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Somatovisceral Influences on Emotional Development

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Abstract

Frameworks of emotional development have tended to focus on how environmental factors shape children's emotion understanding. However, individual experiences of emotion represent a complex interplay between both external environmental inputs and internal somatovisceral signaling. Here, we discuss the importance of afferent signals and coordination between central and peripheral mechanisms in affective response processing. We propose that incorporating somatovisceral theories of emotions into frameworks of emotional development can inform how children understand emotions in themselves and others. We highlight promising directions for future research on emotional development incorporating this perspective, namely afferent cardiac processing and interoception, immune activation, physiological synchrony, and social touch.

Keywords
emotion, development, autonomic nervous system, psychophysiology, interoception

Emotions play a critical role in shaping individuals' experiences, perceptions, and social interactions. Over the course of development, infants' and children's emotion experiences and understanding influence how they interact with and make predictions about their external environment (Buss et al., 2019; Frankenhuis, 2019). Likewise, children's external environments, through social interactions and relationships, affect how emotions are experienced and understood. Emotion understanding, or the ability to recognize and make inferences about one's own and others' emotional states (Box 1), in particular, is critical to effectively navigating one's social environment. Research examining the development of emotion understanding has focused on two primary questions: (1) at what stage of development can infants and children recognize and make predictions about emotions in others? (Hoemann et al., 2020; Ruba & Pollak, 2020); and (2) how do external environmental inputs, like parents' emotional expressions, influence the development of emotion understanding? (Hoemann et al., 2019; Pollak et al., 2019). Both of these approaches have highlighted the role of the external environment in shaping children's emotion understanding. However, emotion understanding is influenced by a complex interplay between both external environmental inputs and internal somatovisceral signals (Burleson & Quigley, 2019; Critchley & Garfinkel, 2017; Norman et al., 2014). Indeed, recent frameworks have proposed a need for examining emotional development in the context of other critical psychological processes, including motor development, cognition, language, and attention (Hoemann et al., 2020; Ruba & Pollak, 2020). In the current manuscript, we highlight afferent somatovisceral cues as another domain that can inform the development of emotion understanding.

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Box 1: What is Emotion Understanding?

Emotion processing refers to a multifaceted suite of psychological and behavioral subcomponents that have been defined and operationalized in a variety of ways (Barrett et al., 2019; Pereira et al., 2019). One such subcomponent is emotion understanding (also referred to as emotion knowledge or emotion reasoning), broadly defined as the ability to understand and make inferences about one's own and others' emotional states (Castro et al., 2016; Voltmer & von Salisch, 2017). Emotion understanding is tightly linked to social cognition and behavior. The ability to understand and reason about one's own and others' emotional states informs social behavior and inferences about others' social behavior (Olsson & Ochsner, 2008; Reschke et al., 2017; Spunt & Adolphs, 2019). It also underlies complex affective responses like empathy, which reflects the ability to perceive, understand, and respond to others' emotional states (Decety, Norman, et al., 2012). Despite the recognition that emotion understanding is one aspect of emotion processing, the ways in which it has been measured have not been consistent. Emotion understanding has been measured using tasks that assess a range of varying aspects including an individuals' ability to monitor and perceive their own internal states, distinguish their feelings from those of others, and recognize, interpret, and discriminate emotions in others (Grühn et al., 2013; Lagattuta & Kramer, 2021; Nummenmaa et al., 2012; Pollak & Kistler, 2002; Smith, Norman, et al., 2020). How emotion understanding is conceptualized also differs depending on the developmental stage being studied. Research on emotion understanding in adults has focused on both individuals' ability to monitor and represent emotions in themselves and recognize and understand emotions in others, along with their ability to distinguish their own feelings from those of others (e.g., Lane et al., 1990; Schlegel & Scherer, 2018; Skerry & Saxe, 2015). In contrast, studies with infants and children have focused primarily on their ability to recognize, label, discriminate, and make inferences about others' emotional states (e.g., Gagnon et al., 2010; Ruba et al., 2017; Smith, Leitzke, et al., 2020; Zieber et al., 2014). Afferent somatovisceral signals play a role in emotion understanding, being a critical aspect of one's ability to represent their own emotional and feeling states, but also influencing how an individual uses environmental information to represent the emotions of others (Garfinkel et al., 2014; Gray et al., 2010). Here, we focus on how somatovisceral afferent signals may influence this latter piece, given its prominence in the literature on emotional development. However, the ability to represent the emotions of others is linked to and likely affected by one's representations and regulation of their own emotion states.

Somatovisceral models of emotion describe how afferent signals from the periphery interact with circuits in the central nervous system (CNS) to influence both emotional states and emotion attributions (Burleson & Quigley, 2019; Norman et al., 2014). Somatovisceral afferents project information about the internal state of the body from the skin, joints, muscles, and viscera to the CNS (Cacioppo & Berntson, 1992; James, 1884). Bidirectional communication between the periphery and CNS, particularly, as it relates to emotion understanding, has only minimally been incorporated into research examining emotional development. Emotional responses in infants are thought to be primarily mediated by reflexive somatovisceral states, with a shift occurring as prefrontal cortical areas develop and start to exert increased regulatory control over peripheral systems (Decety et al., 2011; Quigley et al., 2021). Additionally, peripheral physiological states have been tied to experiences of negative and positive affect in both infancy and early childhood (Brooker & Buss, 2010; Buss et al., 2005; Shih et al., 2018). However, this research has primarily focused on how external information (e.g., caregiver interaction or fear-eliciting paradigm) changes internal states (e.g., heart rate and indices of parasympathetic and sympathetic activation). More research is necessary to understand how internal states, through afferent somatovisceral signals, influence children's experiences of emotions and how they perceive and interpret emotions in others (Koenig, 2020). In adults, there is extensive literature describing the influences somatovisceral information has on affective processes (Berntson et al., 2003; Harrison et al., 2010; Seth & Friston, 2016), including emotion understanding (Critchley & Garfinkel, 2017; Shah et al., 2017; Tsakiris et al., 2021). Integrating this perspective with research on emotional development could enhance understanding of children's affective responses and their perceptions of emotional information.

Here, we aim to unify a broad literature into a novel framework for understanding the role of afferent somatovisceral activity in children's emotion understanding. We apply an integrative lens to bridge across research assessing the role of external inputs in children's emotion understanding with research implicating a critical role for somatovisceral afferents in these processes. We start by reviewing somatovisceral models of emotion, illustrating how afferent signals, through central and peripheral somatovisceral signaling pathways, interact with external environmental influences to shape emotion experience and perception. We report the origins of this work in adults and outline the implications it has for understanding emotional development. We then examine evidence from the childhood literature suggesting that these afferent somatovisceral pathways play a role in the development of a number of emotion processes and that early environmental factors, particularly those related to safety, influence the development of these afferent somatovisceral pathways. We end by presenting illustrative examples of how a somatovisceral perspective could inform developmental research on emotion understanding. We discuss cardiac reflexes, interoception, the immune system, physiological synchrony, and social touch as areas of interest for current and future research investigating the role of afferent signals in emotion development. We highlight how incorporating a role for somatovisceral influences could inform and expand our understanding of emotional development.

Emotion Theories and Emotional Development

Dating back to William James (1884) and Walter Cannon (1929), theorists have disagreed about the structure of emotion and affective experience. These debates have centered on whether emotions are discrete experiences that are distinct in function and characterized by specific patterns of psychological and physiological activation (Ekman, 1992; Izard, 2007; Panksepp, 2005) or are constructed categories resulting from interpretations of diffuse psychological and physiological reactions to the environment, often posited to be organized along the dimensions of valence and arousal (Barrett et al., 2019; Posner et al., 2005; Russell, 2017). Evidence for each perspective is somewhat mixed (for review see Barrett et al., 2019; Hamann, 2012). Discrete views cite findings suggestive of coherent and specific patterns of peripheral physiological, neural, and behavioral patterns of activity associated with certain basic emotions in support of their perspective. For example, in meta-analytic studies, physical disgust has been linked to coactivation of parasympathetic and sympathetic cardiac outflow (Kreibig, 2010) along with high levels of co-occurrence with the expected stereotypical facial expression (Durán & Fernández-Dols, 2021). However, evidence is less consistent for other emotions (Durán & Fernández-Dols, 2021; Kreibig, 2010). Some studies using multivariate pattern classification to synthesize across autonomic or neural measures find unique multimodal constellations of activity for distinct emotions, potentially suggestive of discrete emotion experiences (Kragel et al., 2018; Kragel & LaBar, 2014, 2016). In contrast, dimensional and constructivist views point to meta-analytic evidence that suggests overlap in physiological activation patterns between different emotions (Kreibig, 2010; Siegel et al., 2018), overlap in neural circuitry across categories of emotion (Lindquist et al., 2012), and univariate pattern classifiers that suggest the categorization of neural responses is dependent on aspects of valence and arousal rather than the specific emotion category (Camacho et al., 2019; Chang et al., 2015). While there continues to be a discussion about the contextual, individual, and methodological factors that may play a role in these conflicting findings (Cacioppo et al., 2000; Critchley & Harrison, 2013), they suggest current frameworks may not adequately account for the range of variability in emotion experience and understanding.

In the field of emotional development, debates regarding the structure of emotion take the same basic form. Early theorists argued that emotions are discrete, characterized by stereotyped behavioral and physiological responses, and appear early in infancy and remain stable over the course of development (Izard, 2007; Oster, 1981). While many perspectives have moved away from a focus on emotions as stereotyped, preprogrammed responses (Camras & Witherington, 2005; Walle & Campos, 2012), research on emotional development continues to be grounded in discrete approaches; the focus has been on testing children's ability to recognize and label stimuli characteristic of a specific emotion (Barrett et al., 2019; Ruba & Pollak, 2020). Some of this evidence does indicate children can discriminate emotion categories early in infancy. Studies examining differences in looking times find that newborns appear to be able to discriminate happy from sad and fearful expressions (Farroni et al., 2007; Field et al., 1982, 1983) and 5-month-olds have been demonstrated to be able to discriminate happy from negative facial expressions (Bornstein & Arterberry, 2003; Kestenbaum & Nelson, 1990; Nelson et al., 2006). However, other research using similar paradigms has found different results. Some studies indicate there is minimal evidence for three- and four-month-olds being able to discriminate positive from negative facial expressions (Barrera & Maurer, 1981; Young-Browne et al., 1977) or that 4-month-olds may be able to discriminate multimodal happy expressions from anger and fear, but not sadness (Flom et al., 2018; Flom & Bahrick, 2007; Montague & Walker-Andrews, 2001).

Given these inconsistencies, dimensional approaches, especially constructivist theories, have garnered recent attention as having more explanatory power for how infants and young children understand emotions in others. Indeed, the results described above can be interpreted as supporting a dimensional viewpoint. Many of the studies that find evidence for infants' ability to discriminate different emotion expressions find that they are primarily able to discriminate expressions of different valences (i.e., positive from negative emotional expressions; but see Ruba et al., 2017; White, 2019 for contrasting viewpoints). In a constructivist perspective, infants and young children initially organize emotions along the dimensions of valence and arousal, with emotion categories gradually appearing as experience (e.g., exposure to emotion words) shapes category formation (Barrett, 2017; Hoemann et al., 2019). In support of this, evidence suggests that children group emotion words based on the dimensions of valence and arousal, rather than discrete emotion categories (Nook et al., 2017). However, other research indicates how children group emotion stimuli is primarily accounted for by valence, and less so by arousal or discrete emotion categories (Woodard et al., 2021). These inconsistencies together suggest a need for alternative approaches toward capturing emotion understanding in infants and children.

One limitation across both discrete and dimensional approaches towards emotional development is the focus on how external factors (i.e., emotion language exposure, caregivers, early environment) influence children's ability to discriminate and understand different emotion expressions. Recent frameworks proposing a need to consider emotional development in the context of other domains of development (i.e., motor, cognitive) have only minimally addressed how the development of afferent peripheral systems may play a role in children's emotion understanding (Barrett et al., 2019; Hoemann et al., 2019; Ruba & Pollak, 2020). Additionally, research assessing emotional development often implicitly creates a false dichotomy between emotion experiences and emotion understanding, studying one irrespective of the other. However, children's own emotional states, via somatovisceral afferent systems, likely interplay with higher level cognitive processes involved in emotion understanding, changing how children perceive and make inferences about emotions in others. The following section briefly reviews the somatovisceral afference model of emotion (SAME), highlighting how incorporating the influence of somatovisceral afferents may aid in understanding emotion development.

The Somatovisceral Afference Model of Emotion

The SAME (Cacioppo et al., 1992) proposes a framework through which ascending somatovisceral signals impact emotion processing and represents an alternative model to discrete and dimensional approaches that could provide further insight into how emotions and emotion understanding develop. This idea originated with William James, who described emotions as feeling that occurs during distinct bodily changes that follow the perception of an evocative stimulus (James, 1884). However, both discrete and dimensional theories of emotion have shifted away from a Jamesian view, in which emotion arises from the perception of bodily changes, toward a perspective in which emotions originate in the brain. While the CNS coordinates emotion responses, it is not solely responsible for eliciting emotional states communication and integration with peripheral signals also play a role. Indeed, over the last 20 years there has been a resurgence in research suggesting afferent signals from the periphery influence both emotion experiences and emotion understanding (Critchley & Garfinkel, 2017; Paulus & Stein, 2010; Seth & Friston, 2016).

The SAME provides a framework to conceptualize the impact of ascending somatovisceral signals on the experience of emotion while accounting for seemingly disparate features from other prominent emotion theories (i.e., discrete; dimensional/constructivist) (Cacioppo et al., 1992). The SAME asserts that somatovisceral afferents impact emotional processes along a continuum (Cacioppo & Berntson, 1992; Norman et al., 2014). On one end, ascending somatovisceral cues are recognizable as emotion-specific patterns. For example, research on respiratory patterns associated with certain emotions has shown that there is some consistency between persons in the breathing rhythms that are linked to specific emotional states (Boiten, 1998; Jerath & Beveridge, 2020; Noguchi et al., 2012). Furthermore, practicing distinct breathing patterns has been shown to induce specific emotional states (Philippot et al., 2002). On the other end of the SAME continuum, somatovisceral afferents can be undifferentiated and require interpretation through active cognitive and perceptual processes that are influenced by context. A classic illustration of this type of emotional experience comes from Schachter and Singer's (1962) study in which they administered epinephrine to participants and found that the resulting feelings of arousal were attributed to different emotions (anger or elation) depending on context. Here, vague somatovisceral patterns are still influencing emotion states; but, they necessitate cognitive evaluation to disambiguate the signal and determine the specific emotion being experienced.

A key contribution of the SAME is that it acknowledges that individual variation in psychobiological traits and prior experience can impact somatovisceral signals and how they are interpreted. Emotion states in a given moment are subject to comparison to similar circumstances in the past. Further, the pathways enabling communication between somatovisceral signals and the CNS are shaped by experience, which, in turn, affects the perception and regulation of somatovisceral signals in the future. In this way, somatovisceral afferents are integrated with existing information in the CNS, and subsequently impact emotional processes through descending regulatory circuits that can modify ascending signals (Burleson & Quigley, 2019; Cacioppo & Berntson, 1992; Norman et al., 2014). Ongoing calibration of emotion perception and regulation by somatovisceral afferents, as well as through interoceptive awareness of those afferents, suggests that the integration of subjective and physiological information plays a central role in how individuals perceive and interact with their environments. However, we still understand relatively little about how this integration occurs early in development.

Central Processing of Somatovisceral Signals

Somatovisceral pathways connecting the brain and body use both humoral and neural signals (Critchley & Harrison, 2013; Figure 1). Afferents carry information about peripheral states via the cranial nerves and project to the brainstem, specifically to the nucleus tractus solitarius, medulla, and midbrain which output to the thalamus and, subsequently, to cortex (Smith et al., 2017). Importantly, as somatovisceral signals ascend the neural hierarchy, they become increasingly integrated with other afferent information. The cortical region arguably most involved in this integration is the insular cortex, which receives input from all afferents. Patients suffering lesions to the insula, as well as disruptions to peripheral afferent mechanisms like those with autonomic failure or sympathectomies, have shown deficits in emotional processing, sometimes described as an affective numbness (Berntson et al., 2019; Goldstein, 2012), further linking somatovisceral afference to emotional experience.

The mechanisms regulating afference are additionally subject to top-down control through the Central Autonomic Network (CAN). The CAN consists of multiple interconnected cortical areas including the insula, medial prefrontal cortex (mPFC), orbitofrontal cortex, and anterior cingulate cortex (ACC), as well as limbic regions like the amygdala and hypothalamus (Benarroch, 1993; Koenig, 2020). The CAN regulates the sympathetic nervous system (SNS) and parasympathetic nervous system (PNS) branches of the autonomic nervous system (ANS) through monosynaptic projections to the brainstem regions described above. These branches then dually innervate most organ systems in the body and permit rapid

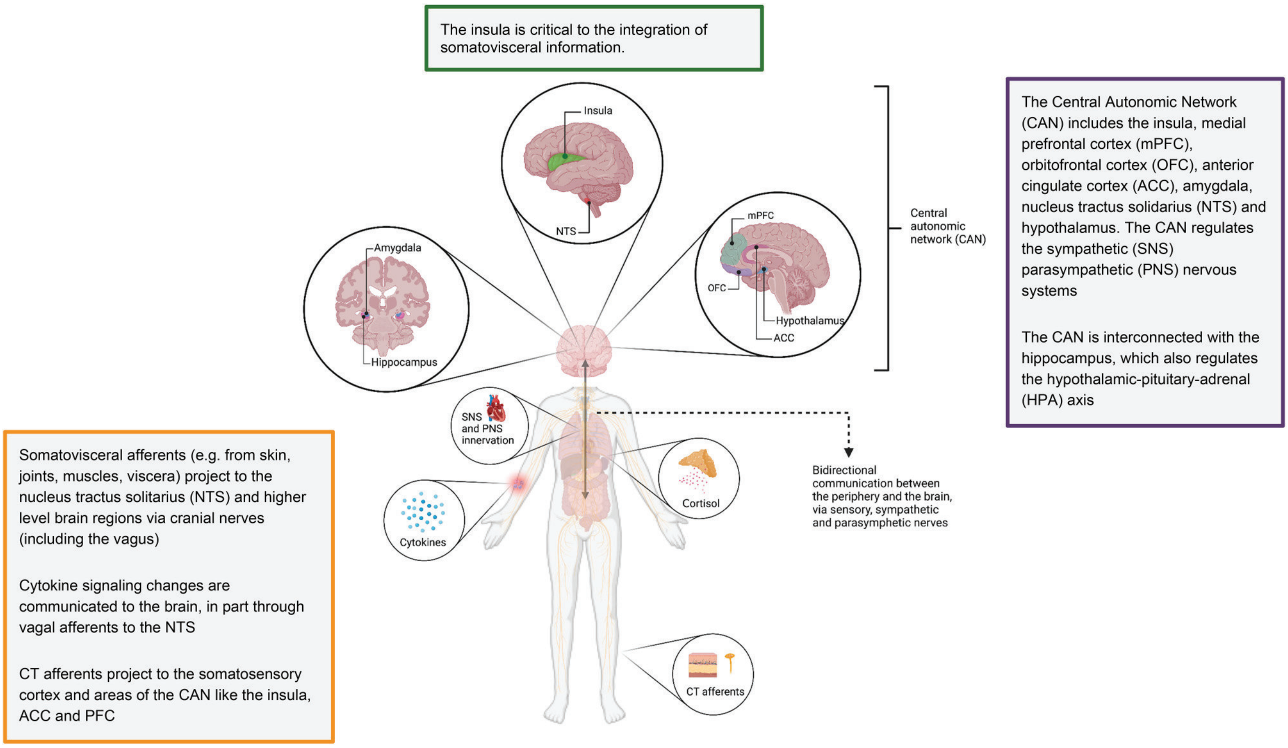

Figure 1. An overview of the central and peripheral pathways involved in the integration and processing of somatovisceral signals.

communication between the periphery and the CNS (Berntson et al., 2017; Ding et al., 2020). ANS activation during a typical stress response shows a stereotypical pattern with SNS cardiac outflow increasing and inversely, PNS cardiac outflow decreasing (Berntson et al., 2017). When these patterns of ANS functioning occur at rest, they have been associated with negative affect (Balzarotti et al., 2017; Bleil et al., 2008; Friedman, 2007). However, fear is also associated with immobilization and high PNS outflow by way of amygdala projections to the periaqueductal gray (Roelofs, 2017), highlighting the complexity of mapping specific emotions to peripheral states. In a more general sense, measures of SNS excitation and PNS inhibition have been shown to reflect activity in the CAN (Porges, 2011; Smith et al., 2017). The CAN is additionally connected to the hippocampus, which plays a role in regulating hypothalamic-pituitary-adrenal (HPA) activity and cortisol production (Gunnar, Doom, et al., 2015; McEwen, 2007). The integrative nature of the CAN in coordinating humoral and neural afferents, as well as efferent signals, is essential to emotion because it permits parallel processing across multiple levels of the neuraxis. Synergistic processing of interoceptive and exteroceptive sensory systems by the CAN allows for rapid perception and regulation of emotions (Benarroch, 1993; Norman et al., 2014). Adapting to dynamic contexts requires continuous updating of circumstances and expectations in concert with an individual's current needs and motivations. The distributed nature of inputs and outputs to the CAN provides a framework by which subjective and physiological aspects of emotions affect one another and interact with the environment (Berntson et al., 2012). This highly interconnected neural architecture results in emotions being continuously coordinated with changing motivations, external factors, and somatovisceral environments.

A Role for Somatovisceral Afference in Emotional Development

Research has identified a number of neural mechanisms involved in developmental changes in emotion processing across childhood and adolescence. Many of the brain areas implicated in emotional development overlap with the structures of the CAN, suggesting a tight link between emotional development and coordination of somatovisceral inputs. In particular, CAN structures including the mPFC, cingulate cortex, and amygdala, along with peripheral systems such as the ANS, experience rapid growth and development during infancy and early childhood (Hill et al., 2010; Levitt, 2003; Porges & Furman, 2011) and are associated with developmental changes in emotion processing (for review see Callaghan & Tottenham, 2016; Casey et al., 2019).

The amygdala undergoes extensive structural and morphological changes during the first 2 years of life and is thought to be critical to early emotional responding. Research finds strong amygdala reactivity to emotional stimuli in childhood, which gradually decreases across adolescence and into early adulthood (Decety, Michalska, et al., 2012; Gee, Gabard-Durnam, et al., 2013; Vink et al., 2014). In contrast, prefrontal cortical areas, which play a critical role in executive functioning and self-regulatory processes along with complex emotion processes, including emotion regulation, learning, and understanding, are slower to develop (Gee et al., 2018; VanTieghem & Tottenham, 2018; Zhang et al., 2019). Decreases in amygdala responses to emotional stimuli during adolescence and early adulthood are paralleled by increases in reactivity in prefrontal regions, particularly the mPFC and ventro mPFC (vmPFC) (Decety, Michalska, et al., 2012; Gee, Gabard-Durnam, et al., 2013; Vink et al., 2014). During this period, shifts in amygdala-prefrontal connectivity also occur, with connectivity during passive emotion viewing moving from a positive functional connection (from amygdala to PFC) in childhood towards a negative one in adolescence (Gee, Humphreys, et al., 2013). These changes in connectivity are suggestive of increased inhibition of the amygdala by the prefrontal cortex, and have been linked to increased emotion-regulatory abilities (Gaffrey et al., 2021; Silvers et al., 2017).

While little research has examined how these neural changes are related to the processing of afferent somatovisceral information, evidence suggests afferent signaling is a critical component of infants' and children's early emotion responding. Processing of afferent signals by the brainstem and amygdala in infancy and early childhood facilitates reflex responses that coordinate distress reactions in the context of hunger, discomfort, and pain, as well as relaxation in the presence of satiation, caregivers, and safety cues (Hostinar & Gunnar, 2013; Porges, 2011). In particular, the ANS is thought to play a critical role in both communications of afferent information from the periphery and facilitation of these reflex responses. The vagus nerve of the PNS has been linked to the regulation and coordination of feeding, breathing, and vocalizing, among other essential life processes (Porges & Furman, 2011). There is also evidence that the ANS undergoes a number of structural and functional changes during early childhood which parallel alterations in the amygdala and PFC. Longitudinal studies found increased engagement of the PNS during the first 5 years of life (Alkon et al., 2011; Harteveld et al., 2021). This period is also characterized by changes in patterns of ANS reactivity. Research suggests that typical infants (< 2 years) demonstrate sympathetic dominance which gradually transitions to parasympathetic dominance, characterized by rapid withdrawal of PNS inhibition during stress or challenge by 3 years old (Stephens et al., 2021; Zeytinoglu et al., 2020). These changes in ANS functioning are thought to at least partially reflect the coordination of autonomic and brainstem reflexes with developing cortical areas, like the medial PFC, involved in cognitive and affective regulatory processes that enable social engagement (Porges, 2011). Indeed, changes in ANS functioning during development, particularly increased regulation of the SNS by the PNS, have been linked to the same emotion and self-regulatory processes as the prefrontal cortex (Beauchaine et al., 2007; Calkins, 2013; Roubinov et al., 2021). Together this suggests a tight developmental link between central systems and peripheral systems critical to both emotional development and afferent processing.

Early Experience Shapes Emotional Development Through Changes in the CAN

Further evidence for the utility of a somatovisceral perspective comes from research finding that early experiences with threat and safety in the environment, especially those related to caregiving, play a role in the development of inhibitory circuits associated with social and emotional outcomes (Gunnar, Hostinar, et al., 2015; Sanchez et al., 2015; Sullivan & Opendak, 2020). Indeed, in rodent pups and nonhuman primate infants, early maternal presence engages the vmPFC and ACC, which down-regulates amygdala and HPA responses to threats in the environment (Courtiol et al., 2018; Opendak et al., 2019). In children, parental presence is linked to dampened cortisol responses (Hostinar et al., 2015; Seltzer et al., 2010) and amygdala reactivity to stress (Gee et al., 2014) as well as reduced fear of stimuli previously associated with threat (Tottenham et al., 2019). Disruption of typical early caregiving inputs appears to result in reduced inhibition of amygdala and HPA circuits by the prefrontal cortex (Debiec & Sullivan, 2017; Gunnar, Hostinar, et al., 2015). Rodent pups and infant primates reared by an abusive mother demonstrate hyper-reactivity of the HPA-axis and altered structure and function of the amygdala and prefrontal cortex (Nephew et al., 2017; Rincón-Cortés & Sullivan, 2016; Spinelli et al., 2009). In humans, early maltreatment is associated with altered prefrontal-amygdala connectivity, especially when viewing emotional stimuli (Fan et al., 2014; Gee, Gabard-Durnam, et al., 2013; Herringa et al., 2013). This body of literature indicates early environmental influences, particularly those linked to caregiving, shape the development of the cortical and subcortical circuits, like the CAN, involved in the processing of somatovisceral afferents.

These neural changes related to early caregiving experiences have been associated with both children's emotional responding and how they perceive and interpret emotions in others. In children exposed to maltreatment, reduced prefrontal-amygdala connectivity is linked to increased sensitivity and attention to cues of threat in the environment (VanTieghem & Tottenham, 2018; Wolf & Herringa, 2016). For example, children exposed to physical abuse identify anger in facial expressions faster and earlier than nonmaltreated peers (Pollak & Sinha, 2002; Shackman & Pollak, 2014). They are also more likely to perceive anger in emotional situations, as early as preschool age (Pollak et al., 2000). In children exposed to early maltreatment, reduced PFC-amygdala connectivity also mediates the relationship between maltreatment and anxiety and depressive symptoms (Herringa et al., 2013; Pagliaccio et al., 2015). These results are typically interpreted as early external factors shaping the development of central neural circuits critical to emotional responding and processing. These neural regulatory changes, in turn, can shift how children perceive and respond to emotional information in their future environments (Pechtel

& Pizzagalli, 2011; Smith & Pollak, 2020). In this interpretation, peripheral reactivity to emotional stimuli is modulated by descending CNS projections that have been shaped by prior experience. However, this focus on top-down regulatory mechanisms could be expanded to study how caregiving relationships shape afferent signaling, and in turn, how somatovisceral afference influences emotion understanding in others.

Central circuits shaped by early experience are also critical to the integration and processing of afferent somatovisceral information (Smith et al., 2017; Thayer & Lane, 2009). This overlap suggests that these early influences may additionally impact how ascending somatovisceral information from the periphery is processed. Early caregiver relationships are thought to play a critical role in moderating the development of the vagus nerve, described above as a key mediator of afferent signals from the periphery to the CNS through coordination with regulatory cortical areas (Porges & Furman, 2011). This is indicative of the role for caregiver influence on somatovisceral pathways.

The bulk of research on the effects of early experience has focused on how experiences related to external environmental inputs (i.e., differences in caregiving and exposure to potentially stressful events) shape brain development in ways that have implications for emotion processing. To date, there has been little research directly examining whether afferent somatovisceral signals influence how infants and young children perceive and experience their emotional world. However, research with non-human animals suggests that afferent vagal signals may play a role in changes in PFC-amygdala activity and connectivity (Seryapina et al., 2017). Additionally, a study of infants with cardiac abnormalities found that they showed delayed structural brain maturation (Licht et al., 2009). One proposed mechanism for these delays is altered afferent signaling (Wernovsky et al., 2005), particularly from the vagus (Koenig, 2020). While much more research examining the development of central and peripheral systems, especially how afferent signals are processed and shape brain development, is needed, this work is suggestive of a role for early afferent signals shaping emotional development through changes in the PFC and amygdala. Below, we highlight four lines of investigation that suggest that incorporating a role for somatovisceral afferent influences on emotional development can inform how children perceive and understand emotions. These include research examining the relationship between emotional processing and afferent cardiac signaling and interoception, immune activation, physiological synchrony, and social touch.

Afferent Cardiac Influences on Emotional Processing and Interoception

In adults, there is evidence that afferent cardiac signals influence both an individuals' own emotion experiences and how they understand or make inferences about emotions in others. For example, variability in blood pressure has been linked to differences in physical (Delgado et al., 2014; Makovac et al., 2020) and social (Inagaki & Gianaros, 2022) pain sensitivity and depressive symptoms (Montano, 2020). In children and adolescents resting blood pressure has been associated with differences in anger expression and regulation (Ewart & Kolodner, 1994; Howell et al., 2007; Starner & Peters, 2004), as well as other positive and negative mood states (Meininger et al., 2004). In adults, having high blood pressure, even within a nonclinical range, is associated with poorer recognition of emotion in others (McCubbin et al., 2011, 2014; Shukla et al., 2019). These effects are thought to be at least partially mediated by afferent cardiac signals from baroreceptors, a mechanoreceptor critical to the regulation of blood pressure (see Box 2; Herrmann-Lingen & al'Absi, 2018; McCubbin et al., 2011). In support of this, evidence suggests that individuals respond to and interpret emotional stimuli differently during baroreceptor activation. For example, administering painful stimuli during the phase of the cardiac cycle that coincides with afferent cardiac signaling by the baroreceptors (ventricular systole) results in reduced ratings of pain and dampened nociceptive responding (Edwards et al., 2003; McIntyre et al., 2008). Additionally, individuals demonstrate enhanced detection and perceived intensity of fearful faces (Critchley & Garfinkel, 2017), higher perceived intensity of disgust faces (Gray et al., 2012), and improved conditioned fear learning and memory (Garfinkel et al., 2021) when stimuli are presented during baroreceptor activation. Together, this body of work points to a role for afferent cardiac signals in shaping how individuals experience and understand emotions in others.

Box 2: Afference, Baroreceptors, and Blood Pressure

The baroreceptor reflex is an afferent mechanism that helps to stabilize blood pressure (BP) during shifts that occur due to posture, behavior, and environmental stimulation, among other influences (for overview see Berntson et al., 2019; Feher, 2012). As a mechanoreceptor, it responds to stretching of the arterial wall (indicative of raised BP) by intensifying PNS inhibitory cardiac outflow and reducing SNS cardiac excitation, which returns BP to a more typical range. This occurs through an automatic brainstem circuit involving several medullary nuclei of the CAN that regulate PNS and SNS activity. Baroreceptors project afferent signals each time the heart pumps blood through the aorta to the body, momentarily increasing arterial stretch and pressure. In addition to facilitating the regulation of BP, baroreceptor activation has been linked to shifts in emotion perception and understanding (Edwards et al., 2003; Garfinkel & Critchley, 2016; Gray et al., 2012; McIntyre et al., 2008). These effects are thought to be partly a result of baroreceptor afferent triggered changes in PNS and SNS activity (Herrmann Lingen & al'Absi, 2018; McCubbin et al., 2011). While more research is necessary to clarify the mechanisms through which baroreceptor activation influences emotion understanding, this body of work points to a role for afferent cardiac signals in shaping how individuals experience and understand emotions in others.

The effects of afferent cardiac signaling on emotion understanding appear to be additionally modulated by an individual's own sensitivity to internal afferent signals.

Interoception refers to the ability to sense and perceive afferent somatovisceral signals from the periphery (Azzalini et al., 2019; Critchley & Garfinkel, 2017). There continues to be debate about how to best define and measure interoception. Much of the research has focused on how accurate individuals are at detecting and tracking internal bodily sensations, like their heart beat, which is referred to as interoceptive accuracy (Garfinkel et al., 2015). Individuals with greater interoceptive accuracy perceive emotional stimuli to be more arousing than those with lower interoceptive accuracy (Dunn et al., 2010; Köteles et al., 2020). Further, interoception appears to affect how emotional responses are regulated. Individuals with higher interoception, measured in a variety of ways, show a greater capacity to cognitively reappraise or suppress emotions (Füstös et al., 2013; Kever et al., 2015; Schwerdtfeger et al., 2019). These effects can be interpreted within a predictive coding framework, in which the automatic generation of probabilistic expectations about internal and external stimuli is thought to play a critical role in defining emotion states (Ainley et al., 2016; Barrett, 2017; Barrett et al., 2016). Poor integration of unexpected interoceptive and exteroceptive information with one's predictions may contribute to individuals with lower interoceptive sensitivity demonstrating decreased emotion regulation and reduced sensitivity to afferent effects on emotion understanding. Ongoing calibration of emotion perception and regulation by somatovisceral afferents, as well as through interoceptive awareness of those afferents, suggests that the integration of subjective and physiological information plays a central role in the development of emotion understanding.

While there are minimal studies directly examining the influence of afferent cardiac signaling and variability in sensitivity to those signals on children's emotion experiences and understanding, there is some evidence for similar effects in infants and children (for review see Fotopoulou & Tsakiris, 2017; Murphy et al., 2017). Inducing states of stress, which results in changes in peripheral states that reduce the time between baroreceptor afferent cardiac signals, is associated with changes in how children recognize and interpret emotions in others. In particular, acute stress shifts children towards categorizing morphed facial expressions on an anger-fear continuum as fearful rather than anger (Chen et al., 2014). This is similar to the findings described above of enhanced detection of fearful faces in adults when presentation coincides with afferent cardiac signaling.

There is also evidence suggestive of differences in interoceptive sensitivity contributing to children's emotion processing. Heartbeat-evoked potentials are event-related potentials time-locked to the heartbeat that is thought to index cortical processing of cardiac activity. These signals have been linked to interoceptive sensitivity in adults (Katkin et al., 1991; Pollatos & Schandry, 2004) and are apparent early in development (by 9 months; Fairhurst et al., 2014; Löken et al., 2009). Additionally, children with high interoceptive awareness demonstrate increased anxiety symptoms (Eley et al., 2004). Growing evidence also suggests interoceptive sensitivity in children is associated with emotional intelligence and perceptions of stress (Eley et al., 2004; Koch & Pollatos, 2014) as well as increased emotion regulation (Opdensteinen et al., 2021; Schaan et al., 2019). Together, this is suggestive of important individual differences linked to both afferent signaling and sensitivity to that signaling that may shape how children understand emotions in others. Research employing methods that involve presenting emotional stimuli at different phases of the cardiac cycle along with novel tasks aimed at assessing interoceptive sensitivity in infants and young children (see Maister et al., 2017; Schaan et al., 2019 for examples) could help better elucidate exactly how somatovisceral signals impact emotion understanding over development.

Early Experience, Immune Activation, and Emotional Processing

Immune signals from the periphery represent another critical source of somatovisceral afferent information. Peripheral immune activity has been implicated in altered emotional and motivational responding. Inflammatory proteins, like cytokines, become active during immune challenges, and also during stress. They communicate with the brain via a number of afferent pathways including activation of vagal and humoral pathways (see Dantzer, 2018 for review). In adults, this type of afferent immune signaling has been associated with motivational and affective shits, including increased negative affect, decreased social motivation, and altered emotion processing (Dantzer et al., 2008; Maydych et al., 2018; Murray & Schaller, 2016). There is also some evidence that peripheral inflammation changes how individuals perceive and interpret emotions in others. Peripheral inflammation is associated with delayed recognition of and lower intensity ratings of facial expressions typically associated with sadness (Piber et al., 2020). Inducing a peripheral immune response, via the administration of endotoxin, results in reduced accuracy in labeling emotions in faces (Moieni et al., 2015) and altered neural responding during an emotion recognition task (Kullmann et al., 2014). Together, this literature suggests peripheral inflammation is associated with motivational and affective shifts that have implications for emotion processing.

There is evidence for similar effects of afferent immune signaling on emotion processing in children. Disruptions of early parental relationships, studied through maltreatment or reported quality of parental relationships, have been linked to increased levels of peripheral inflammation in children (Fagundes et al., 2013; Hostinar et al., 2018; Kuhlman et al., 2017). This increased inflammation in turn is associated with processes critical to the ability to understand and interpret emotions in others. These include increased sensitivity to cues of threat in the environment through altered neural connectivity in emotion regulation networks (Nusslock et al., 2019). This suggests that one mechanism through which early experience may influence emotion understanding is via altered afferent immune signaling. Indeed, the neuroimmune network hypothesis (Nusslock & Miller, 2016) proposes that early stress creates a positive feedback loop that links emotional processes, low-grade inflammation, and physical and mental health outcomes through crosstalk between neural and immune systems. This model provides an example of how incorporating approaches that focus on the bidirectional interplay between somatovisceral and external input can advance our understanding of emotional development. However, this research is still relatively nascent (Hostinar et al., 2018; Kuhlman et al., 2019). There is a need for further work examining the mechanisms through which early experience influences immune functioning, and how immune functioning influences children's emotional outcomes, like emotion understanding.

Emotional Contagion and Physiological Synchrony

Emotional contagion, which refers to the automatic transmission of emotional states between individuals (Hatfield et al., 1994), is fundamental to social behavior and social connection, especially early in life. Emotional contagion serves as a fast and effective way to understand and respond to the emotional states of others (van Kleef & Côté, 2022) and has been demonstrated to be present in infancy and early development (Brown et al., 2017; Decety et al., 2016). Emotional contagion is thought to be, in part, facilitated by afferent somatovisceral signals and provides an illustration of how examining somatovisceral afference can inform emotional development. During emotional contagion, external stimuli such as others' emotional expressions influence the observer's internal environment by eliciting comparable physiological changes in their body (Behrens et al., 2020; Dimitroff et al., 2017), which may then facilitate a shared emotional state. Indeed, this physiological synchrony, or the matching of biological states between two individuals, has been demonstrated across the lifespan and linked to parallel changes in emotional and affective states (Davis et al., 2018; Palumbo et al., 2017). For example, individuals high in empathy who viewed videos of people experiencing stress demonstrated cardiac responses that correlated with those of the people undergoing stress on video (Dimitroff et al., 2017).

Emotional contagion and physiological synchrony are thought to aid in infants' and children's ability to perceive and understand emotional information in others, as well as their social behaviors (Olsson et al., 2018; Waters et al., 2014). Physiological synchrony between mothers and infants and young children has been demonstrated using heart rate (Waters et al., 2014; Woltering et al., 2015), vagal activity (Lunkenheimer et al., 2015), skin conductance (Ham & Tronick, 2009), temperature (Ebisch et al., 2012; Manini et al., 2013), and HPA responses (Hibel et al., 2014; Ruttle et al., 2011). Synchrony is particularly pronounced when mother and child are undergoing structured play or stressful interaction together as compared to free play (Davis et al., 2018; Palumbo et al., 2017). This synchrony has been demonstrated to impact subsequent emotional experiences. For example, the physiological synchrony of heart rate during a personally negative discussion between parent and child is associated with a greater ability to overcome negative emotions after the negative interaction (Woltering et al., 2015). Additionally, physiological synchrony measured using heart rate between mother and infant after the mother had undergone a stressful-negative event in the laboratory is associated with increased avoidance on the part of the infant (Waters et al., 2014). Together this literature suggests sharing of physiological states between social connections plays a role in influencing children's early emotional experiences and thus may shape the development of a range of emotional processes. Research examining physiological synchrony between parents and infants and young children and how it relates to how they perceive, interpret, and understand emotions in others could provide increased insight into how the parental child relationship shapes emotional development.

Social Touch and Shared Emotion States

Social touch provides a key illustration of how somatovisceral afference influences the sharing of emotional states (for review see Burleson & Quigley, 2019) and emotional development in general. Social touch from a trusted other activates unmyelinated C-tactile (CT) fibers that innervate the skin near hair follicles (Löken et al., 2009). This activation of CT afferent fibers elicits feelings of pleasantness (Löken et al., 2009; McGlone et al., 2014; Sailer et al., 2020) that have additionally been linked to increases in efferent vagal activity (Triscoli et al., 2017). CT afferents project to both the somatosensory cortex and areas of the CAN that are involved in affective processing and interoception (insular, anterior cingulate, and prefrontal cortices), further implicating this somatovisceral signal in emotional processing (Björnsdotter et al., 2009; Gordon et al., 2013). Social touch has also been demonstrated to facilitate physiological synchrony, which in turn, can alter emotional processes. For example, forearm stroking has been shown to increase synchrony measured through skin conductance responses in couples (Chatel-Goldman et al., 2014), which subsequently influenced pain sensitivity and empathy. Similar effects have been found for hand holding (Reddan et al., 2020), although the mechanisms for this are less clear; the palms of the hand have historically been thought to be devoid of CT fibers (Cruciani et al., 2021; but see Watkins et al., 2021 for evidence suggesting this may not be the case). Research showing that variability in individuals' touch preference and history shape the magnitude of their CT-elicited pleasantness ratings (Sailer & Ackerley, 2019) is furthermore suggestive of a developmental influence on this experience.

In infancy, social touch is a critical signal of support and safety (Colegrove & Havighurst, 2017; Thrasher & Grossman, 2019). In particular, touch between child and mother affects the transmission of emotion, and the maturation of the autonomic and CNSs (Butruille et al., 2017; Feldman et al., 2014; Feldman & Eidelman, 2003). Touch between infant and mother facilitates sharing of the negative emotions associated with stress from mother to infant (Waters et al., 2017). Depending on the external environment, infants/children may receive more or less social touch. For example, urban parents tend to spend less skin-to-skin contact time with their infants as compared to parents from rural areas (Keller et al., 2009) and there is evidence that the types of touch used to soothe infants may vary across cultures (Carra et al., 2014). In the same way that different types of parenting practices related to motor stimulation appear to have consequences for motor development (Karasik & Robinson, 2022), differences in the use of social touch may influence emotional development. Evidence suggestive of this comes from research on maternal depression. Depressed mothers engage in less social touch with their infants (Mantis et al., 2019), and maternal depression in turn has been linked to altered emotion processing in infants and young children (Astor et al., 2020; Bornstein et al., 2011; Meiser et al., 2015; Væver et al., 2015). While research on postpartum depression and altered emotion processing in infants and children has focused on the types of facial expressions infants are exposed to as a potential mechanism, it is possible alterations in other types of emotional inputs (i.e., social touch) also play a role via somatovisceral systems. Research in infants and young children examining the frequency of social touch, its relation to critical afferent pathways (i.e., ANS functioning), and its association with emotion understanding, could provide insight into how these afferents then affect emotional experience and development in stages of infanthood and childhood.

Conclusions and Future Directions

The human capacity to respond to a range of internal and external stimuli with immense flexibility is mediated at least partially by emotions. Here, we have proposed a novel theoretical framework for understanding emotional development, which incorporates a role for integration and coordination across somatovisceral and neural signaling pathways in the development of both emotion experiences and understanding in others. Prior work using both discrete and dimensional views of emotion has greatly illuminated our understanding of emotional development. However, these approaches may be too narrowly focused on how children recognize emotion categories in others, and how environmental influences alter neural regulatory mechanisms. Emotion understanding is a more dynamic process than measurement through the recognition of discrete face expressions, or even other types of emotional stimuli, indicates. Emotion experience and understanding depend not only on environmental inputs, but also on internal somatovisceral pathways between the brain and periphery, and in particular, on ascending signals. Recent work suggests that bidirectional influences between central and peripheral, namely vagal, systems impact the development of emotion regulatory processes (Koenig, 2020). Using frameworks of emotion understanding that are inclusive of dimensional/discrete approaches and peripheral-central crosstalk, like the SAME model, may aid in integrative expansions of this work.

Research across subfields of affective neuroscience, including interoception and psychoneuroimmunology, has demonstrated that somatovisceral afference affects emotion perception and experience. Additionally, these relationships vary developmentally with age; older adults demonstrate weakened sensitivity to somatovisceral afferent inputs (Mendes, 2010, 2016). However, to date, we know relatively little about how somatovisceral afference influences emotion processing in infancy and early childhood. Research on emotional development in children has focused on how external cues from the environment and caregivers shape central circuits essential to emotion processing. These circuits do indeed regulate peripheral activity and emotions through top-down mechanisms. But, they also process bottom-up, ascending somatovisceral signals and include neural inhibitory connections that control and moderate reflexes in infancy. Further, these circuits continue developing until young adulthood, suggesting that emotion understanding in children may be especially prone to somatovisceral influences.

Being able to make inferences about one's own and others emotional states is uniquely important for social species. Existing perspectives on emotion (discrete and dimensional models) do not appear to adequately account for the data; incorporating approaches and methods that could illuminate theoretical discrepancies can only advance our understanding of emotional development. Measures that can provide insight into somatovisceral afference, including electrocardiogram (for heart rate, PNS activity, and ventricular systole) and impedance cardiography or skin conductance (for SNS activity), are easily collected and less subject to data loss due to movement in young children and infants than many the neural measures (fMRI, fNIRS, EEG). Many markers of peripheral activity linked to somatovisceral afference, such as resting blood pressure and heart rate, are commonly collected in health-related settings, and collaboration could facilitate exploration of questions linked to the role of somatovisceral afference in emotional development. Utilizing these measures to further elucidate how somatovisceral afference influences children's emotion understanding, particularly related to interoception and afferent cardiac processing, ascending inflammatory signals, social touch, and physiological synchrony, represent potentially fruitful avenues for research aiming to advance understanding of emotional development.

Recent theoretical perspectives have proposed that emotional development is likely dependent on a broad range of other developmental competencies, including motor, language, and cognitive development (Hoemann et al., 2020; Ruba & Pollak, 2020). These perspectives propose that in order to understand how children recognize and interpret emotions in others, it is critical to move beyond infants' and children's performance on classic emotion recognition tasks to examine performance in the context of these other developmental domains. We suggest that somatovisceral afference represents an additional such domain, given its importance to affective functioning, the development of peripheral physiological systems, and communication with the CNS. Research aimed at elucidating how afferent somatovisceral signals influence infants' and children's emotion perception and experience, can provide a more comprehensive understanding of emotional development across the lifespan. This is not an easy task and requires integration across several subfields in psychology. However, we believe this type of multilevel integrative research can greatly inform our understanding of how children experience and develop emotions, and uncovering the mechanisms underlying these processes will allow for greater insight into how to support healthy emotional development in children in the future.

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