., 2022; Pearson and Pfeifer, 2022; Vig et al., 2022). Unlike unidimensional tools such as the BPQ or SAQ, the MAIA was designed to measure multiple dimensions of interoception, encompassing eight subscales across five dimensions (Mehling et al., 2018; Mehling et al., 2012). Using only a subset of these subscales can lead to an incomplete assessment of interoceptive dimensions. Additionally, combining subscales that measure different dimensions, may obscure specific agerelated changes within each dimension. To better understand these changes, future research should report individual subscale results when using the MAIA, allowing for a more nuanced examination of age-related differences in IB.

The three patterns identified in this review highlight the complex relationships between age-related changes in interoception and psychophysiological processes. While some aspects decline with age, others suggest compensatory mechanisms and protective factors. We conclude by proposing future research directions on interoceptive ageing:

Although physiological theories suggest an overall decline in sensory and interoceptive functions with age (Costello and Bloesch, 2017; Kuehn et al., 2018; MacCormack et al., 2022; Mendes, 2010), future studies should examine individual differences in interoceptive ageing, similar to

those observed in cognitive ageing (Salthouse, 2012). Understanding these differences could offer valuable insights into the affective and cognitive trajectories of older adults. Two intriguing hypotheses could be explored: Firstly, whether older adults with lower IAcc exhibit less negative affect (Haustein et al., 2023; Ulus and Aisenberg-Shafran, 2022), and whether those with higher IAcc demonstrate better cognitive functioning (Haustein et al., 2023). Secondly, and more controversially, research could investigate whether interoception acts as a protective factor against cognitive decline, including neurocognitive impairment and dementia (Abrevaya et al., 2020; Hazelton et al., 2023). To test these hypotheses, a comprehensive assessment of interoceptive sensitivity across various dimensions (Suksasilp and Garfinkel, 2022) is necessary, alongside the inclusion of neurocognitive and affective measures within different research paradigms. A refined understanding of interoceptive ageing could help predict individual strengths and weaknesses of older adults' cognitive and affective states, with opportunities for targeted interoceptive interventions. For example, while it might not appeal to some older adults to enhance their interoceptive sensitivity and potentially increase emotional volatility, others might find that a heightened awareness of internal bodily states aids internal thought processes such as memory and boosts overall cognitive functioning. Socioemotional selectivity theory (Carstensen, 2006; Carstensen et al., 2011) explains the age-typical positivity effect, whereby older adults prioritise positive experiences due to increased awareness of mortality. Improving older people's interoceptive sensitivity is unlikely to counteract these positive experiences but might assist in bolstering cognitive functioning to support overall senescent wellbeing.

Investigating how various interoceptive dimensions (both adaptive and maladaptive (Farb et al., 2015; Mehling et al., 2018; Mehling et al., 2012)) relate to body image and BDD in young and older adults could offer valuable insights into the potentially protective role of interoceptive sensitivity on body image disturbance and associated mental health issues. Additionally, it could enhance our understanding of broader aspects of BR and agency in later life.

Investigating the functional significance of interoceptive dimensions across the lifespan would elucidate whether higher-order subjective dimensions of interoception (e.g., IB, metacognitive insight) might become more prominent and reliable to older adults than noticing lower-order internal bodily sensations (e.g., IAcc).

Future qualitative research could explore older adults' subjective internal bodily sensations, thereby enriching our understanding of interoceptive experiences developed over a lifetime of exposure to embodied visceral feedback. Qualitative experiences of interoception are likely to expand our understanding of how they shape emotion, cognition, and BR in older age, including decision-making and behaviours within health-related contexts.

CRediT authorship contribution statement

Gaby Pfeifer: Writing, literature search and screening, Formal analysis, Data curation, Conceptualization. **Sophie Cawkwell:** Literature search and screening, review and editing.

Funding

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

Declaration of competing interest

None.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ijpsycho.2024.112483.

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