Brain evidence of allostatic and interoceptive dysfunction in psychopathy

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Abstract

The search for brain mechanisms of psychopathy has diverse potential starting points. In this review, we propose taking an approach that begins with the question: why do we need a brain? Adopting this starting point requires examining evolutionary evidence, which indicates that brains evolved to anticipate and meet the needs of the body before they arise (i.e., *allostasis*), and that brains, in service of this aim, continually model and sense the internal conditions of the body (i.e., *interoception*). These fundamental functions of the nervous system are carried out in part by the allostatic-interoceptive system, which spans brainstem nuclei, subcortical structures, and large-scale cortical networks (i.e., default mode, salience, and somatomotor networks). Psychopathy is related to alterations of the brain's allostatic-interoceptive system, particularly the cortical extent, in terms of its myeloarchitecture, task-based neural activity, and functional connectivity. Synthesizing evidence of these alterations, we propose that psychopathy is marked by an impaired integrative capacity of the allostatic-interoceptive cortices, resulting in visceromotor signals that lack rich contextual details and that regulate the viscera in a relatively context-insensitive manner. Impoverished visceromotor signals may also hinder the allocation of attention to signals that are relevant to allostasis. However, the extant neuroimaging evidence supporting these hypotheses is highly heterogeneous. We consider two proposals for resolving this heterogeneity, grounded in neuroanatomy and organizing principles of biological systems. Uncovering the brain bases of psychopathy and aggression will likely require moving toward a science of individual brains regulating individual bodies in the context of an ever-changing environment.

1. Introduction

The scientific push to identify brain mechanisms associated with psychopathy is motivated by the disorder's destructive nature. People with psychopathy are notoriously callous, remorseless, deceitful, and impulsive (Crego & Widiger, 2015; Hare, 2003; Hart & Cook, 2012), and are more likely than their non-psychopathic peers to commit both violent (Gillespie et al., 2023; Monahan et al., 2001; Reidy et al., 2015) and non-violent crime (Anderson et al., 2018; Harris et al., 1991), even following formal punishment (Anderson et al., 2018; Leistico et al., 2008). In addition to the physical and emotional suffering they inflict on victims (Reidy et al., 2015), psychopathic people incur an enormous financial cost to society: in the US, the annual cost associated with the disorder is estimated to range from $245 billion to $1.6 trillion (Gatner et al., 2023; Kiehl & Hoffman, 2011). Developing effective interventions will be critical to mitigating these costs, and yet, despite some initial results demonstrating the promise of multiple intervention approaches (e.g., Baskin-Sommers et al., 2015; Caldwell et al., 2006, 2007; Fleming et al., 2022; Olver et al., 2013), there is a lack of evidence-based treatments for psychopathy targeting etiologically relevant mechanisms (Hecht et al., 2018).

The search for brain mechanisms of psychopathy has countless potential starting points. Efforts toward this end often take an inductive approach that begins with a symptom of interest and ends with a biological 'signature' of that symptom in the brain, which ideally generalizes across patients. However, a different approach that is perhaps more likely to produce biologically plausible and clinically useful results is deductive, and starts with the question: why do we need a brain? Starting from this question requires examining the natural selection pressures under which nervous systems evolved. Those pressures included the need to survive predation, produce offspring, and maintain metabolic resources. Over hundreds of millions of years, animals under these and other selection pressures grew larger bodies with more complex internal systems, evolutionary adaptations that conferred advantages in locomotion and versatility (Sterling & Laughlin, 2015). Thus, brains likely evolved to fulfill one central aim: to coordinate the internal systems of the body (e.g., the cardiovascular, digestive, musculoskeletal, and respiratory systems) and to meet the needs of those systems before they arise (Barrett, 2017; Sterling, 2012; Sterling & Laughlin, 2015). This process is called allostasis (Sterling, 2012). Allostatic regulation, unlike homeostatic control, is a metabolically efficient strategy by which the nervous system flexibly adjusts the internal systems of the body in a context-appropriate manner (Sterling, 2012). To achieve this, the brain continually senses and, by some accounts, models the internal conditions of the body, a process called interoception (Barrett & Simmons, 2015; A. D. Craig, 2003; Quigley et al., 2021; Seth, 2013). Arguably, the entire nervous system serves this central aim (Barrett, 2017; Sterling & Laughlin, 2015). Yet, one brain system – the allostatic-interoceptive system, distributed across multiple large-scale cortical networks (i.e., default mode, salience, and somatomotor networks), subcortical regions (e.g., hypothalamus, dorsal amygdala), and brainstem nuclei (e.g., nucleus tractus solitarius, NTS; periaqueductal gray, PAG) – appears to play a primary role in monitoring the internal conditions of the body via ascending viscerosensory signals and transmitting allostatic (or visceromotor) control signals to coordinate the body's internal systems (Kleckner et al., 2017; Zhang et al., 2025).

Here, we combine what is known about the structure and function of the brain's allostatic-interoceptive system with evidence from neuroimaging studies of psychopathy to argue that psychopathy may be a disorder of allostasis and interoception. Section 2 of this review lays out the founding evidence for the brain's allostatic-interoceptive system, derived from tract-tracing studies of non-human animals and from ultra-high field imaging of the human brain. These findings serve as the framework for section 3, which considers neuroimaging evidence suggesting that psychopathy is related to dysfunction of the allostatic-interoceptive system – in terms of its myeloarchitecture, functional connectivity, and task-based activity. However, the psychopathy neuroimaging evidence is highly heterogeneous. Section 4 considers two possible explanations for this heterogeneity: first, that core dysfunction of the allostatic-interoceptive system has cascading effects on the function of virtually the entire brain, producing study-wise heterogeneity in the anatomical locations where psychopathic people display altered activity; and second, that an organizing principle of biological systems known as degeneracy implies that heterogeneity across individuals and instances is a defining feature of brain function. Finally, section 5 considers the implications of these findings for the empirical study and theoretical understanding of psychopathy, aggression, and violence.

2. The Brain's Allostatic-Interoceptive System

To outline the brain's allostatic-interoceptive system, we will trace the flow of ascending viscerosensory signals from the body's internal organs to the cerebral cortex (section 2.1, **Figure 1**). The descending visceromotor pathways, which enlist largely the same primary structures as the viscerosensory pathways, are also briefly reviewed (section 2.2). Evidence for these pathways derives primarily from tract-tracing studies, in which an anatomical tracer is injected into one region of the brain of a non-human animal, flows along axons that project toward the region (i.e., if the tracer is retrograde) or away from the region (i.e., if the tracer is anterograde), and is examined in the ex vivo brain to visualize axons and regions of termination (Lanciego & Wouterlood, 2020). In addition, recent ultra-high field (7T) fMRI analyses have corroborated these pathways in humans, leveraging increased signal and spatial resolution to observe the functional interactions of small brainstem and subcortical structures (Zhang et al., 2025).

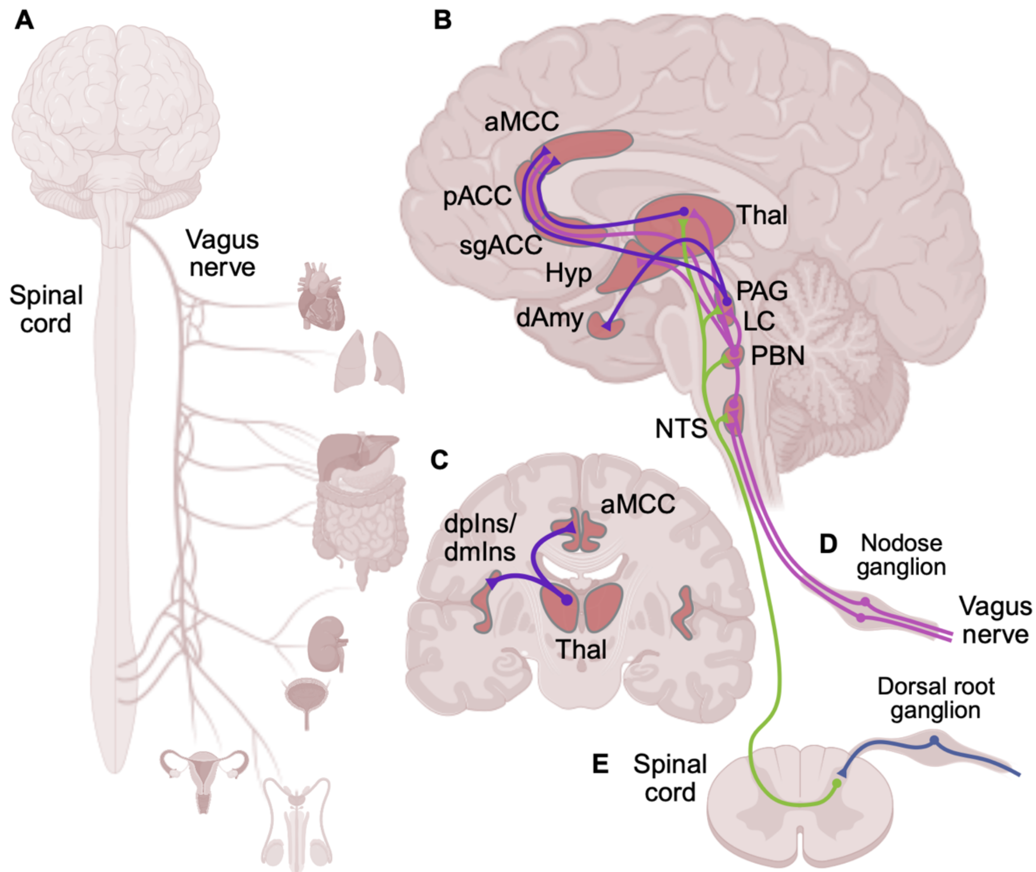

Figure 1. Summary illustration of viscerosensory pathways and key centers in the human brain. Depicted are A) the length of the two primary viscerosensory pathways to the brain (the vagus nerve and spinal cord) ascending from the body's internal organ systems, B) sagittal view of the midline of the brain, C) coronal view of the brain, D) nodose ganglion of the vagus nerve, and E) section of the spinal cord. Viscerosensory signals following the vagus nerve (pink) with cell bodies in the nodose ganglion terminate in NTS and then pass to PBN, PAG and thalamus. Signals are then relayed from PBN, LC, PAG, and thalamus to hypothalamus, dorsal amygdala, insula (including dorsal posterior insula, known as primary interoceptive cortex), and cingulate cortices. Viscerosensory signals with cell bodies in the dorsal root ganglion enter the spinal cord (lamina 1), ascend the spinothalamic tract (green), and terminate in NTS, PBN, PAG, and thalamus. For brevity, some monosynaptic projections and key centers are not shown (see Zhang et al., 2025). Figure created in https://BioRender.com based on Critchley & Harrison (2013). Abbreviations: aMCC, anterior midcingulate cortex; pACC, pregenual anterior cingulate cortex; sgACC, subgenual anterior cingulate cortex; Thal, thalamus; Hyp, hypothalamus; dAmy, dorsal amygdala; PAG, periaqueductal gray; LC, locus coeruleus; PBN, parabrachial nucleus; NTS, nucleus tractus solitarius; dpIns, dorsal posterior insula; dmIns, dorsal mid insula.

2.1. Ascending Viscerosensory Signals

Viscerosensory signals are conveyed to the brain along two primary pathways: the vagus nerve (cranial nerve X) traveling up the abdomen and front of the neck, and the spinal cord (Berthoud & Neuhuber, 2000; A. D. Craig, 2003; Critchley & Harrison, 2013; Jänig, 2022; Moore, 2024; Terasawa & Brewer, 2024). Signals following the vagus nerve synapse first in the NTS of the medullary brainstem (**Figure 1**), as well as in adjacent nuclei including area postrema and the dorsal motor nucleus of the vagus (Berntson & Khalsa, 2021; Critchley & Harrison, 2013; Jänig, 2022; Shaffer et al., 2023; Terasawa & Brewer, 2024). From NTS, these signals are passed to multiple brainstem nuclei – including the parabrachial nucleus (PBN) and locus coeruleus (LC) of the pons; and PAG, dorsal raphe (DR), ventral tegmental area (VTA), and superior colliculus (SC) of the midbrain – and subcortical structures – including dorsal amygdala, hypothalamus and dorsomedial thalamus (Critchley & Harrison, 2013; Jänig, 2022; Terasawa & Brewer, 2024; Zhang et al., 2025). From PBN, one of the main secondary synapses of ascending vagal signals, these signals are additionally passed to substantia nigra (SN) and PAG of the midbrain and to striatum, dorsal amygdala, hippocampus, hypothalamus, lateral geniculate nucleus (LGN), and dorsomedial thalamus (Critchley & Harrison, 2013; Jänig, 2022; Terasawa & Brewer, 2024; Zhang et al., 2025). Monosynaptic projections between these brainstem and subcortical structures are complex and widespread (Zhang et al., 2025). Ascending signals following the spinal cord synapse on similar brainstem and subcortical targets, with projections directly from spinal cord terminating in NTS, PBN, LC, and thalamus (Critchley & Harrison, 2013; Terasawa & Brewer, 2024).

From the brainstem and subcortex, viscerosensory signals are passed to the cerebral cortex, with the terminal regions corresponding to the default mode, salience, and somatomotor networks (Kleckner et al., 2017; Zhang et al., 2025). The dorsal posterior insula (of the somatomotor network) is the main site of viscerosensory cortical representation (i.e., ‘primary interoceptive cortex’; A. D. Craig, 2002). Much like primary sensory cortices in exteroceptive domains (e.g., primary visual cortex), dorsal posterior insula receives dense thalamic projections carrying interoceptive signals, as well as direct projections from PBN (Cechetto, 2014; Zhang et al., 2025). These viscerosensory terminations are organized topographically along an anteroposterior axis (Evrard, 2019). Viscerosensory signals also arrive to dorsal mid insula, which preserves the topographic organization of the dorsal posterior insula (Evrard, 2019; Schneider et al., 1993), and to ventral anterior insula (salience network). Beyond the insula, viscerosensory signals arrive to subgenual anterior cingulate cortex (sgACC; default mode network), pregenual anterior cingulate cortex (pACC; default mode network), and anterior midcingulate cortex (aMCC; salience network; Kleckner et al., 2017; Zhang et al., 2025). These insula and cingulate regions are ‘rich club hubs’ with dense connectivity profiles that facilitate communication and functional integration between multiple brain networks (Van Den Heuvel & Sporns, 2011, 2013). Additional hub regions (although receiving sparser viscerosensory projections) also contribute to the allostatic-interoceptive system, including default mode network regions of frontopolar cortex, dorsomedial prefrontal cortex, and posterior cingulate cortex (Kleckner et al., 2017; Zhang et al., 2025).

2.2. Descending Visceromotor Signals

In general, descending visceromotor signals coordinating the systems of the body can be traced along tracts similar to the viscerosensory pathways, but in the opposite direction and with notable exceptions in the cortex. Whereas the primary viscerosensory cortical site is the dorsal posterior insula, the primary visceromotor cortical structures include ventral anterior insula and sgACC (Cechetto, 2014; Devinsky et al., 1995; Evrard, 2019; Vertes, 2004). Stimulating anterior insula and sgACC directly modulates cardiovascular function (e.g., heart rate and blood pressure; Kaada, 1951a; Oppenheimer et al., 1992; Verberne, 1996; Oppenheimer, 2006, 2007; Resstel & Corrêa, 2006) and respiratory function (Kaada et al., 1949; Kaada, 1951b), demonstrating their critical roles in issuing descending visceromotor signals. Other cingulate structures, pACC and aMCC, are also considered to perform visceromotor functions (Chanes & Barrett, 2016; Kleckner et al., 2017; Zhang et al., 2025). From these cortical sites, visceromotor signals project to many of the structures in the viscerosensory pathway, including mediodorsal thalamus, hypothalamus, dorsal amygdala, striatum, PAG, DR, SC, SN, VTA, and PBN (An et al., 1998; Zhang et al., 2025). In the subcortex, the hypothalamus is a critical visceromotor structure (Thompson, 2003; Vertes, 2004), sending dense downward projections and mediating the release of regulatory hormones (Clarke, 2015).

2.3. Viscerosensory Signals Modulate Cognition and Global Brain Activity

Before examining the architecture and function of the allostatic-interoceptive system in psychopathy, it is worth underlining the system's influence in organizing cognitive phenomena and activity across the whole brain. Far from being background signals that are compartmented from so-called 'higher level' cognitive structures, signals from the heart, lungs, and other internal systems of the body actively shape ongoing activity throughout the nervous system (for reviews, see Bolt et al., 2025; Engelen et al., 2023; Theriault et al., 2025; Tort et al., 2025).

While several allostatic-interoceptive regions are known for their role in regulating the body (e.g., hypothalamus, NTS, PBN, PAG), others are classically considered to play crucial roles in exteroceptive sensory processing or other cognitive domains. For example, LGN and SC are known for their roles in vision and visuomotor function (receiving dense projections from the retina; Apter, 1945; Ellis et al., 2016), SN, VTA and striatum for their roles in reward processing and skeletomotor function (Arber & Costa, 2022; Cataldi et al., 2022), and the hippocampus for its central role in memory (Bird & Burgess, 2008; Burgess et al., 2002; Topolnik & Tamboli, 2022). Yet each of these 'cognitive' regions has bidirectional connections with multiple cortical and subcortical regions of the allostatic-interoceptive system, suggesting that viscerosensory and visceromotor signals interface with exteroceptive sensory signals and signals related to cognitive domains (Engelen et al., 2023; Theriault et al., 2025; Tort et al., 2025) even at relatively early stages of sensory processing (e.g., in LGN and SC). Corroborating this hypothesis, the systolic period of the cardiac cycle (i.e., when the heart pumps blood) effectively suppresses sensory sampling of visual (Sandman et al., 1977; McIntyre et al., 2007; Salomon et al., 2016; Ren et al., 2022), auditory (Cohen et al., 1980; X.

Yang et al., 2017), somatosensory (Al et al., 2021; Motyka et al., 2019), and nociceptive signals (Wilkinson et al., 2013). In the domain of memory, stimulating the vagus nerve in both humans and non-human animals improves memory consolidation (Clark et al., 1998, 1999; Ghacibeh et al., 2006; Jacobs et al., 2015; Ura et al., 2013).

Moreover, allostatic-interoceptive signals shape brain-wide dynamics via neurochemical and electrical oscillatory means. Present in this system are brainstem source nuclei for neuromodulatory systems that regulate the central and peripheral nervous system, including the noradrenergic (LC), dopaminergic (SN, VTA, hypothalamus), and serotoninergic systems (DR; Benarroch, 2012; Sclocco et al., 2018). Also present are nuclei, such as the PAG, that utilize multiple neurochemicals, including endogenous opioids and the primary excitatory and inhibitory neurotransmitters in the nervous system, glutamate and gamma-aminobutyric acid (GABA), respectively (Benarroch, 2012; Sclocco et al., 2018). Each of these source nuclei circulates neurotransmitters throughout cerebellum, subcortex, and cortex via widespread connections (**Figure 2**), enabling fast and flexible switching over time through a range of whole-brain states (Shine, 2019). Modulatory nuclei also project toward the periphery, affecting tissue throughout the body in the service of visceromotor control (see, for example, the central role of noradrenaline in sympathetic control of the viscera; McCorry, 2007) and skeletomotor control (see the central contributions of dopamine to skeletomotor activity; Arber & Costa, 2022; Cataldi et al., 2022).

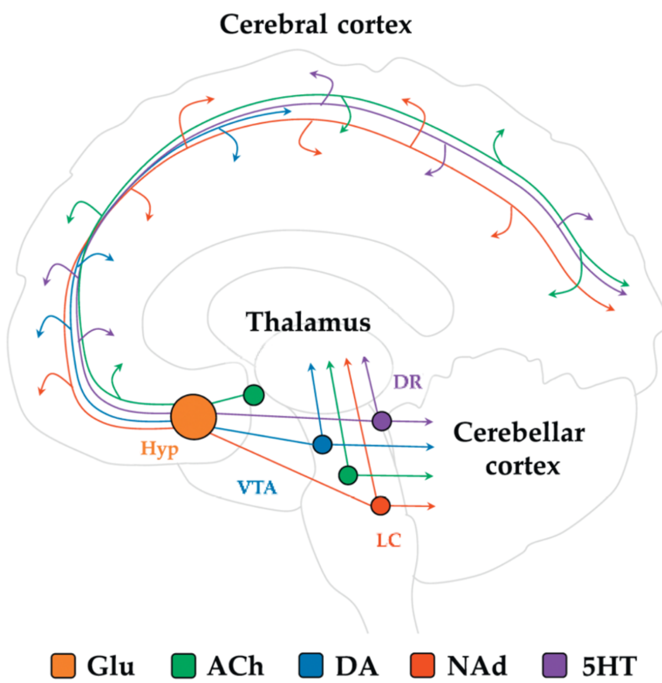

Figure 2. Source nuclei for neuromodulatory systems, present in the brainstem and subcortical aspects of the allostatic-interoceptive system, circulate dopamine (in blue), noradrenaline (in red), and serotonin (in purple) throughout the brain. Abbreviations: DR, dorsal raphe; Hyp, hypothalamus; VTA, ventral tegmental area; LC, locus coeruleus; Glu, glutamate; ACh, acetylcholine; DA, dopamine; NAd, noradrenaline; 5HT, serotonin. Adapted with permission from Shine (2019).

Mounting evidence suggests that the breathing cycle coordinates brain-wide neural oscillations (for review, see Tort et al., 2025). Briefly, in rodents, the breathing cycle modulates the membrane potential of individual neurons (Jung et al., 2022; Juventin et al., 2023) and the spiking activity of neuronal populations (González et al., 2023), and synchronizes prefrontal and sensory cortices, hippocampus, olfactory bulb, thalamus, and amygdala at theta (5-10 Hz; Tort et al., 2018; Karalis & Sirota, 2022) and gamma frequencies (30-120 Hz; Zhong et al., 2017; Herrero et al., 2018). In humans, who breathe more slowly than rodents, the breathing cycle couples cortical and subcortical regions at gamma frequencies and modulates neural activity at a broader range of lower frequencies, including delta (0.5-4 Hz), theta, alpha (8-13 Hz), and beta (13-30 Hz; Zelano et al., 2016; Jiang et al., 2017; Kluger & Gross, 2021; Q. Yang et al., 2022).

Altogether, these characteristics suggest that allostatic and interoceptive signals are intricately woven into the fabric of the brain, potentially placing allostasis at the core of brain function (Theriault et al., 2025). Whatever else the brain is doing at any given time – remembering, perceiving, attending, making decisions, emoting – it appears to be doing in concert with the rhythms of the internal conditions of the body in service of allostasis (Barrett, 2017; Engelen et al., 2023; Theriault et al., 2025; Tort et al., 2025; Zhang et al., 2025).

3. Dysfunction of the Brain's Allostatic-Interoceptive System in Psychopathy

The structure and function of the brain's allostatic-interoceptive system appears to be altered in psychopathy, according to single-study and meta-analytic evidence from diffusion-weighted tractography, resting-state functional connectivity, and task-based blood-oxygen-level-dependent (BOLD) activity. The sum of this evidence suggests that psychopathy is marked by impaired allostasis and an altered capacity for visceromotor signals to guide the allocation of attention. Relevant results are reviewed in sections 3.1-3.3 and synthesized with regard to allostatic dysfunction in section 3.4.

3.1. Reduced Myeloarchitectural Integrity of the Allostatic-Interoceptive System in Psychopathy

Psychopathy has been related to diminished structural integrity of white matter tracts connecting regions within the allostatic-interoceptive system, in particular the uncinate fasciculus and cingulum (**Figure 3D**). The uncinate fasciculus is a hook-shaped bundle of white matter fibers that connects several allostatic-interoceptive regions, passing from the amygdala through ventral anterior insula to innervate frontopolar cortex and sgACC (Ebeling & Cramon, 1992; Horel & Misantone, 1976; Thiebaut De Schotten et al., 2012). Reduced integrity of the uncinate fasciculus has been reliably observed in relation to psychopathy, in the right hemisphere (M. C. Craig et al., 2009; Motzkin et al., 2011; Sobhani et al., 2015; Sundram et al., 2012; Wolf et al., 2015), left hemisphere (Dotterer et al., 2019), and bilaterally (Hoppenbrouwers et al., 2013; Vermeij et al., 2018). Conversely, the number of bilateral uncinate fasciculus streamlines may be greater in psychopathy (Guo et al., 2025), potentially suggesting more fibers within this tract. A more extensive tract, the cingulum links multiple allostatic-interoceptive regions, including default mode and salience network hubs, and also connects these regions to other networks (e.g., dorsolateral prefrontal cortex in the frontoparietal network; Kappers et al., 1936; Mufson & Pandya, 1984; Morris et al., 1999; Heilbronner & Haber, 2014). More specifically, the cingulum bundle can be divided into four portions: a subgenual portion carrying axons between sgACC, pACC, aMCC, frontopolar cortex, orbitofrontal cortex, and dorsolateral prefrontal cortex; an anterior dorsal portion carrying axons between sgACC, pACC, aMCC, dorsolateral and dorsomedial prefrontal cortices, ventrolateral frontal cortex, frontopolar cortex, orbitofrontal cortex, and thalamus; a posterior dorsal portion carrying axons between sgACC, aMCC, dorsolateral and dorsomedial prefrontal cortices, frontopolar cortex, orbitofrontal cortex, and thalamus; and a temporal portion carrying axons between posterior cingulate cortex, thalamus, amygdala, and the hippocampal formation (i.e., the subiculum; Heilbronner & Haber, 2014). In psychopathy, reduced integrity has been observed in the left dorsal cingulum (i.e., averaged across anterior dorsal and posterior dorsal portions; Sethi et al., 2015) and right cingulum (i.e., averaged across the entire bundle; Dotterer et al., 2019). Conversely, psychopathy may be related to a greater number of bilateral cingulum streamlines (Guo et al., 2025).

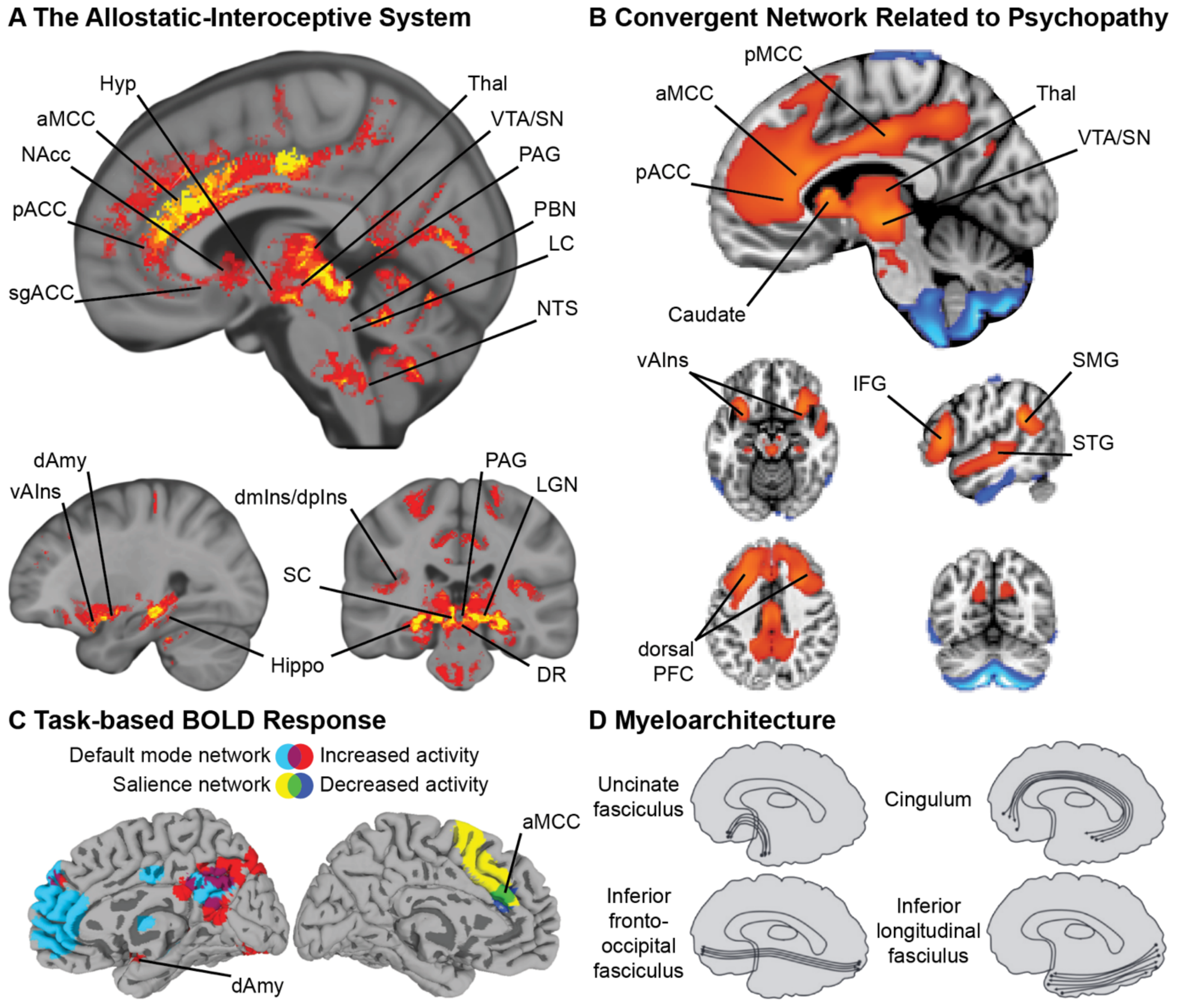

Figure 3. A) The allostatic-interoceptive system, identified via functional connectivity analyses of ultra-high field (7 Tesla) imaging data from healthy adult human subjects (Zhang et al., 2025). Seed regions were 21 cortical, subcortical and brainstem regions that in tract-tracing studies of non-human animals have shown extensive monosynaptic and polysynaptic connections to the viscera via the vagus nerve and spinal cord. Regions in red were functionally connected to 15 of 21 seed regions, while regions in yellow were functionally connected to all 21 seed regions. Figure adapted with permission from Zhang et al. (2025). B) The psychopathy network, identified through normative network mapping of coordinates where psychopathy was related to increased or decreased activity in 23 fMRI studies (i.e., separate functional connectivity analyses were conducted for each study's coordinates; Dugré & De Brito, 2025). Warm colors represent regions that were positively functionally connected to the heterogeneous coordinates whose activity was related to psychopathy, while cool colors represent regions that were negatively functionally connected to these coordinates. Figure adapted with permission from Dugré & De Brito (2025). C) Regions showing consistently increased or decreased task-based BOLD response in meta-analyses of 25 fMRI studies (Deming & Koenigs, 2020). Findings are displayed to show overlap with the default mode network and salience network. Figure adapted with permission from Deming & Koenigs (2020). D) White matter tracts whose integrity has been linked to psychopathy, as measured by fractional anisotropy in diffusion-weighted tractography. Figure adapted with permission from Dotterer et al. (2019) Abbreviations: aMCC, anterior

midcingulate cortex; dAmy, dorsal amygdala; dmIns, dorsal mid insula; dpIns, dorsal posterior insula; DR, dorsal raphe; Hippo, hippocampus; Hyp, hypothalamus; IFG, inferior frontal gyrus; LC, locus coeruleus; LGN, lateral geniculate nucleus; NAcc, nucleus accumbens; NTS, nucleus tractus solitarius; pACC, pregenual anterior cingulate cortex; PAG, periaqueductal gray; PBN, parabrachial nucleus; PFC, prefrontal cortex; pMCC, posterior midcingulate cortex; SC, superior colliculus; sgACC, subgenual anterior cingulate cortex; SMG, supramarginal gyrus; SN, substantia nigra; STG, superior temporal gyrus; Thal, thalamus; vAIns, ventral anterior insula; VTA, ventral tegmental area.

Two additional tracts linking the allostatic-interoceptive system to other networks have been implicated, namely the inferior fronto-occipital fasciculus and the bilateral inferior longitudinal fasciculus (**Figure 3D**). The inferior fronto-occipital fasciculus sprawls from the frontal to occipital and parietal lobes via the temporal lobe, carrying axons between cortical allostatic-interoceptive regions (i.e., frontopolar cortex of the default mode network) and regions in dorsal attention (e.g., superior parietal cortex), frontoparietal (e.g., posterior parietal cortex), and visual (e.g., extrastriate occipital cortex) networks (Mayo, 1823; Meynert, 1884; Curran, 1909; Catani et al., 2002; Giampiccolo et al., 2025). Nearby, the inferior longitudinal fasciculus runs from the anterior temporal lobe to occipital cortex and carries axons between subcortical allostatic-interoceptive regions (i.e., amygdala and hippocampus) and regions in other networks (e.g., extrastriate occipital cortex of the visual network; Reil, 1812; Burdach, 1822; Dejerine, 1895; Mori et al., 2002; Catani et al., 2002; Gomez et al., 2015; Latini et al., 2017). In psychopathy, reduced integrity and fewer streamlines have been observed in the left inferior fronto-occipital fasciculus (Dotterer et al., 2019; Guo et al., 2025), along with reduced integrity in the bilateral inferior longitudinal fasciculus (Dotterer et al., 2019). Conversely, more streamlines were observed in the right inferior fronto-occipital fasciculus (Guo et al., 2025).

Thus, the myeloarchitecture within the allostatic-interoceptive system is compromised along the uncinate fasciculus (connecting amygdala to frontopolar cortex and sgACC) and cingulum (connecting sgACC, pACC, aMCC, frontopolar cortex, dorsomedial prefrontal cortex, hippocampus, amygdala, and thalamus). Compromised tracts extending from this system to other networks include the cingulum (connecting to the frontoparietal network), the inferior fronto-occipital fasciculus (connecting to the dorsal attention, frontoparietal, and visual networks), and the inferior longitudinal fasciculus (connecting to the visual network).

3.2. Altered Functional Interactions of the Allostatic-Interoceptive System in Psychopathy

During wakeful rest, psychopathic people have also shown reduced functional connectivity (i.e., the co-fluctuation of the BOLD signal) within the allostatic-interoceptive system, particularly between aMCC and other cortical regions. Specifically, reduced functional connectivity has been observed between aMCC (salience network) and posterior cingulate cortex (default mode network; Pujol et al., 2012), between aMCC and ventral anterior insula (salience network; Contreras-Rodríguez et al., 2015), and between aMCC and ventral mid insula (salience network; Ly et al., 2012). Reduced cortico-subcortical connectivity within this system has also been observed, including between aMCC and the hypothalamus (Contreras-Rodríguez et al., 2015), between aMCC and dorsal amygdala (Contreras-Rodríguez et al., 2015), and between frontopolar cortex and amygdala (Motzkin et al., 2011). Finally, reduced information flow has been observed from posterior insula downward to amygdala (Ye et al., 2022).

Moreover, allostatic-interoceptive cortical networks display altered functional interactions with other networks, in particular with the frontoparietal network. In healthy individuals, the default mode, salience, and frontoparietal networks tend to engage in a stereotyped interaction: the ongoing activity of the default mode and frontoparietal network is anticorrelated[1] (Buckner & DiNicola, 2019; Fox et al., 2005; Fransson, 2005), such that the brain continuously fluctuates between states of higher default mode network activity and states of higher frontoparietal network activity, while the salience network plays a role in switching between these two general states (Chand et al., 2017; Chiong et al., 2013; Goulden et al., 2014; Sridharan et al., 2008). In

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[1] Although note that a subsystem of the frontoparietal network (involved in tasks requiring internally directed attention, such as mentalizing) may instead functionally co-activate with the default mode network (Dixon et al., 2018; Kam et al., 2019).

psychopathy, the anticorrelation between the default mode and frontoparietal networks is reduced (from pACC to bilateral posterior parietal cortex and to right dorsolateral prefrontal cortex; Dotterer et al., 2020), suggesting increased competition between the two networks (Deming et al., 2023). Meanwhile, the salience network shows increased connectivity with the frontoparietal network – between aMCC and dorsolateral prefrontal cortex (bilateral in Contreras-Rodríguez et al., 2015; left lateralized in Espinoza et al., 2018) – and exercises a diminished switching role (Deming et al., 2023).

Functional links from the subcortex to other brain networks are also aberrant. The amygdala and hippocampus act less as central hubs (i.e., with fewer functional connections; Tillem et al., 2019), suggesting that these regions receive relatively less information and have less influence on global neural communication. And the amygdala shows reduced connectivity to extrastriate occipital cortex (visual network), not continuously but during a specific brain state marked by relatively weak connectivity across the brain (Espinoza et al., 2019).

In sum, aMCC notably has shown reduced functional connectivity with multiple allostatic-interoceptive regions – posterior cingulate cortex, ventral anterior insula, dorsal amygdala, and hypothalamus – as well as increased connectivity to dorsolateral prefrontal cortex of the frontoparietal network. The salience network may play a diminished role in switching between patterns of default mode and frontoparietal network activity. Lastly, amygdala and hippocampus have shown fewer connections to regions across the brain, making these regions less influential hubs.

3.3. Altered Task-based BOLD Activity of the Allostatic-Interoceptive System in Psychopathy

According to meta-analyses, psychopathic people frequently show both reduced and increased BOLD response in allostatic-interoceptive cortical regions. This altered activity might be considered domain-general, occurring when psychopathic individuals perform a variety of externally focused, cognitively demanding tasks. In the salience network, reduced domain-general BOLD response has been observed in aMCC (**Figure 3C**; Deming & Koenigs, 2020), whereas increased activity has been observed in bilateral dorsal anterior insula (Poeppl et al., 2018). These regions are thought to detect and monitor salient information, and thus in the typical brain these regions tend to increase activity during cognitively demanding tasks (Uddin, 2017). In the default mode network, increased BOLD response has been observed in the posterior cingulate cortex and dorsomedial prefrontal cortex (**Figure 3C**; Deming & Koenigs, 2020). Classically, these regions in the typical brain show decreased activity during cognitively-demanding tasks (Shulman et al., 1997; Raichle et al., 2001; cf. Buckner & DiNicola, 2019; Spreng, 2012), and so the increased activity in psychopathy could be construed as an attenuated task-related deactivation (Freeman et al., 2015; Deming & Koenigs, 2020).

3.4 Synthesis: Impoverished Visceromotor Signals and Altered Attention to Allostatically Relevant Information

Visceromotor cortices (aMCC in particular) exhibit altered functional dynamics and degraded myeloarchitecture in psychopathy. Based on this evidence, we propose that visceromotor signals in the psychopathic person's brain lack the rich contextual details that in the typical brain facilitate regulating the body as a function of an ever-changing environment. The visceromotor signals exiting the anterior cingulate (sgACC, pACC, aMCC) and insula are thought to be integrated summaries of signals that arrive there from multiple sensory modalities (Chanes & Barrett, 2016; A. D. Craig, 2003; Menon & Uddin, 2010; Singer et al., 2009; Uddin, 2015). In psychopathy, the array of multimodal sensory signals arriving to the anterior cingulate (sgACC, pACC, aMCC) may be relatively sparse. Viscerosensory signals arrive there via a degraded uncinate fasciculus, and viscerosensory structures (e.g., dorsal amygdala, hypothalamus) as well as other visceromotor structures (i.e., ventral anterior insula) functionally interact with aMCC in a diminished capacity. Visual signals arrive to the frontopolar cortex via a degraded inferior fronto-occipital fasciculus, and then to anterior cingulate via a degraded cingulum. Impaired sensory integration[2] may even occur at multiple levels of the allostatic-interoceptive system, since visual signals arrive to the amygdala and hippocampus along a degraded inferior longitudinal fasciculus, and these two subcortical nuclei have fewer global functional connections. Many of these white matter tracts carry bidirectional projections (Kleckner et al., 2017; Zhang et al., 2025), suggesting impaired transmission of both ascending viscerosensory and descending visceromotor signals.

If the visceromotor signals lack rich contextual details, then a psychopathic person's allostatic process may be relatively context insensitive. In support of this hypothesis, psychopathic people often show altered physiological responses to environmental perturbations. For example, in a classic study, psychopathic people displayed lower skin conductance response (an estimate of sympathetic nervous system activity) in anticipation of an auditory cue following several pairings with an electric shock (Lykken, 1957). In decades' worth of studies since then, psychopathic people have shown lower skin conductance (as indexed by level, response amplitude, and number of responses) as they anticipated (Aniskiewicz, 1979; Flor et al., 2002; Hare et al., 1978; Rothemund et al., 2012), imagined (Patrick et al., 1994), and experienced (Aniskiewicz, 1979; Arnett et al., 1993, 1997; Hare, 1968; House & Milligan, 1976; Verona et al., 2004) changes in a variety of visual, auditory, and somatosensory stimuli (for review, see de Looff et al., 2022). Likewise, they have shown lower heart rate and greater heart rate variability in response to environmental perturbations (Patrick et al., 1994; de Looff et al., 2022), as well as lower heart rate even in the absence of perturbations caused by an experimenter (i.e., 'resting heart rate;' for review see de Looff et al., 2022).

[2] The Impaired Integration theory first proposed that "psychopathy is characterized by difficulty rapidly integrating multicomponent perceptual information, which in turn influences the quality of mental representations and shapes the development of associative neural networks" (Hamilton et al., 2015, p. 771). The extant data suggest that impaired integration could be a critical feature of allostatic-interoceptive dysfunction.

In addition to diminished sympathetic and parasympathetic control, hormonal control of the body also appears to be context-insensitive in psychopathy. In response to environmental perturbations (e.g., a social stressor), psychopathic people have shown lower levels of cortisol (Cima & Nicolson, 2021), a glucocorticoid that aids in regulating nearly every organ system in the body (Kadmiel & Cidlowski, 2013). Yet, in baseline periods prior to perturbations, their cortisol levels have been consistently higher relative to those of non-psychopathic individuals (for review, see Braz Ferreira et al., 2025), accompanied by higher levels of oxytocin (Mitchell et al., 2013) and testosterone (Roy et al., 2019; South et al., 2023; Stålenheim et al., 1998). These hormones, whose release is mediated by the hypothalamus (Basaria, 2014; Kadmiel & Cidlowski, 2013; Kerem & Lawson, 2021; Scherholz et al., 2019), have diverse regulatory effects on bodily tissues, including aiding metabolic and anti-inflammatory processes (cortisol and oxytocin; Kerem & Lawson, 2021; Scherholz et al., 2019), regulating fluids and electrolytes (cortisol; Scherholz et al., 2019), aiding cell growth (oxytocin; Kerem & Lawson, 2021), and transcribing genes (testosterone; Hiipakka & Liao, 1998).

Moreover, impoverished visceromotor signals may hinder the allocation of attention to signals that are relevant to allostasis (i.e., salient cues, e.g., a visual cue predicting physical harm to the body). Reduced task-based activity of the visceromotor aMCC may reflect disrupted detection of allostatically relevant cues. The salience network (including aMCC) then appears to be less capable of switching the relative activity of the default mode and frontoparietal networks, a dynamic shift that in the typical brain is critical for allocating attention to cognitively demanding tasks (Bednarski et al., 2012; Kelly et al., 2008; Ng et al., 2016). Signals from aMCC that may be involved in this dynamic shift arrive at frontoparietal network regions via a degraded cingulum. As a result, competition with default mode network may impede frontoparietal network processing of the relevant cues. Indeed, psychopathic people display an attentional bottleneck, such that they selectively focus on some cues and disregard other cues, even those that have allostatic relevance (Baskin-Sommers & Brazil, 2022). For example, when psychopathic people viewed two cues – one that predicted and one that did not predict the threat of receiving an electric shock – their anticipatory eye-blink response varied by the cue presentation order (Baskin-Sommers et al., 2011). When the allostatically relevant, threat predicting cue was presented first, they showed a normal startle response, yet when the alternative cue was presented first, their startle response was reduced. We propose that allostasis is central to this attentional bottleneck: psychopathic people prepare the body for action when they detect allostatically relevant cues but enact insufficient bodily control when these cues are obscured by distractors.

4. Heterogeneity of Allostatic-Interoceptive System Dysfunction Across Studies

Notably, the conclusions above are tempered by vast heterogeneity. In many studies the BOLD activity of specific allostatic-interoceptive regions is, in contrast to the above meta-analytic findings, unaltered. For example, in more than half of studies, anterior cingulate cortex (including aMCC) has shown a typical BOLD response (Deming et al., 2024). In another quarter of studies, anterior cingulate showed an altered BOLD response that was situation-specific. Additional allostatic-interoceptive regions have also shown altered task-based BOLD response, though in a minority of studies: altered activity has been observed in individual studies in the amygdala (for review, see Deming et al., 2022) and in the full extent of the insula (i.e., ventral anterior insula (Deming et al., 2020; Nummenmaa et al., 2021), dorsal anterior insula (Decety, Chen, et al., 2013; Poeppl et al., 2018), mid insula (Decety et al., 2014), and posterior insula (Decety et al., 2014; Glenn et al., 2017)). The nature of these alterations (i.e., increased vs. reduced activity) also varies by study (Deming et al., 2022, 2024; Griffiths & Jalava, 2017; Johanson et al., 2020). In fact, separate meta-analyses have observed consistently increased (Deming & Koenigs, 2020) and decreased activity (Poeppl et al., 2018) of the amygdala. Spatial heterogeneity also abounds, as the literature has implicated not only the allostatic-interoceptive system but regions dispersed across all four cortical lobes (for reviews, see Koenigs et al., 2011; Griffiths & Jalava, 2017), with little spatial convergence between studies (Deming et al., 2022, 2024; Dugré & De Brito, 2025). Few functional connectivity findings have been replicated. Simply put, the science of psychopathic brain alterations is all over the map.

Resolving this heterogeneity will be a critical precursor to identifying brain mechanisms of psychopathy with translatable clinical utility. Beginning again with the architecture and evolution of the nervous system, two characteristics of the allostatic brain emerge as potential resolving explanations. First, the visceromotor cortices are well placed to have cascading effects on the function of downstream regions throughout the brain, suggesting the spatially distributed brain alterations can be traced back to core dysfunction within allostatic-interoceptive cortex (section 4.1). Second, in general, brain-behavior mappings vary across individuals and instances, suggesting that person-specific rather than group-aggregate analyses may be better suited to identifying brain dysfunction associated with psychopathy (section 4.2). Heterogeneity, in short, may not be a bug but a defining feature of a brain regulating the body's organ systems amidst constant changes in the internal and external context.

4.1. Heterogeneity Resulting from Core Dysfunction of the Allostatic-Interoceptive System

Visceromotor cortices sit atop multiple hierarchies. We propose that core dysfunction of the allostatic-interoceptive system has cascading effects on activity in regions at lower levels of these hierarchies, resulting in study-wise spatial heterogeneity. New evidence supports this hypothesis. The first hierarchy is the visceromotor pathway, descending from visceromotor cortices (i.e., anterior cingulate and insula) toward the subcortex and brainstem, then toward the internal organ systems via the vagus nerve and spinal cord (**Figure 4B**; see section 2.2). The second hierarchy descends from visceromotor cortices and traverses the majority of the cortex to arrive at primary sensory cortices. Evidence for this cortical hierarchy is grounded in these anatomical principles: 1) cross sections of the cortex are composed of distinct layers (i.e., superficial layers I-III, middle layer IV, and deep layers V-VI), 2) the degree of lamination varies across the cortex (**Figure 4**; Barbas, 2015; Brodmann, 1910; Chanes & Barrett, 2016; García-

Cabezas et al., 2020; Zilles & Amunts, 2012), and 3) the difference in lamination between two regions determines the routing of ascending sensory signals and descending modulatory signals (Barbas, 2015; Barbas & Rempel-Clower, 1997).

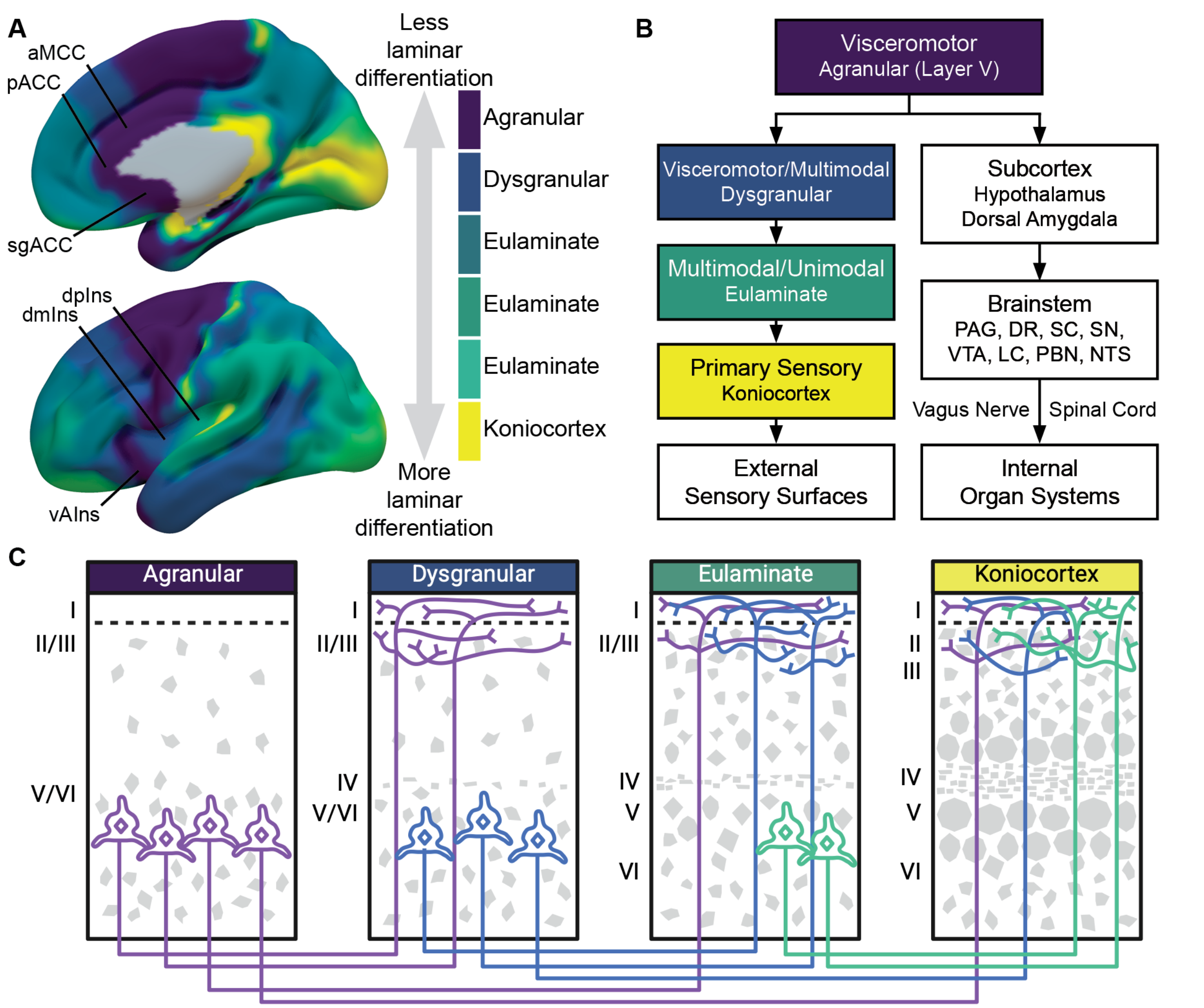

Figure 4. Two neural hierarchies converge on layer V of visceromotor cortices. A) The degree of laminar differentiation varies across the cortex. Visceromotor cortices, including anterior cingulate and ventral anterior insula, have the least laminar differentiation (i.e., agranular), multimodal and unimodal cortices have increasingly more laminar differentiation (i.e. dysgranular and eulaminate), and primary sensory cortices have the greatest degree of laminar differentiation (i.e., koniocortex). Figure displays the cortical laminar gradient according to the von Economo-Koskinas cortical type atlas (Pijnenburg et al., 2021; von Economo & Koskinas, 1925). Note that von Economo & Koskinas (1925) labeled eulaminate cortices 'homotypic.' B) Visceromotor signals descend the cortical gradient toward regions with increasingly more differentiated laminar profiles, arriving at primary sensory cortices and continuing toward external sensory surfaces (e.g., the retina and cochlea). These signals also descend the visceromotor pathway toward subcortex and brainstem, continuing along the vagus nerve and spinal cord toward in body's internal organ systems. C) Along the cortical hierarchy, layer V

neurons in regions with less laminar differentiation project downward to superficial layers (i.e., layers I-III) of regions with more laminar differentiation. Regions with more similar laminar profiles (e.g., agranular and dysgranular) feature more extensive downward projections. Here, two projecting neurons represent these more extensive projections, while one projecting neuron represents the less extensive projections connecting regions with less similar laminar profiles (e.g., agranular and koniocortex). Ascending projections are not shown. Laminar profiles are displayed in gray in the background and labeled in Roman numerals. Figure created in https://BioRender.com based on Barbas (2015). Abbreviations: aMCC, anterior midcingulate cortex; dmIns, dorsal mid insula; dpIns, dorsal posterior insula; DR, dorsal raphe; LC, locus coeruleus; NTS, nucleus tractus solitarius; pACC, pregenual anterior cingulate cortex; PAG, periaqueductal gray; PBN, parabrachial nucleus; SC, superior colliculus; SN, substantia nigra; sgACC, subgenual anterior cingulate cortex; vAIns, ventral anterior insula; VTA, ventral tegmental area.

Descending signals flow from areas with fewer layers toward areas with increasingly more sharply defined layers, or greater laminar differentiation (**Figure 4**; Barbas, 2015; Barbas & Rempel-Clower, 1997). Visceromotor cortices atop the two hierarchies are unique in the cortex as they are composed of four layers, with no layer IV and undifferentiated layers II and III (Barbas, 2015; Zilles & Amunts, 2012). Regions with no layer IV (e.g., ventral anterior insula, sgACC, aMCC; García-Cabezas et al., 2020) lack granule cells and are therefore called agranular (**Figure 4C**). Stepping down the hierarchy, regions with a nascent layer IV (e.g., dorsal mid insula; García-Cabezas et al., 2020) are dysgranular. Next, granular cortices feature six layers including a distinct layer IV, and these regions can be further subdivided based on the sharpness of the definition between layers and the prominence of layer IV (García-Cabezas et al., 2020). Among granular cortices, multimodal and unimodal association areas are eulaminate with a defined but less prominent layer IV, while primary sensory areas (e.g., primary visual cortex) are koniocortices with a prominent layer IV that receives extensive sensory input from the thalamus (Barbas, 2015; García-Cabezas et al., 2020). The cortical hierarchy follows the degree of lamination, descending from agranular and dysgranular visceromotor cortices toward eulaminate regions and then koniocortices (Chanes & Barrett, 2016), as evidenced by gross patterns of structural (Barbas, 2015; Barbas & Rempel-Clower, 1997; Mesulam, 2000) and functional connectivity (Katsumi et al., 2022). Monosynaptic and polysynaptic projections link all levels of the cortical hierarchy, with the most extensive monosynaptic connections occurring between regions with similar degrees of lamination (e.g., agranular and dysgranular; **Figure 4C**; Barbas, 2015).

In agranular cortices, projections descending both hierarchies originate primarily in layer V. From this deep layer, visceromotor signals terminate in the superficial layers (i.e., layers I-III) of dysgranular, eulaminate, and koniocortical regions (**Figure 4C**; Barbas, 2015; Barbas & Rempel-Clower, 1997; García-Cabezas et al., 2019). Signals flowing down the hierarchy continue to follow this general principle: layer V neurons in less differentiated regions project to superficial regions of more differentiated regions (Barbas, 2015; Barbas & Rempel-Clower, 1997; García-Cabezas et al., 2019). Additional connections pass the signal from superficial to deep layers within the cortical column (e.g., within a column of dysgranular cortex; Shipp, 2007). Sensory signals ascending the cortical hierarchy follow the reverse pathway, projecting from superficial layers of cortices with a greater degree of lamination to deep layers of cortices with a lower degree of lamination, terminating ultimately in layer V of agranular cortices. In the subcortically-projecting hierarchy, visceromotor signals also originate in layer V (**Figure 4B**; Cobos & Seeley, 2015; Hodge et al., 2020; Takemoto et al., 2023). In fact, the signals descending the cortical hierarchy are thought to be efferent copies of the visceromotor signals sent toward to the subcortex, brainstem, and internal organ systems (Barrett, 2017). Notably, however, two types of layer V neurons exist – those that project only to other cortical regions and those that project both within the cortex and to subcortex (Baker et al., 2018; Takemoto et al., 2023) – suggesting different populations of neurons may top the two hierarchies. Nonetheless, layer V in visceromotor cortices is positioned to have cascading modulatory effects on activity throughout the brain.

According to recent evidence, in psychopathy visceromotor cortical dysfunction may alter activity in downstream regions in a heterogeneous manner, giving the appearance of spatially scattered loci of BOLD disruptions across studies. In new meta-analyses, the loci of altered task-based BOLD activity showed minimal spatial consistency (Dugré & De Brito, 2025).

Yet, the functional connectivity profiles of these loci converged on a common network (**Figure 3B**). The majority of loci were functionally connected to a network overlapping substantially with the allostatic-interoceptive system, including visceromotor cortices (ventral anterior insula, pACC, aMCC), frontopolar cortex, dorsomedial prefrontal cortex, thalamus, and dopaminergic brainstem nuclei (VTA, SN; Dugré & De Brito, 2025). This network mapping approach reduced study-wise heterogeneity markedly (Dugré & De Brito, 2025). Although each individual study observed altered activity in unique and scattered regions, what these regions shared in common were significant functional interactions with visceromotor cortices. This raises the intriguing possibility, testable with ultra-high field fMRI (Bandettini et al., 2021), that core dysfunction in the psychopathic brain originates in visceromotor cortices in layer V. Indeed, such propagation of dysfunction is common in brain disorders (Fornito et al., 2015).

4.2. Heterogeneity Resulting from Degeneracy

The brain is a degenerate system, meaning that different brain structures are capable of achieving the same functional outcome in separate instances (Albantakis et al., 2024; Edelman & Gally, 2001; Tononi et al., 1999; Westlin et al., 2023). In other words, brain-behavior mappings are many-to-one, with many functional brain patterns mapping to a given behavioral outcome (Waschke et al., 2021; Westlin et al., 2023). Individuals display multiple cortical activation patterns, which vary trial-by-trial, when performing a single perceptual decision-making task (Nakuci et al., 2025). Multiple neural patterns have also been related to separate instances of a single emotion category, including instances of fear, happiness, sadness, anger, disgust, and loss (Raz et al., 2016; Singh et al., 2021; Wang et al., 2024; Wilson-Mendenhall et al., 2015). Different individuals can also engage different brain structures to achieve similar functional outcomes. For example, different individuals have been shown to recruit different brain networks when reading (Seghier et al., 2008) and during experiences of anger and anxiety (Doyle et al., 2022). Degeneracy thus implies heterogeneous brain-behavior mappings across instances (within individuals) and across individuals.

Given degeneracy, the assumption that psychopathy is related to a single neural profile is likely flawed (Deming et al., 2024; Griffiths & Jalava, 2017). Instead, the brain basis of psychopathy is likely to be both context- and person-specific. Psychopathy is not a unique case in this regard. Heterogeneous, person-specific neural profiles have been linked to many psychiatric diagnoses (Haukvik et al., 2023; Segal et al., 2023, 2025). Basic statistical principles also favor the person-specific approach as, in general, the findings of group-aggregate analyses rarely generalize to individuals (Cragg et al., 2019; Estes, 1956; Gallistel, 2012; Hunter et al., 2024; Mattoni et al., 2025). In this light, heterogeneous findings across group-aggregate studies are not the problematic outcome of methodological issues (i.e., variable methods across studies; Griffiths & Jalava, 2017; Koenigs et al., 2011), but rather the expected result of separate attempts to simplify a degenerate system. Advancing the science of brain mechanisms of psychopathy will require replacing group-aggregate analyses with analyses of individuals, consistent with a growing movement called precision psychiatry (Fernandes et al., 2017; Kraus et al., 2023; Laumann et al., 2023; Tiego et al., 2023; Williams & Whitfield Gabrieli, 2025).

5. Implications for Understanding Psychopathy, Aggression, and Violence

Allostasis is the central aim of the nervous system, and probing allostasis may be key to understanding violence. All complex behaviors and mental phenomena – including violence and aggression – are likely best described as strategies for survival, reproduction, and allostasis (Sterling & Laughlin, 2015). The job of clinical scientists may be to identify the allostatic consequences of violent and aggressive behavior, and to replace these strategies with more prosocial strategies that achieve similar allostatic ends. A range of tools are available for advancing these scientific aims, including measures of peripheral physiology (e.g., cardiovascular, respiratory, or gastrointestinal activity; Khalsa et al., 2018; Quigley et al., 2021), imaging of the brain's allostatic-interoceptive system (Kleckner et al., 2017; Zhang et al., 2025), illusory tasks (e.g., the interoceptive rubber hand task or the embreathment task; Monti et al., 2020; Suzuki et al., 2013), and experimental manipulation of viscerosensory signals (e.g., noradrenergic stimulation producing increased cardiorespiratory activity; Teed et al., 2022).

Notably, allostasis may be a core underlying process that unites seemingly disparate empirical and theoretical strands. Studies of the endocrine, cardiovascular, and nervous systems are often treated as separate lines of inquiry. Similarly, separate theories – explaining the physiological (Gao et al., 2012; Hare, 1968; Kimonis, 2023; Montague, 1979), mental (Baskin-Sommers et al., 2011; Baskin-Sommers & Brazil, 2022; Lykken, 1957), and neural (Blair, 2003; Damasio, 1994; Hamilton et al., 2015; Kiehl, 2006; Moul et al., 2012) correlates of psychopathy and aggression – are often described as incompatible. We would propose that the contents of these seemingly disparate strands are simply corollaries of allostasis. In other words, measures of a person's biology or mental experience, whether that experience is cognitive or emotional, are empirical observations of the current output of a nervous system that is continually sensing and regulating the body for survival, irrespective of whether or not that nervous system is being perturbed by an experimenter.

Thus, the current allostatic perspective obviates the practice of inferring a person's mental state from measures of biology (i.e., reverse inference; Krueger, 2017). This practice is common and established in the science of psychopathy and aggression. Fear is often inferred from observations of the skin conductance response (e.g., Armstrong et al., 2019; Lykken, 1957, 1995), the eye-blink startle response (e.g., Baskin-Sommers et al., 2011; Patrick, 1994; Patrick et al., 1993), and amygdala activity (e.g., Blair et al., 2004; Johanson et al., 2020; Lozier et al., 2014; Marsh & Cardinale, 2014). Stress is inferred from measured cortisol levels (e.g., Blankenstein et al., 2022; Braz Ferreira et al., 2025). Empathy is inferred from amygdala, insula, and anterior cingulate activity (e.g., Decety, Chen, et al., 2013; Decety, Skelly, et al., 2013; Kaseweter et al., 2022). However, inferring mental state from biology is unwarranted and is likely to be inaccurate, since many brain states (Nakuci et al., 2025; Raz et al., 2016; Singh et al., 2021; Wang et al., 2024; Wilson-Mendenhall et al., 2015) and many physiological patterns

(McVeigh et al., 2024) can map to the same mental experience, and a single brain state (Lindquist et al., 2012) or physiological pattern (Hoemann et al., 2020) can map to many different mental experiences. Fruitful new lines of inquiry might instead consider these biological measures for what they are: correlates of the brain's allostatic process. Taking this perspective opens countless promising questions. What are the consequences of aggressive behavior for the brain's regulation of the body's cardiovascular, respiratory, digestive, immune, endocrine, and musculoskeletal systems? What states of these systems precede spontaneous aggressive behavior? How do perturbations to these systems mitigate aggressive behavior (e.g., Im, 2021; Pels & Kleinert, 2016; Qureshi et al., 2021; Raine et al., 2020; Wagner et al., 1999)?

Applying this allostatic perspective empirically will require considering each person in their current context. The strategies implemented by the brain to regulate the body depend on the person's current resources and what is available to them in their external environment. In considering person- and context-specificity, the allostatic perspective differs from theories of psychopathy positing that physiological (Hare, 1968) and neural dysfunction (Blair, 2003; Damasio, 1994; Kiehl, 2006) is stable and persistent. To examine person- and context-specificity, future studies should sample individuals deeply across many contexts and across many instances of the same context (Hoemann et al., 2023; Kraus et al., 2023; Laumann et al., 2023; Tiego et al., 2023). Deep sampling may eventually produce interventions for aggressive behavior that are personalized and delivered with precise timing (Fernandes et al., 2017).

Finally, imaging the brainstem and cortical layers – in particular the brainstem nuclei of the allostatic-interoceptive system, deep layers of agranular visceromotor cortices, and superficial layers of granular sensory cortices – will be necessary for uncovering the mechanistic interactions that support allostasis and interoception. To date, a handful of studies have observed relationships between psychopathy and brainstem function (Decety, Skelly, et al., 2013; Deming et al., 2020; Geurts et al., 2016; Yoder et al., 2015). Yet, in each of these studies voxel sizes were ≥ $3mm^3$, roughly equal to the average cross-sectional diameter of a single brainstem nucleus (Afshar et al., 1978), suggesting that these prior studies lacked the spatial resolution to isolate activity in individual brainstem structures. And to date no study of psychopathy has examined the function of individual cortical layers. Ultra-high field fMRI enables imaging small brainstem nuclei and thin cortical layers (Bandettini et al., 2021; Hansen et al., 2024), making this a powerful tool for characterizing the allostatic-interoceptive system.

6. Conclusion

Beginning with the question ‘why do we need a brain?’ bears a useful new framework for probing the brain mechanisms of psychopathy and aggression, one centered on the fundamental process of allostasis. In the course of evolutionary history, animal bodies have developed more complex internal systems, and survival success has depended in large part on the ability of the brain to coordinate these systems. To do so efficiently, the brain anticipates the needs of the body and meets them before they arise (Barrett, 2017; Sterling, 2012; Sterling & Laughlin, 2015). Psychopathy might best be understood as a disorder of this fundamental process. Dysfunction of the visceromotor cortices, apparent in converging lines of neuroimaging evidence, could reflect an impaired capacity to form richly integrated visceromotor signals. Impoverished visceromotor signals would have multiple consequences, including hindering the allocation of attention to allostatically relevant cues, impairing the top-down modulation of global brain activity, and producing altered visceromotor and skeletomotor strategies for meeting the body’s current allostatic needs. Critically, these strategies will depend on the person, the status of their internal resources, and the possibilities available to them in their environment, suggesting that future work should take a precision psychiatry approach to identify brain mechanisms at the level of the individual.

Abbreviations

ACh – acetylcholine

aMCC – anterior midcingulate cortex

BOLD – blood-oxygen-level-dependent

DA – dopamine

dAmy – dorsal amygdala

dmIns – dorsal mid insula

dpIns – dorsal posterior insula

DR – dorsal raphe

GABA – gamma-aminobutyric acid

Glu – glutamate

Hippo - hippocampus

Hyp – hypothalamus

IFG – inferior frontal gyrus

LC – locus coeruleus

LGN – lateral geniculate nucleus

NAcc – nucleus accumbens

NAd – noradrenaline

NTS – nucleus tractus solitarius

pACC – pregenual anterior cingulate cortex

PAG – periaqueductal gray

PBN – parabrachial nucleus

PFC – prefrontal cortex

pMCC – posterior midcingulate cortex

SC – superior colliculus

sgACC – subgenual anterior cingulate cortex

SMG – supramarginal gyrus

SN – substantia nigra

STG – superior temporal gyrus

Thal – thalamus

vAIns – ventral anterior insula

VTA – ventral tegmental area

5HT – serotonin

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