# Aging bodies, brains, and emotions: The physiological hypothesis of emotional aging

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**Abstract**

Longstanding evidence finds that healthy older adults tend to experience greater positivity, equanimity, and well-being in daily life. Prominent psychological theories of emotional aging tend to focus on cognitive pathways such as shifting motivations and accumulated cognitive resources (e.g., attentional control, expertise) to explain observed emotional aging effects. In this chapter, we introduce the physiological hypothesis of emotional aging (PHEA). At its core, the PHEA proposes that physiological aging contributes to emotional aging, wherein age-related changes to the peripheral body and how the brain represents and regulates the peripheral body (e.g., interoception) should result in age-related changes to emotional experience and associated socioemotional perceptions and behaviors, i.e., emotion communication. Importantly, the PHEA argues that the dynamics of physiological aging (e.g., increased dysfunction, greater afferent noise from the viscera and peripheral transmission pathways, reduced interoception) may in turn facilitate the increased importance of cognitive pathways in late life emotional outcomes and functions. As such, the PHEA provides an integrative neuroscience approach to emotional aging that highlights the importance of physiological health and aging across the body and brain while providing an interpretive framework that complements existing cognitive theories of late life emotion. This chapter introduces core arguments of the PHEA, unifies existing evidence on physiological, interoceptive, and related neural aging as relevant for emotional aging, and forecasts new directions and implications for late life socioemotional functioning and interpersonal behaviors.

**Keywords:** aging, emotion, interoception, psychophysiology, brain

Healthy older adults (> 60 years) tend to exhibit more positive and fewer negative emotions, more emotional stability and reduced reactivity, and more adaptive responding to interpersonal conflicts and daily life stressors than their younger counterparts (e.g., Birditt & Fingerman, 2005; Carstensen et al., 2011). However, older adults may be more susceptible to certain social affective difficulties, such as alexithymia (i.e., difficulty identifying and describing emotions), reduced regulatory flexibility, and errors in interpersonal perceptions and affect-based decisions (Eldesouky & English, 2018; Mattila et al., 2008; Schlegel et al., 2020). To date, psychological theories explain these emotional benefits and difficulties by focusing on cognitive factors that change with age. Age-related emotional benefits are attributed to shifting motivations or greater expertise, whereas difficulties are attributed to deteriorating executive control.

The *physiological hypothesis of emotional aging* (PHEA) proposes that physiological aging should be an important parallel pathway of emotional aging. Over time, maturational changes to nervous system structure and function (e.g., peripheral nerve demyelination) as well as increasing physiological dysfunction (e.g., systemic inflammation, hypertension, neuropathy) produce greater afferent noise from the viscera and along peripheral transmission pathways to the brain (i.e., interoceptive dysfunction). In parallel, the brain must increasingly rely upon its accumulated priors and exteroceptive situational cues to compensate for physiological senescence, resulting in a more prediction-bound aging brain that is less reliant on sensory—especially interoceptive—feedback. Building on this model of the aging body-brain, the PHEA hypothesizes that emotions and affect-based behaviors will become less coupled with ongoing peripheral changes in late life. These weakening links between body and mind ("maturational dualism"; Mendes, 2010) mean that older adults may experience a "mellowing" of emotional arousal. Similarly, late life emotional processes should become anchored in "cognitive" and situational processes (e.g., semantic knowledge, cultural scripts; emotion beliefs; end-of-life motivations; situational cues)—with all the incumbent benefits and vulnerabilities entailed.

The PHEA provides an integrative neuroscience approach to late life emotion that highlights the importance of body-brain health and aging while providing an interpretive framework that complements existing cognitive theories of emotional aging. In this chapter, we first describe common models of emotional aging and elaborate on the PHEA's core arguments. Drawing upon constructionist and predictive brain models of emotion, we unify existing evidence on physiological, interoceptive, and neural aging in emotion alongside evidence that the aging brain and emotions are increasingly prediction-driven rather than sensory-driven. We close by forecasting new directions and implications for late life socioemotional functioning, communication, and health.

## Psychological Theories of Emotional Aging

Most psychological theories of emotional aging propose cognitive explanations for age-related emotional differences. *Socioemotional selectivity theory* (SST) hypothesizes that as the end-of-life approaches, older adults' narrowing time perceptions motivate them to prioritize more positive, meaningful experiences and to minimize negative experiences (Carstensen et al., 1999). Similarly, the *selection, optimization, and compensation with emotion regulation* framework (Urry & Gross, 2010) emphasizes the importance of older adults' available cognitive resources (i.e., cognitive control, executive functioning, knowledge) in determining how older adults use emotion regulation. Other models (Blanchard-Fields, 2007; Labouvie-Vief et al., 1989; Magai et al., 2006; Ong & Bergeman, 2004) argue that emotion expertise and skills honed over a lifetime help older adults better understand, navigate, and manage their emotional lives in adaptive ways. The *strength and vulnerability integration* (SAVI) model further proposes that accumulated cognitive behavioral strategies help older adults anticipate and minimize exposure to negative or highly arousing situations (Charles, 2010). However, when highly evocative situations are unavoidable or circumstances hinder cognitive behavioral strategies, physiological arousal is more costly for older adults due to declines in physiological flexibility and recovery relative to younger adults. Alternately, *dynamic integration theory* (Labouvie-Vief, 2003) emphasizes age-related cognitive declines in exacerbating older adults' vulnerability to highly arousing situations. Together, these common theories suggest that older adults' motivations and cognitive resources are central mechanisms of desirable emotional outcomes such as equanimity, emotion regulation efficacy, and positivity.

In contrast, physiological models focus on the role of age-related nervous system degradation as a pathway underlying age-related emotional changes. The *aging brain model* (Cacioppo et al., 2011) suggests that emotional aging is a by-product of age-related changes in amygdala-hippocampal function, which causes negative stimuli to be less arousing for older adults. *Maturational dualism* (Mendes, 2010) instead focuses on peripheral nervous system aging, pointing to neuropathy (i.e., cell death) and demyelination amongst peripheral nerves as pathways by which mental states including emotions become more disembodied in later life. The SAVI can also be considered a physiological model, because it suggests that age-related declines in physiological flexibility and recovery make older adults more vulnerable to aversive, highly arousing events, which they then seek to avoid or mitigate with cognitive behavioral resources. The PHEA builds upon these physiological model precursors to provide an updated integrated systems framework for understanding how the aging body-brain and related processes (i.e., interoception) contribute to emotional aging. Importantly, rather than seeing physiological aging as a competing explanation relative to cognitive aging, the PHEA explicitly hypothesizes that physiological, interoceptive, and neural aging may facilitate older adults' reliance on accumulated priors (e.g., knowledge), cognitive behavioral skills (e.g., expertise in employing regulatory strategies), and situational

affordances (e.g., bias towards exteroceptive vs. interoceptive cues) for constructing emotion experiences, interpersonal perceptions, and judgments.

## The Physiological Hypothesis of Emotional Aging

At its core, the PHEA argues that the aging body-brain should have several downstream impacts on late life emotional experiences, perceptions, and socioemotional functioning, including emotion communication. Physiological or biological explanations for emotional aging are not new (Cacioppo et al., 2011; Mendes, 2010; Uchino et al., 2010). However, age-related physiological changes, even in "normative" aging, are complex (Lakatta, 1993). Comparing age differences in a single physiological marker (e.g., heart rate) is likely insufficient to test physiological aging. This is because any given measure on its own cannot account for differential rates of aging (e.g., between the cardiovascular vs. gastric systems) nor cross-system aging effects (e.g., within sympathetic and parasympathetic nervous system coordination). Likewise, focusing on singular brain regions (e.g., amygdala) may be similarly insufficient because central modeling and management of the periphery is enacted across networks of brain regions. The PHEA adapts constructionist predictive brain models of emotion to better consider these multi-system complexities.

### Emotions Are Constructed from Interoception and Prior Experiences

The brain's functional architecture can be parsed into broadly-distributed intrinsic networks supporting mental states and behaviors (Barrett & Satpute, 2013; Lindquist & Barrett, 2012). In the context of emotion, these distributed networks are domain-general, in that they are not specifically or consistently activated during any one emotional experience or perception—but rather play a broader role across many instances of emotion (Lindquist et al., 2012, 2016). Core networks commonly observed during younger adult emotion include the salience, default mode, dorsal attention, and frontoparietal networks (Doyle et al., 2022; Kleckner et al., 2017; Touroutoglou et al., 2015). Modern constructionist accounts of emotion propose that emotions emerge from the dynamic coaction of these domain-general networks, iteratively fusing together an individual's internal model of the world (e.g., concepts, prior experience, beliefs) with ongoing sensory inputs from the body and external world (Hoemann & Barrett, 2019; MacCormack & Lindquist, 2017). The *theory of constructed emotion* ((Barrett, 2017, 2018) draws inspiration from predictive brain models to identify pathways by which physiology and representations thereof (i.e., *interoception*) contribute to emotion (Allen et al., 2022; Katsumi et al., 2022; Kleckner et al., 2017; Quigley et al., 2021; Seth & Friston, 2016). A core hypothesis is that the brain's fundamental function is to manage and enact *allostasis.*

Allostasis occurs as the brain adaptively maximizes survival and energy balance by making "best guesses" about the body's needs for action in each context within the constraints of ongoing physiological resources (Katsumi et al., 2022; McEwen, 2017; Schulkin, 2011; Shaffer et al., 2022; Sterling & Laughlin, 2015). Allostasis is likely orchestrated via the function of the *allostatic interoceptive network* (AIN). The AIN was identified via resting state fMRI analysis of young adult participants, tract-tracing studies in non-human animals, and the flow of predictions and prediction errors within cortical layers and between cortical layers and subcortical and brainstem centers involved in visceromotor regulation (Katsumi et al., 2022; Kleckner et al., 2017). AIN topography maps onto two well-known intrinsic brain networks—the default mode and salience networks—which are connected via hubs that serve as major information thoroughfares in the brain (Kleckner et al., 2017).

These networks and their brain structures support many interoceptive and allostatic functions: they receive and monitor ascending peripheral projections, help efferently regulate visceral functions, and support the representation of prior experiences (Kleckner et al., 2017; Menon, 2015; Seeley et al., 2007). Interoceptive processing in these regions is thought to reflect the brain's modeling of afferent peripheral feedback while allostatic processing in these regions is thought to reflect the brain's efferent predictive control of the periphery in relation to interoceptive modeling (Sennesh et al., 2022). Consistent with their hypothesized role in visceromotor regulation and interoception, AIN-related networks and regions are also consistently observed in neuroimaging studies of hunger, inflammation, pain, physiological arousal, psychological stress, and emotion (Ginty et al., 2017; Lindquist et al., 2012, 2016; MacCormack et al., 2020; Satpute et al., 2019; Simmons et al., 2013; Xia et al., 2017).

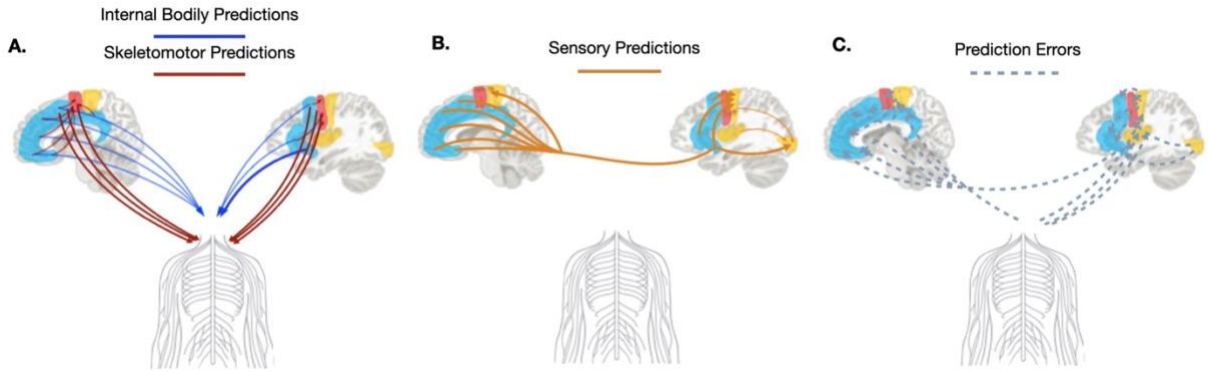


**Figure 1.** The allostatic interoceptive network (AIN) enacts regulating and representing ongoing bodily states. **A.** The AIN helps construct emotion instances via initial efferent visceromotor predictions based on prior experiences. **B.** Copies of visceromotor predictions are sent to sensory cortices to shape incoming sensory perceptions. **C.** Prediction errors are received from exteroceptive sensory cortices and afferent peripheral signals to update the next iteration of predictions. Adapted with permission from Barrett (2017).

In service of allostasis, cortical limbic areas within the AIN such as the orbitofrontal cortex, anterior cingulate cortex, temporal pole, and ventral anterior insula extract information from the current environment to generate predictions about how the body might need to act based on prior experiences in similar environments (Barrett, 2017) (**Figure 1A**). These predictions are projected to visceromotor centers (e.g., amygdala, basal ganglia, periaqueductal gray) to marshal peripheral physiology for behavior (Barrett, 2017; Kleckner et al., 2017). In parallel, visceromotor predictions are sent to the primary exteroceptive cortex (e.g., visual, auditory, olfactory, gustatory, etc. cortex), primary motor cortex, and interoceptive sensory cortex (e.g., the posterior insula) to shape the meaning of incoming sensations from the world and body in line with initiation predictions (Chanes & Barrett, 2016) (**Figure 1B**). In this manner, anticipatory predictions shape perceptions, unless incoming sensory signals are sufficiently different from predictions, in which case "prediction errors" from exteroceptive modalities (e.g., visual cortex) and interoceptive modalities (e.g., posterior insula) help update the next iteration of predictions (**Figure 1C**).

Thus, information from external environments alongside internal bodily "environments" dynamically contribute to mental events, including emotions. Critically, sensory predictions and prediction errors likely give rise to affect. Affect—feelings of pleasantness or unpleasantness (*valence*) and activation or acquiescence (*arousal*)—is thought to arise from the brain's central representations of the body's internal milieu in relation to its world (Barrett & Bliss-Moreau, 2009; Hesp et al., 2019; MacCormack & Lindquist, 2017). Valence and arousal are features of the body's state in the world, not unlike dimensions of brightness (in vision) or loudness (in audition). The difference is that brightness and loudness represent features of the external world, whereas valence and arousal represent features of the internal world (Barrett & Bar, 2009).

Altogether, the theory of constructed emotion hypothesizes that emotions (i.e., experience, perception) emerge from the brain predicting and making meaning based upon its exteroceptive and allostatic/interoceptive representations, accumulated knowledge, and executive functions which influence how information is integrated, processed, and shifted in/out of conscious awareness. But these components are not static. They develop and change with experience in context-sensitive ways within the individual ontogeny and beyond. Constructionist work increasingly grapples with how emotions develop in the first place, from birth into childhood, with an emphasis on concept and language acquisition in early life emotional development (Hoemann et al., 2019; Lindquist et al., 2015).

But as lifespan development theories have long affirmed (Baltes, 1987), development does not stop in adulthood. Instead, maturation and aging reflect the continual process of the brain finetuning itself to its environments based on prior experiences while navigating the changes that accompany physical maturation and senescence. To understand how emotions change with age, we must first consider how the

domain-general components underpinning emotion are changing (MacCormack et al., 2020, 2021a; MacCormack & Lindquist, 2017). The PHEA draws upon this principle of domain-general aging to hypothesize that emotional aging is rooted in *allostatic aging* (i.e., the AIN, peripheral physiology, interoception) and the *aging predictive brain*. We discuss these next.

**Emotional Aging is Rooted in Allostatic Aging**

***Allostatic Interoception Network Aging.*** The AIN is primarily studied in young adults. However, its structure and function are not static across the lifespan. It develops with brain maturation from birth into early childhood, expanding from isolated brain regions into a coherent network (Atzil et al., 2018). Although the AIN itself has not been studied in childhood, the constituent default mode network continues to develop across childhood into early adolescence (6-12 years) and resembles the spatial topography of the young adult network (aged 18-28) by age 12 (Fan et al., 2021). There are also age-related changes to the AIN during mid-to-late adulthood. Older adults show smaller grey matter volumes within hubs of the AIN (e.g., insula, dorsal anterior cingulate cortex) relative to younger adults (He et al., 2014). These structural changes may precede functional changes. For example, within-AIN functional subnetworks are differentially affected by aging. Touroutoglou and colleagues (2018) found age differences in the dorsal vs. ventral salience subnetwork connectivity, which may reflect a disconnect between regions that send predictions (e.g., ventral anterior insula) and those that represent prediction errors and incorporate them into ongoing experience (e.g., dorsal anterior insula).

The brain's ascending arousal system, which overlaps with the AIN in several regions (e.g., thalamus, periaqueductal gray) also declines in functional connectivity with age, mediating age-related connectivity differences within and between the AIN (Guardia et al., 2022). This suggests that AIN aging may be partially rooted in altered arousal processing in the brainstem. Dysregulation of the brain and body's neurochemical systems for regulating arousal (e.g., norepinephrine, dopamine, orexin) increase with age (Mather, 2020), producing states of chronic hypoarousal. The body-brain compensates for chronic hypoarousal by elevating tonic levels of arousal-related neurotransmitters, but this may come at costs to these systems' adaptive flexibility and range.

***Peripheral Aging.*** Even amidst healthy aging, all physiological systems age [e.g., *brain* (Fjell & Walhovd, 2010); *cardiovascular* (Amery et al., 1978); *integumentary* (Fenske & Lober, 1986); *musculoskeletal* (Frontera, 2017); *respiratory* (Lalley, 2013); *digestive* (Russell, 1992); *endocrine* (Cai et al., 2012); *reproductive* (Pellicer et al., 1995); *immune* (Akha, 2018)]. These aging systems likely impact emotional aging in different ways and to different extents, but as an example, we discuss cardiovascular aging, given its common focus in affective science (e.g., examination of heart rate, heart rate variability, blood pressure changes during stress and emotion; (Blascovich & Mendes, 2010)). The cardiovascular

system undergoes major changes during aging, with cardiovascular disease a leading cause of death for adults over the age of 65 (Global Burden of Cardiovascular Diseases Collaboration, 2018). Blood pressure increases with age as collagen increases and elastin decreases in the arteries, contributing to arterial stiffness (Paneni et al., 2017). Such vascular changes influence aortal contributions to age-related increases in systolic blood pressure alongside decreases in diastolic blood pressure (Steppan et al., 2011). Together, cardiovascular aging manifests as *decreases* in heart rate and cardiac output at rest alongside *increases* in blood pressure at rest and during task reactivity (Amery et al., 1978; Uchino et al., 2005, 2010). The flexible coupling between respiratory and cardiovascular systems is also disrupted, reflected in age-related decreases in heart rate variability (Grossman & Taylor, 2007; Umetani et al., 1998).

The peripheral nervous system also ages. As early as midlife, peripheral nerves show signs of structural and functional aging, i.e., the loss of nerve fibers, increased nerve demyelination, and decreases in regenerative and reinnervation capabilities (Melcangi et al., 2000; Palve & Palve, 2018; Sato et al., 1985; Verdú et al., 2000). Neuropathy also becomes increasingly prevalent (Bouhassira et al., 2008). From the perspective of the brain sensing the body, accumulating peripheral dysfunctions may result in even less precise signals from the already relatively unmylenated peripheral nerves, which are also slower, more "noisy," and unreliable. As such, it may become harder for the brain to predict and pinpoint the nature and meaning of afferent signals, i.e., *alexisomia*.

***Interoceptive Aging.*** Finally, as the body-brain matures and ages, these combined effects should produce interoceptive aging. Interoception reflects the processes by which "the nervous system anticipates, senses, and integrates signals originating from the body" (Quigley et al., 2021; p. 29). Although initial evidence is limited, studies show that older adults perform worse on heartbeat perception tasks used to index interoceptive accuracy or sensitivity (Khalsa et al., 2009; Murphy et al., 2018; Nusser et al., 2020). Similarly, older adults report being less interoceptively aware relative to younger adults (Murphy et al., 2018), in line with age-related perceptual decrements in pain, temperature, respiration, and hunger (Altose et al., 1985; Frank et al., 2000; Lasch et al., 1997).

Taken together, physiological aging brings fundamental shifts in how the brain represents the periphery alongside aging of peripheral systems and body-brain transmission pathways. With increasingly slower, noisier, less reliable physiological signals, it follows that the aging brain may over time rely less upon afferent feedback in favor of situated predictions extracted from an individual's life history.

## Emotional Aging Reflects Shifts from a Sensory-Driven to More Prediction-Driven Brain

Emerging evidence suggests that the brain operates through hierarchical generative models that proactively predict incoming sensory signals to enact behavioral responses (motor movements, physiological reactions) optimized to that organism's environments (Barbas, 2015). This predictive

processing occurs wherein the brain generates "best guess" predictions (*prediction signals*) based on prior experience that anticipate incoming signals from the exteroceptive environment and interoceptive milieu. Unanticipated information (*prediction error*) occurs when there is some degree of discrepancy between the expected and observed sensory signals. The greater the discrepancy or prediction error, the greater the brain needs to encode mispredicted sensory signals in service of updating predictions (i.e., *learning*).

Thus, as predictive dynamics unfold over time, the neural processes of development, maturation, and aging reflect the continual refinement of a given brain's generative predictions and learning, tailored to its environments and experiences. In early life, sensory-driven processing is crucial for helping the brain learn. This is evident from infancy: infants use statistical learning to extrapolate from sensory probabilities in their environment to derive situation-specific and generalized knowledge (i.e., rational constructionism; Xu & Griffiths, 2011). Thus, as age increases, so too does individuals' accumulated knowledge. This knowledge, rooted in culture, language, and life history, provides priors that guide future predictions. When priors are correct, they are strengthened. When incorrect, prediction errors help initiate encoding for learning. Prediction-driven processing is more efficient and less metabolically costly than sensory-driven processing, weighting mental inference towards past priors.

However, from midlife onwards, sensory feedback gradually weakens, as degradation of sensory organs and their transmission pathways reduces the precision, reliability, speed, and clarity of sensory inputs to the brain. Importantly, age-related degradation to external sensory modalities is more consciously noticeable and can be "corrected" (i.e., with corrective eye lenses, hearing aids). Yet aging of internal physiological systems and their interoceptive pathways is more complex and may be more difficult to notice unless detectable disease or dysfunction is present. As such, the aging brain may ultimately become more prediction-bound and less reliant on sensory feedback—especially interoceptive feedback.

Together, these changes in predictive processing set the stage for older adult brains to be particularly efficient in situations that their predictions are fine-tuned to anticipate. In these cases, sensory feedback is less critical because experience is largely driven by predictions (e.g., a grandchild's birth is joyful; a friend's death is saddening). But when confronted with stimuli that do not fit with predictions, declines in sensory feedback may become more costly. If sensory prediction errors are small, the older adult brain may simply downweight the importance of these errors due to noisier, less reliable sensory feedback. In this case, the relevant data distributions supporting situated predictions remain largely unchanged and little to no learning (i.e., prediction updating) occurs. But when confronted with strong sensory prediction errors that cannot be discounted, such as in particularly novel, unexpected, or threatening situations, the older brain can still update its priors and react, but this process likely requires a

more intense, metabolically costly response to signal prediction error, relative to younger individuals with greater physiological flexibility.

These tradeoffs between prediction-driven and sensory-driven processing may explain why older adults are more vulnerable when aversive, highly arousing situations are unavoidable and unexpected, as noted by the SAVI. Furthermore, if sensory feedback is noisy and unreliable, this may lead to greater learning errors (e.g., anchoring on the wrong pieces of sensory feedback; incorrectly integrating multisensory data) or may produce greater uncertainty about what that feedback means. Early work already demonstrates these neural prediction-sensory tradeoffs in older vs. younger adult auditory, visual, and sensorimotor perceptions (Chan et al., 2021; Hsu et al., 2021; Moran et al., 2014; Ruzzoli et al., 2012; Wolpe et al., 2016). The PHEA hypothesizes that these prediction-sensory tradeoffs should especially extend to interoceptive feedback, impacting late life emotion.

## Evidence for the Physiological Hypothesis of Emotional Aging

The PHEA is a new model of emotional aging with little published work formally testing all model paths (**Figure 2**). However, growing evidence is consistent with the notion that age-related changes to the AIN, peripheral physiology, and their communication (e.g., interoception) should result in late life emotional experiences and affect-based behaviors that are less coupled with ongoing peripheral changes. As a result of this "decoupling," late life emotional processes should become more anchored in "cognitive" processes and exteroceptive, situational heuristics. We next integrate existing evidence implicating physiological and predictive brain aging in emotional aging.

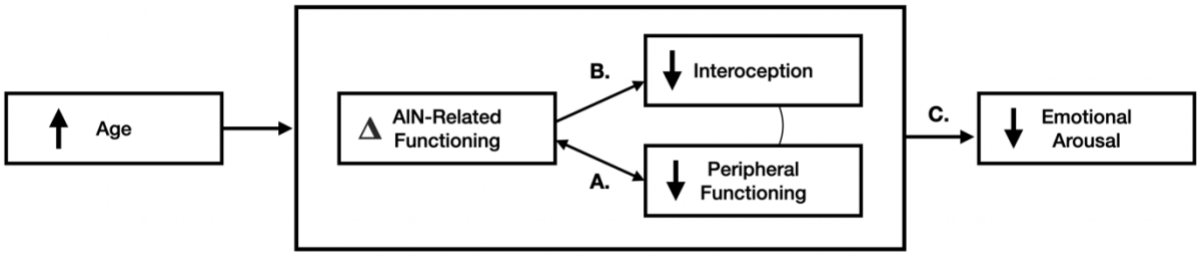


**Figure 2.** The physiological hypothesis of emotional aging, depicting the effect of aging on **(A.)** bidirectional relations between peripheral functioning and the AIN, resulting in **(B.)** age-related decrements to interoception. Altogether, these age-related changes in the body-brain and interoception should contribute to **(C.)** age-related changes in emotional processing, e.g., less intense high arousal emotional experiences. Note this figure does not depict the PHEA proposal that physiological aging supports older adults' reliance on predictions (e.g., knowledge, expertise) and exteroceptive cues.

**Age-Related Decoupling of the Body and Emotion**

Initial evidence has begun bridging physiological and interoceptive links to emotional aging. Older adults' emotional experiences typically involve less intense physiological changes relative to younger adults. Older adults exhibit reduced reactivity to diverse emotion inductions, social conflicts, and stressors across the autonomic nervous system, skin conductance, cortisol, etc. (e.g., Mikkelsen et al., 2019; Neiss et al., 2009; Tsai et al., 2000; see meta-analysis in Uchino et al., 2010). Similarly, age moderates the relation between interoceptive accuracy and emotional reactivity (Mikkelsen et al., 2019), such that younger adults' interoceptive accuracy is closely tied to their emotional reactivity, whereas older adults show no relationship between the two.

But studies also show mixed evidence for age-related differences in the concordance between emotion reports and physiological measures. Older adults reporting or expressing more intense emotions, especially low arousal emotions such as sadness, show either greater physiological reactivity relative to younger adults (Lohani et al., 2018; Wu et al., 2021) or comparable reactivity (Kunzmann & Grühn, 2005; Steenhaut et al., 2018). The PHEA explains this mixed evidence by pointing out that sadness is typically low arousal. Physiological reactivity and interoception, due to their neurobiology, are more frequently tied to *high arousal* states, suggesting that weakened links between the body and emotion should be more pronounced for high arousal emotions and states (e.g., stress, anxiety, anger) but not necessarily low arousal emotions and states. Indeed, this decoupling between interoceptive sensations and emotions is observed particularly in older adults' self-reported high arousal emotions relative to younger and midlife adults (MacCormack et al., 2021a). The mixed relation observed between physiological changes and low arousal emotions may also be due to between-sample differences in the extent of older adults' physiological and interoceptive aging. Extremely healthy samples vs. more normative healthy samples could exhibit different physiological profiles. Future work should consider these factors while testing whether older adults show preserved concordance for other low arousal emotions beyond sadness such as contentment, boredom, etc.

Importantly, the PHEA does not hypothesize that older adults will *always* be less physiological reactive or arousable than younger adults. Older adults may have a more limited capacity or range for mounting robust physiological responses relative to younger adults—especially for high arousal reactions requiring greater physiological arousal (e.g., cardiac pre-ejection period, skin conductance, blood pressure flexibility as per Uchino et al., 2010). But older adults also possess a wealth of knowledge about socio-emotional contexts, supporting more fine-tuned predictions and behaviors. As such, the observed relation between older adult physiology and emotion will depend not only upon a given older adult's degree of physiological aging (and related interoceptive and neural processes), *but also* upon whether emotional situations and stimuli align with their predictions.

For example, it is well-established that physiological arousal is typically evoked in response to novel, uncertain, unpredictable, or highly salient stimuli and situations (e.g., Tomaka et al., 1993). Common features of "stressors" are that they are uncertain, unpredictable, and involve self-relevant threats to identity or safety (Lebois et al., 2016). Yet most emotion induction tasks such as viewing emotional pictures or film clips—or social stressors where older adults must navigate an interpersonal conflict—may simply be more predictable and within the bounds of older adults' range of prior experiences compared to younger adults. In these contexts, being more prediction-driven is advantageous. The brain can efficiently draw upon its "best guess" predictions to tailor subsequent emotions and behaviors. Greater familiarity, certainty, or predictability translates to lower physiological reactions, and lower prediction error translates to less physiological and emotional arousal.

Yet in contexts where older adults are confronted with situations or stimuli that involve greater uncertainty, unpredictability, effort, or difficulty (i.e., wherein older adults cannot easily compensate with priors), then older adults should mount a robust response within the bounds of their physiological range. However, to mount this kind of response, older adult bodies may need to expend more physiological resources and take longer to recover, leading to more severe physiological costs and consequences. As such, older adult declines in afferent feedback may be relatively costly, reducing flexible adaptation and recovery. In this way, the PHEA builds on SAVI's hypotheses about older adult physiological vulnerabilities. Similarly, these situation-specific vulnerabilities complement SST, wherein older adults are motivated to promote pleasant, low arousal states. Presumably, positive and/or low arousal contexts are more likely to be predictable, controllable, familiar, etc. In this vein, we next consider the importance of the aging brain and its accumulated predictions.

**The Aging Predictive Brain in Emotion**

Although the AIN has only recently been characterized, longstanding work in the affective neuroscience of aging literature implicates age differences in the AIN with emotion. In a recent meta-analysis summarizing older vs. younger adult neural changes during in-scanner emotion induction and perception tasks, there were significant age differences in activation and coactivation among nodes of the AIN (MacCormack et al., 2020). Notably, younger adults exhibited more reliable functional activity and coactivation between AIN structures such as the amygdala, thalamus, posterior insula, and midcingulate cortex. These regions are well-established for their roles in enacting visceromotor control, processing "raw" interoceptive signals, and flagging incoming salient sensory signals.

On the other hand, older adults exhibited more reliable functional activity and coactivation between structures such as the dorsal anterior cingulate, anterior insula, dorsomedial prefrontal cortex, and several frontal regions. Observed regions largely comprised the dorsal salience and default mode

networks, which are implicated in mentalizing, executive function, and autobiographical narratives. We speculate that these age differences during emotion likely reflect domain-general patterns wherein younger brains are more sensory-driven during emotion construction (e.g., posterior insula, amygdala)—while older brains are more prediction-driven, extrapolating from richer representational priors.

More generally, the PHEA interprets convergent findings on older adults' greater emotion expertise as consistent with the aging predictive brain hypothesis. Older adults have amassed a wealth of semantic knowledge and lay theories about the causes, concomitants, and consequences of emotions and related situations. Richer knowledge should boost older adults' emotional complexity (Labouvie-Vief et al., 1989; Ong & Bergeman, 2004) while helping them better anticipate and select situations in line with emotional goals while better managing and interpreting emotional events (e.g., Coats & Blanchard-Fields, 2008; Isaacowitz et al., 2017; Livingstone et al., 2018; Shallcross et al., 2013). As such, relative to within-cohort peers, older adults with richer knowledge and more diverse life experiences arising from education, social network size, geographic or cultural mobility, etc. should presumably have predictions that better generalize across situations. In this way, more diverse life experiences may be protective, helping these older adults encounter fewer unpredictable situations (and incur fewer associated costs) relative to peers.

Altogether, age-related sensory/prediction tradeoffs may not only mean that older adults are motivated to seek out meaningful, positive situations due to narrowing time horizons, but also because those situations reduce costs to older adults' more limited physiological resources. Together, both the SST (i.e., temporal motivations) and the SAVI and PHEA (i.e., physiological costs) suggest that older adults should be more likely to select and modify their socioecologies than younger adults. Indeed, older adults are more likely to prune problematic relationships, minimize social confrontations and conflicts, and select socially passive behaviors accordingly (Antonucci et al., 2004; Birditt & Fingerman, 2005; Charles et al., 2009). However, this social pruning and minimizing may also leave older adults more vulnerable to loneliness and fewer social support systems in the face of stressors and loss.

Interestingly, when considering emotion regulation strategies, older adults appear more likely to prefer and/or employ situation selection and modification (e.g., Livingstone & Isaacowitz, 2015) but other studies show no age differences (e.g., Isaacowitz et al., 2015; Sands et al., 2018). Additionally, although SST suggests that older adults should select positive stimuli and situations more over those that are neutral or negative, Sands and colleagues (2018) found that older adults preferred neutral stimuli over positive high arousal stimuli. This may suggest that older adults prefer and select for low arousal experiences and situations (Isaacowitz & Ossenfort, 2017; MacCormack et al., 2021a; Sands et al., 2016, 2018; Sands & Isaacowitz, 2017)—which are presumably less eventful, more predictable, and require

fewer physiological, cognitive, and behavioral resources. Otherwise, there is little evidence that older adults are actually better than young adults at volitional emotion regulation (Isaacowitz, 2022).

Finally, the PHEA also suggests that late life declines and dysfunctions in interoceptive signaling should not only lead the aging brain to rely more on its accumulated predictions, but also to rely more on exteroceptive or situational rather than interoceptive cues to guide emotion construction and inference. Consistent with this hypothesis, MacCormack et al. (2021a) showed that in a cognitive task, older adults were less likely to associate interoceptive sensations (e.g., heartbeat, blood pressure) with emotion categories; this was especially the case for stereotypically high arousal emotion categories such as anger, fear, and disgust. Instead, older adults characterized emotion categories along "external" dimensions of situational (e.g., harm, danger) and nonverbal (e.g., scowling, clenched fists) features. Furthermore, not only did older adults report more positive and low arousal emotions over negative and high arousal emotions in daily life relative to younger adults, but older adults also reported fewer, less intense interoceptive sensations during emotions and greater occurrences of external sensations (nonverbal and situational features) during emotion.

These findings are consistent with studies of alexithymia across the age span, wherein older adults show greater externally-oriented thinking than younger adults (Gunzelmann et al., 2002; Lane et al., 1998), suggesting that older adults may be more likely to anchor on external cues and features in emotion inference. Older adults' externally-oriented thinking has been related to greater inhibition in recalling negative affective information (Dressaire et al., 2015). Insofar as alexithymia is underpinned by interoceptive difficulties (Brewer et al., 2016), one possible interpretation is that older adults' decreased physiological flexibility, arousal, and interoception may lead them to rely on exteroceptive, situational cues during emotion processing. In turn, this external focus may make it easier for older adults to ignore, not notice, or inhibit unpleasant arousal cues in favor of more comfortable, pleasant, low arousal cues.

Altogether, these findings across neuroimaging, cognition, and behavior support the PHEA's hypothesis that in the face of physiological aging, late life emotions may become more rooted in older adults' predictions based on external, situational cues and less on internal, interoceptive cues. As such, older adults' conceptual knowledge, beliefs, mindsets, and appraisals may play an even stronger role in determining the qualia of their resultant emotional experiences, perceptions, and social affective functioning when compared to younger adults. On the one hand, older adults should have greater expertise in selecting, optimizing, and compensating while navigating their social affective lives. Yet without robust sensory prediction errors to support information encoding and updating, older adults may become more suspectable to false beliefs, false memories, and prediction mismatches (Bernstein et al., 2011; Chen, 2002; Ruzzoli et al., 2012; Schacter et al., 1997), with greater difficulties in adjusting expectations, recovery from expectancy violations, and underreaction or overreaction in responses.

Similarly, without robust interoceptive feedback, older adults may rely more upon exteroceptive prediction errors, leading to an externalized focus in their emotional processing.

## Implications and Future Directions

Altogether, the PHEA provides an integrative neuroscience and constructionist approach for modeling the role of body-brain aging in emotional aging. Nervous system aging alongside increasing physiological dysfunction produce greater afferent noise along body-brain transmission pathways. The aging brain must use accumulated priors and situational cues to compensate for physiological senescence; as such, the aging body-brain thrives in prediction-consistent situations but is less flexible to prediction violations. In turn, emotion becomes less coupled with ongoing peripheral changes—and more dependent upon older adults' accumulated cognitive resources and situational affordances. Whereas other chapters in this volume discuss emotional communication shifts *between* individuals with age, the PHEA argues that age-related communication shifts *within* an individual—between body and brain—can contribute to emotional aging. We close by considering social affective implications and next steps.

### Social Affective Implications

**Emotional communication.** One implication of physiological aging is that older adults may be less likely to understand, describe, and communicate using interoceptive features, anchoring instead on exteroceptive features (i.e., visual; Costello & Bloesch, 2017) or socially abstract features (Borghi & Setti, 2017). When using bodily maps of emotions, older adults tend to report fewer, weaker bodily sensations, suggesting that emotion schemas become less interoceptively-anchored (Volynets et al., 2020). Similarly, older adults are less likely to associate interoceptive sensations with emotion categories but instead anchor emotions in externally-visible nonverbal cues or abstract situational features (MacCormack et al., 2021a). In turn, older adults are more susceptible to externally-oriented thinking in alexithymia. Interoception is increasingly recognized as foundational for emotional awareness, insight, and communication (Tsakiris & De Preester, 2018). Given that alexithymia and impoverished emotional awareness are implicated in depression (Bamonti et al., 2010), interoceptive aging may make it more difficult for older adults to identify and communicate their feelings, which could contribute to perceptions of social isolation and geriatric depression. Difficulties with interoceptive communication in emotion could also translate to difficulties pinpointing and describing somatic vs. affective sensations, evidenced by higher rates of somatization in late life (Mattila et al., 2008).

**Interpersonal and emotion perception.** Many studies show that older adults are less accurate at identifying others' mental states, including emotions, relative to younger adults (e.g., Lima et al., 2014; Ruffman et al., 2008). On the one hand, these findings may be due to task design artifacts (e.g., static,

posed faces, contextless backgrounds, length of stimulus exposure) or the skills being assessed (Castro & Isaacowitz, 2019). For example, social familiarity reduces age differences in emotion perception accuracy (Stanley & Isaacowitz, 2015). Similarly, when older adults are provided with situationally-rich information, perception accuracy improves (Sze et al., 2012). A PHEA-aligned interpretation is that older adults have less afferent affective, interoceptive information to guide inferences about contextless, ambiguous stimuli. Once task designs allow older adults to draw upon richer situational predictions, they can better perceive others' emotional states and intentions.

Convergent evidence in young adults finds that higher interoceptive accuracy reduces the misattribution of physiological arousal during social perception—both in terms of facial perceptions and social trait judgments (Feldman et al., 2022a, 2022b) and can reduce susceptibility to social influence in decision-making (Von Mohr et al., 2022). Although speculative, older adults may be more susceptible to social misattributions—especially of uncertain or ambiguous stimuli—without robust, clear interoceptive signals (unless they are able to compensate with knowledge from prior experience or situational cues)—which may help explain why older adults tend to be more trusting towards strangers, less likely detect deception, and exhibit higher credulity (Castle et al., 2012; Ruffman et al., 2012; Shao et al., 2019). In line with this hypothesis, older adults in a high arousal state are more susceptible to false advertisements than younger adults (Kircanski et al., 2018), perhaps because older adults' poorer interoceptive accuracy affords less insight into the source of their arousal.

**Affective learning and decisions.** Physiological signals, arousal, and interoception are also strongly implicated in affect-based learning and behaviors, e.g., risk-taking (Critchley & Garfinkel, 2018; Dunn et al., 2010; MacCormack et al., 2021b). Arousal signals are particularly important when stimuli are ambiguous or uncertain (Critchley et al., 2001; FeldmanHall et al., 2016; Herman et al., 2021). On the one hand, more frequent low arousal states could impart a "clear head" wherein older adults are less often biased by physiological influences during decisions. However, older adults may be more vulnerable to miscalculations of risk, over-optimism, and inflexible updating without robust afferent signals or related prediction errors at their disposal to guide ambiguous, uncertain decisions, including during high arousal (Chowdhury et al., 2014; Liebherr et al., 2017; Sullivan et al., 2021).

**Perceptions of older adults.** Above, we have discussed intrapersonal and interpersonal implications of physiological aging from the older adult perspective, such as how aging physiology (i.e., physiological systems, arousal and interoception thereof) might in turn alter how older adults communicate, perceive emotions and intentions in others, and make certain decisions. However, physiological aging could also over time produce shifts in how *other* people perceive and react to older adults too. For example, older adult facial expressions can be more difficult to interpret with negative rather than positive expressions being easier to process in older faces (Craig & Lipp, 2018, 2018). Given

that perceivers can detect facial cues about individuals' internal bodily states such as their heartbeats or sickness (Axelsson et al., 2018; Galvez-Pol et al., 2022), aging of physiological systems may in turn translate to changes in how others perceive these low-level facial cues in older adults. One possibility is that older adult faces may, as a result, differ in their expressions of arousal, in turn shifting how perceivers interact with older adults, such as during a social conflict. Similarly, as arousal can be expressed in vocalizations (Filippi et al., 2017), this may be another avenue by which age-related shifts in older adults' physiology alter how perceivers infer affective content expressed by older adults.

**Future Directions**

The PHEA proposes that body-brain aging should over time help facilitate the emergence of commonly observed late life patterns in emotional experience, wellbeing, and socioemotional functioning, including emotion communication. Yet to date, most evidence reviewed herein examines cross-sectional age differences and correlates. Age differences observed thus far in physiological reactivity and recovery, interoception, and the AIN may be due to birth cohort or mortality selection effects. Thus, establishing longitudinal within-person effects is critical for testing the PHEA. Physiological aging—at least in healthy adults—is slow and gradual on the scale of years or decades. Future work should use measurement burst designs with frequent sampling intervals to help characterize rates of aging in interoception, the AIN, etc.

In addition to capturing within-person effects, experimental designs could help test hypotheses about older adults' reliance on accumulated predictions and exteroceptive cues. Paradigms could manipulate situational or stimuli predictability, ambiguity, or uncertainty to test whether older adults are more vulnerable and less flexible when faced with these types of situations and stimuli. Other studies could test whether older adults' emotional and arousal-related appraisals and beliefs play a stronger role in determining outcomes. For example, reappraising arousal was more effective at buffering older adults' physiological reactivity (Gurera & Isaacowitz, 2022), perhaps because older adult brains are more prediction-driven.

Another important direction is using integrative assessments of physiological functions, interoception, and the AIN. Physiological aging is heterogeneous, occurring at different timescales, rates, and level of pathology depending on the function or system (Polidori, 2021), Yet most emotional aging studies focus on age differences in cardiovascular reactivity. Assessments that focus on a single measure or modality may fail to capture broader systemic dysfunctions, such as age differences in physiological coordination (Berntson et al., 2008). Similarly, timeseries approaches may reveal age differences in acute physiological dynamics (Gates et al., 2015). However, focusing exclusively on peripheral physiology is misguided. The aging body can only contribute to emotional aging via the aging brain. Emotional aging

studies should examine the brain systems that model and regulate peripheral function, interoception, and arousal. In turn, interoceptive aging may be an important moderator determining the extent to which afferent physiological signals become incorporated into emotion and behavior.

Finally, throughout this chapter, we have focused on healthy aging of the body, brain, and emotion. However, if physiological aging contributes to emotional aging, then this holds important implications for health and disease contributions to late life emotional wellbeing. Positive health behaviors presumably help slow age-related changes to physiological functioning and interoception, delaying or minimizing the extent to which body-brain aging contributes to emotional aging. In these cases, older adults' emotional differences may be better explained by age-related changes in life circumstances (e.g., retirement) or temporal motivations (i.e., SST). As such, future studies should document how health factors and behaviors may exacerbate vs. minimize the relative roles of physiology, interoception, and the AIN in emotional aging. Similarly, preclinical disease risk factors (e.g., hypertension, systemic inflammation) in early and middle-aged adulthood—and related health inequities arising from chronic adversity, local environmental pollution, poverty, and discrimination—may not only accelerate later disease emergence but also midlife and geriatric mood disorders via impacts on physiological functioning, interoception, and the AIN. More diverse samples (e.g., representative community samples; cross-cultural samples) are critical for understanding how the aging body-brain and communication therein contribute to both intrapersonal and interpersonal socioemotional outcomes in mid- and late life.

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