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The psychobiology of emotional development: The case for examining sociocultural processes

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Abstract

Psychobiological techniques to assess emotional responding have revolutionized the field of emotional development in recent decades by equipping researchers with the tools to quantify children's emotional reactivity and regulation more directly than behavioral approaches allow. Knowledge gained from the incorporation of methods spanning levels of analysis has been substantial, yet many open questions remain. In this prospective review, we (a) describe the major conceptual and empirical advances that have resulted from this methodological innovation, and (b) lay out a case for what we view as the most pressing challenge for the next decades of research into the psychobiology of emotional development: focusing empirical efforts toward understanding the implications of the broader sociocultural contexts in which children develop that shape the psychobiology of emotion. Thus, this review integrates previous knowledge about the psychobiology of emotion with a forward-looking set of recommendations for incorporating sociocultural processes into future investigations.

KEYWORDS

ANS psychophysiology, culture, emotion reactivity, emotion regulation, neurophysiology

1 | INTRODUCTION

Psychobiological techniques to assess emotional responding have revolutionized the field of emotional development in recent decades by equipping researchers with novel tools to quantify children's emotion reactivity and regulation. Knowledge gained from integration of methods spanning levels of analysis has been substantial, yet many open questions remain. In this prospective review, we first describe the conceptual and empirical advances that have resulted from investigations that have capitalized on these methodological innovations and forwarded our understanding of how emotion reactivity and regulation processes are implemented in the brain and reflected in downstream peripheral psychophysiology. As children are continually impacted by their sociocultural environments, in the second section of the paper we discuss the need for developmental affective neuroscience to focus empirical efforts toward understanding the broader cultural contexts in which children develop that shape the psychobiology of emotion. We review extant research from cultural neuroscience that has informed understanding of culture and biological interactions in shaping emotional responding, and we point out the gaps in current knowledge that could usefully be addressed with psychobiological methods. Throughout this review, we highlight how developmental psychobiological approaches provide complementary insight into behavioral approaches, by dissociating similarities and differences in emotional development across behavioral and biological levels of analysis. We end with two prospective recommendations for future research into the psychobiology of children's emotion reactivity and regulation: to integrate the cultural and developmental affective neuroscience perspectives, and to strive to create a representative and generalizable knowledge base. Specific directions for work in each of these areas are suggested, as a call to researchers to consider collecting, reporting, and potentially incorporating sociodemographic data in their experimental designs.

2 | EMOTION REACTIVITY AND REGULATION

Among the psychological processes that are the basis for smooth social interaction, emotion reactivity and emotion regulation play pivotal roles. Emotion reactivity refers to an individual's threshold, intensity, and duration of arousal (Rothbart & Derryberry, 1981). For instance, a child is thought of as being high on negative emotion reactivity if the child displays frequent, intense, and rapid distress responses to situations that are frustrating. A child's tendency to display negative reactivity may be observed in both social and nonsocial situations. In the context of a social interaction, such a characteristic response may be elicited and expressed in situations where the child is provoked, threatened, asked to share, or required to respond to any number of other social demands. Conversely, emotion regulation refers to the processes by which an emotional response is altered, maintained, or discontinued (e.g., Gross, 2015; Thompson, 2011). Research has shown that emotion reactivity and emotion regulation are overlapping but separable processes that differentially predict behavioral and psychological health outcomes (Cole, Martin, & Dennis, 2004; Davies, Sturge-Apple, Cicchetti, Manning, & Zale, 2009; Gross, 2015), and both carry important consequences for later functioning. Additionally, extant work demonstrates that the ability to manage emotion is needed to maintain healthy relationships (Blair & Raver, 2015) and foster social competence (Calkins, Gill, Johnson, & Smith, 1999). On the other hand, certain developmental disorders are marked by deficits in emotion reactivity and regulation, which influence the motivation and ability to respond to others' needs (Michalska et al., 2017; Michalska, Zeffiro, & Decety, 2016). Failure to acquire the skills required to manage emotional responses may lead to difficulties in social interaction (Calkins, 1994; Cicchetti, Ackerman, & Izard, 1995; Rubin, Coplan, Fox, & Calkins, 1995). For example, children who display aggressive behaviors toward their peers may do so because they have developed inappropriate strategies for regulating anger (Eisenberg, Fabes, Nyman, Bernzweig, & Pinuelas, 1994; Quiñones-Camacho & Davis, 2018). Understanding how these emotion reactivity and regulatory behaviors are implemented in the brain and reflected in downstream peripheral psychophysiology has been a major focus of the last few decades of research in developmental psychobiology.

3 | NEUROPHYSIOLOGICAL APPROACHES TO UNDERSTANDING EMOTION REACTIVITY AND REGULATION

The neurophysiological approaches that have been most usefully applied to the understanding of children's emotion reactivity and regulation in the recent history of this area of developmental science include event-related potentials (ERPs) and neuroimaging (functional magnetic resonance imaging/fMRI; functional near-infrared spectroscopy/fNIRS) techniques. The noninvasive nature of these methodologies has revolutionized researchers' ability to study neural processes and correlates of emotional behaviors in structured laboratory paradigms.

3.1 | Event-related potential (ERP) approaches

Electroencephalogram (EEG) provides a noninvasive measure of electrical activity in the brain that is recorded via scalp electrodes. The EEG signal is the result of the summation of synchronous firing of postsynaptic neuronal potentials (Davidson, Jackson, & Larson, 2000). Various measures of emotional functioning can be derived from the signal acquired from electrodes at specific scalp locations. The temporal resolution of EEG is one of the most notable benefits of this technique—responses are characterized very precisely, on the scale of milliseconds. One downside of this method is a lack of spatial precision, as it does not provide clear evidence of signal localization. Most relevant to our discussion of emotion reactivity and regulation is the computation of ERPs from the EEG signal, which has emerged as a valuable tool for assessing children's emotional responding during structured laboratory challenge tasks.

The continuous electrical changes in the brain that are captured by the EEG signal can be time-locked to specific events, like stimulus presentation, and the associated positive and negative voltage changes are known as ERPs. The late positive potential (LPP) is the ERP component that has been most robustly linked to emotional arousal/reactivity and regulatory processes (see Brooker et al., 2018 and Hajcak, MacNamara, & Olvet, 2010 for reviews that also describe the other ERP components implicated in emotional processes). The LPP is thought to reflect facilitated attention to emotion (e.g., Cuthbert, Schupp, Bradley, Birbaumer, & Land, 2006; Quiñones-Camacho, Wu, & Davis, 2018), is greater when viewing affective as opposed to neutral stimuli, and is modulated by deliberate attempts to regulate emotion (Foti & Hajcak, 2008; Hajcak, Dunning, & Foti, 2009). Thus, the LPP has been construed as a marker of emotion reactivity mechanisms (arousal resulting from exposure to evocative stimuli), and attenuation of LPP (e.g., reductions in LPP magnitude on "regulate" compared to "just view" types of trials) is thought to mark effective regulation of that reactivity/arousal. Limited research has examined the LPP in children and adolescents, but it has been established in children as young as 5 years (Dennis & Hajcak, 2009) and can be modulated by effective use of emotion regulation strategies (like reappraisal—thinking differently about one's emotions to reduce their intensity). For example, Babkirk, Rios, and Dennis (2014) showed that modulation of the LPP predicts emotion regulation strategy use in school-aged children, indicating that this ERP may be a neural marker of adaptive emotional development. The emotion regulation strategies children used during disappointing and frustrating laboratory tasks were observed, and the children who showed more reappraisal-related modulation of the LPP at age 5 were using more adaptive strategies to manage their disappointed and frustrated feelings both concurrently and 2 years later. Thus, researchers have taken advantage of the child-friendly noninvasiveness and temporal resolution of ERP techniques to begin to identify developmental change in early-emerging biomarkers of emotional arousal. In addition, investigations of the extent to which the LPP is modulated by active regulatory attempts give insight into children's broader emotional development. Though more work is needed to establish other emotion regulation processes (e.g., harmonious parent–child interactions, dynamic shifting between different emotion regulation strategies) that may also attenuate the LPP in childhood, ERPs represent a very promising psychobiological tool for clarifying the neural correlates of emotion reactivity and regulation.

3.2 | Neuroimaging approaches

Noninvasive neuroimaging techniques such as fMRI and fNIRS provide functional information that is complementary to ERPs and enables the study of the development of the brain's functional architecture. As with ERPs, neuroimaging approaches provide the unique opportunity to quantify neural underpinnings of online affective processes and assess emotional reactions directly, in real time, thus reducing biases from self-reports and retrospective recall (Michalska, Gardiner, & Hughes, 2018). The growing field of developmental affective neuroscience has capitalized on these techniques to begin to illuminate the neurobiological bases of children's complex emotional tendencies and abilities. Moreover, it has sought to elucidate early-emerging biomarkers of risk for affective disorders, including disruptive behavior disorder, conduct disorder and mood and anxiety disorders (Gold et al., 2016; Michalska et al., 2016; Michalska, Decety, Zeffiro, & Lahey, 2015; Wakschlag et al., 2017). Below we enumerate some of the strengths and limitations of neuroimaging techniques for the study of emotion reactivity and regulation.

3.3 | fMRI

fMRI measures changes in the local concentrations of oxyhemoglobin and deoxyhemoglobin (i.e., the blood-oxygen-level-dependent/BOLD signal) associated with neuronal activity through sensitivity to local changes in magnetic susceptibility (Ogawa et al., 1992). The prime advantages of fMRI include high spatial resolution (on the order of millimeters) and deep brain structure coverage, both of which have generated novel insights into the development of neural networks involved in emotion reactivity and regulation (Gee et al., 2013; McRae et al., 2012; Pfeifer et al., 2011). Among the main limitations, most relevant to developmental affective neuroscience are the very low tolerance of motion and high acoustic noise. For children, many aspects of participating in a neuroimaging experiment can be challenging and potentially more stressful compared with adults, as their capacity to regulate emotions is still developing (Luna, Garver, Urban, Lazar, & Sweeney, 2004). Thus, anxiety caused by the fMRI experiment itself may potentially cloud developmental neuroimaging data on emotion reactivity and may do so for some children more than others (Michalska, Gardiner et al., 2018; Pecukonis, Anderson, Sadikova, & Redcay, 2017; Shechner et al., 2013).

Another limitation is that fMRI is only an indirect measure of neuronal activity—the BOLD response is thought to be generated by excitatory synaptic activity (Logothetis, Pauls, Augath, Trinath, & Oeltermann, 2001) leading to localized changes in blood flow in response to glutamate release (Attwell & Iadecola, 2002). Importantly, the development of the neurovascular coupling mechanism or "hemodynamic response function" (HRF) is only partially understood (see Harris, Reynell, & Attwell, 2011 for a review). Thus, for task-based fMRI studies examining emotional processes early in development, one common concern is the potentially immature neurovascular coupling mechanism. The best ways to detect BOLD signal using task-based fMRI in young children remain an active area of research, but age-specific HRFs should at least be considered in developmental studies focused on infancy and early childhood (Arichi et al., 2012).

3.3.1 | Emotion reactivity

Neuroimaging investigations of emotion reactivity have focused on the neural underpinnings of children's responses to the emotions of others, either by using evocative stimuli that happen to be social in nature (e.g., facial expressions, scenarios depicting people) or in tasks designed to assess interpersonal dynamics. In most such paradigms, children are asked to observe images or short clips of people expressing various emotions, while lying inside a brain scanner and responding to explicit or implicit questions about their experience using a button box. This tradition established an important foundation of elemental emotional abilities, such as affective responsivity to (often negative or aversive) emotional faces. For instance, witnessing others in fear, pain, or distress elicits an automatic aversive emotional response and recruits brain structures engaged in experiencing nociceptive pain, including supplementary motor area (SMA), anterior insular cortex (AIC), and parts of the cingulate cortex (ACC) (Decety & Michalska, 2010; Michalska, Kinzler, & Decety, 2013). These responses in turn correlate with subjective experiences of emotion responsivity (Kanske, Böckler, Trautwein, & Singer, 2015, although see Michalska et al., 2013). As several key regions to understanding and experiencing emotions undergo considerable remodeling from childhood to adolescence, a few studies have captured continuous functional changes in this response across age. For example, one fMRI study examined age-related changes associated with reactivity to others in distress in participants from middle childhood to adulthood (Decety & Michalska, 2010). Results indicated that the younger the participants, the more strongly the SMA, posterior insula, and amygdala were recruited when they watched clips of people in distress. The degree of activation in posterior insula was inversely correlated with age, whereas a positive correlation with age was found in the AIC. The posterior insula receives interoceptive information from the body, via the ventromedial nucleus of the thalamus, such as pain, temperature, hunger, and thirst. Considerable evidence suggests that this activity is then re-represented in the AIC, where it is integrated with higher cognitions (Craig, 2003, 2004). Activation in the AIC correlates directly with subjective feelings from the body and with emotional feelings, thus positioning it as a hub for subjective emotional experience (Craig, 2004), a point to which we return later. In other words, what develops is children's ability to compute a higher order/cognitive representation of bodily activity related to feelings of distress and aversive affect.

Recent work examining emotional changes during development complements these findings by specifically addressing whether age predicts changes in the way children respond to both negative affective and neutral stimuli (Silvers et al., 2017a, 2017b). Focusing on the amygdala, implicated in the detection and responding to motivationally salient stimuli such as threats (Monk et al., 2008), this work documents that youth exhibit heightened emotion reactivity and bilateral amygdala recruitment not only to aversive but also to neutral stimuli, relative to adults. Thus, it appears that the amygdala, together with the posterior portion of the insular cortex (Decety & Michalska, 2010; Decety, Michalska, & Kinzler, 2011), exerts a stronger influence on emotional processing during development than adulthood (Casey, Jones, & Hare, 2008), potentially leading children to view emotional and nonemotional stimuli through a valenced lens. Alternatively, age-related changes in amygdala and insula reflect heightened attention and orientation toward social cues (Silvers et al., 2017a, 2017b). Taken together, this work suggests that emotion reactivity attenuates with age and that aversive affective cues are interpreted in increasingly specialized and cognitive ways across development.

3.3.2 | Emotion regulation

Brain imaging research has also sought to provide insight into the neural underpinnings of emotion regulation in childhood and adolescence by examining the effects of using specific instructed strategies to change emotional experience. Most of this work has focused on cognitive reappraisal, a strategy that involves reframing or thinking differently about a stimulus to change one's feelings. Though children can use and describe cognitive strategies like reappraisal from as young as 5–6 years (e.g., Babkirk et al., 2014; Davis, Levine, Lench, & Quas, 2010; Dennis & Hajcak, 2009), the ability to use them well continues to develop throughout childhood and adolescence (Dougherty, Blankenship, Spechler, Padmala, & Pessoa, 2015; McRae et al., 2012; Silvers et al., 2012). fMRI studies of emotion regulation strategy use have provided evidence of age-related changes in lateral prefrontal cortex (LPFC) recruitment (McRae et al., 2012), amygdala modulation (Pitskel, Bolling, Kaiser, Crowley, & Pelphrey, 2011), and more recently, the integration of these two components in the *ventrolateral PFC-amygdala pathway hypothesis* set forth by Silvers and colleagues (Belden, Luby, Pagliaccio, & Barch, 2014; Silvers et al., 2017a, 2017b). Future work in this area can build on these important insights about the neural patterns supporting emotion regulation to test additional aspects of regulatory skill beyond single strategies (e.g., examinations of flexible or dynamic strategy use across an unfolding event; Bonanno & Burton, 2013).

3.4 | fNIRS

Recent advances in applying functional imaging technology to infants, specifically the advent of functional near-infrared spectroscopy (fNIRS), have made it newly possible to study the very early developing brain at work. fNIRS is an optical imaging method that measures hemodynamic responses from cortical regions, enabling the localization of brain activation (Lloyd-Fox, Blasi, & Elwell, 2010). Other neuroimaging techniques that are well established in older youth and adults have been limited in their use with infants and very young children because of methodological concerns. For instance, fMRI data collection requires participants to lie motionless in a spatially confined, dark, and noisy tube for up to an hour, a task that is nearly impossible for very young children. While fMRI has been used with infants, this work is restricted to the study of sleeping or sedated infants. fNIRS is an excellent alternative approach for research with young children, because it can accommodate a large degree of motion, meaning that children are able to sit on their parent's lap and behave normally while stimuli are presented. Moreover, unlike fMRI, fNIRS systems are portable, which means that studies of children's emotional responding in more naturalistic evocative settings than can be approximated in the laboratory are possible. One limitation of fNIRS, however, is its limited spatial resolution and reach—it cannot collect responses from deeper (subcortical) brain structures and in this respect provides less information than can fMRI. However, fNIRS can measure localized patterns of hemodynamic responses in cortical regions, thus enabling comparisons with adult fMRI data in these regions (Grossmann, 2013).

In the last decade, there has been a surge of fNIRS studies with infants, including a number of studies that have looked at prefrontal cortex activation during a wide range of experimental tasks (see Grossmann, 2013 for a review). This work has shed new light on the developing functionality of the cortex at very young ages, suggesting functional specialization of the medial and lateral prefrontal cortex (PFC) much earlier in development than was previously thought. As noted above in our description of fMRI research on the neural patterns of activation that are implicated in emotion regulation, the LPFC region of the cortex appears to be responsible, at least in part, for emotion regulation. fNIRS studies have thus provided important knowledge about brain development in infancy and early childhood that other neurophysiological methods could not generate.

Recent fNIRS work has capitalized on the advantages of the technique to begin identifying the possible biological mechanisms that underlie emotion reactivity and regulation in childhood. Perlman, Luna, Hein, and Huppert (2014) used fNIRS to examine PFC correlates of frustration in 3- to 5-year-old children. Frustration was induced by a computer game paradigm in which the child won a prize that was later stolen from them by a dog. Specific patterns of cortical activation across the phases of the task were examined and revealed important cortical localization of emotion reactivity and regulation. More activation was detected in MPFC when the prize was obtained, whereas more activation was detected in the LPFC when children were frustrated by losing the prize, suggesting a specific role of the LPFC in emotion regulation.

A recent paper by Grabell et al. (2017) examined linkages between children's facial muscular movements and concurrent neural activation in an emotion regulation challenge context. Notably, this pairing of observable emotion behavior with concurrent neurophysiology is typically not available with neuroimaging techniques like fMRI, or if it is, the behavioral component of emotional responding (eye tracking, facial expressions) is constrained by requirements of the apparatus (move as little as possible). The 3- to 7-year-old children in this study completed a validated, frustrating computer task, while facial expressions and LPFC activation were recorded. Results showed that positive expressions accompanied by eye constriction during frustration were related to stronger LPFC activation. Mapping neural activation onto concurrent emotional expressions enables researchers to parse emotion regulatory neural processes from overt behavior, a long-standing methodological problem in this area. Thus, the integration of fNIRS with other methodological approaches to provide more comprehensive insight into the developmental processes at play represents a promising direction for future research into children's emotion reactivity and regulation.

4 | PSYCHOPHYSIOLOGICAL APPROACHES TO UNDERSTANDING EMOTION REACTIVITY AND REGULATION

The autonomic nervous system (ANS) has two coordinated branches that jointly support a wide range of functioning, including emotional responding. The parasympathetic nervous system (PNS) modulates the body's viscera and neuroendocrine systems to maintain homeostasis and self-regulation, and to promote recovery from a stressor or challenge. The sympathetic nervous system (SNS) mobilizes resources to meet environmental demands (Berntson, Quigley, & Lozano, 2007). Under conditions of immediate challenge, suppression of parasympathetic input to the heart may not be sufficient to enable adaptive responding, and thus, activation of the sympathetic system (equipping the body to respond to challenge by increasing heart rate and oxygen flow) is additionally necessary for response mobilization. In other words, both systems are activated by environmental stress or challenges, but serve distinct functions. Specifically, Porges' highly influential Polyvagal Theory (e.g., Porges, 2003, 2007, 2009) suggests that the PNS is responsible for social engagement processes, whereas the SNS is responsible for challenge-related responses (Dickerson & Kemeny, 2004).

The ANS is thought to play an important role in determining individual differences in the intensity and duration of emotional experiences, including how someone experiences or responds to an emotion (Porges, 2007). The physiological basis for effective emotion regulation may lie in the functioning of the parasympathetically mediated vagus nerve, which is also implicated in the control of attention, emotion, and behavior. Originating in several areas in the brainstem, the vagus is a family of neural pathways which enable bidirectional communication between the brain and internal organs. Multiple measures of peripheral physiological reactivity are directly influenced by cortical and subcortical brain regions, including posterior and anterior insula, anterior cingulate, and vmPFC (Michalska, Feldman et al., 2018). Thus, a common noninvasive psychophysiological metric of emotion regulation is respiratory sinus arrhythmia (RSA), which refers to the periodic fluctuations in heart rate that are associated with breathing (Shader et al., 2018). A growing body of research suggests that individual differences in RSA underlie regulatory behaviors (e.g., Beauchaine, 2001; Calkins & Keane, 2004; Hastings et al., 2008; Porges, 2007).

Respiratory sinus arrhythmia can be usefully leveraged as an index of emotional and regulatory function either as a measure of basal parasympathetic function (i.e., resting RSA) or reactivity to challenge (El-Sheikh, 2005; Wang, Lü, & Qin, 2013). Greater parasympathetic dominance over the heart while the individual is at rest is reflected in higher RSA and is generally associated with slower heart rate and dampening of the sympathetic nervous system's effect on the heart (Bell & Calkins, 2012). Higher resting RSA levels are related to the capacity to adaptively respond to challenge, better self-regulation, and more adaptive outcomes broadly construed (Calkins & Keane, 2004; Liew et al., 2010), including more positive and less negative affect, less emotion dysregulation, and greater use of more effective emotion regulation strategies (Calkins, Propper, & Mills-Koonce, 2013).

Greater RSA reactivity (e.g., a change from resting to task levels) under conditions of challenge is largely viewed as an adaptive response pattern (see Graziano & Derefinko, 2013, and Holzman & Bridgett, 2017 for quantitative reviews). For example, less pronounced RSA reactivity has been associated with poor emotion regulation and extreme emotional responses (Buss, Davidson, Kalin, & Goldsmith, 2004; Buss, Davis, Ram, & Coccia, 2017; El-Sheikh, Harger, & Whitson, 2001; Gentzler, Santucci, Kovacs, & Fox, 2009), whereas more pronounced RSA reactivity during challenges relates to more positive and less negative affect, less emotion dysregulation, and more effective emotion regulation strategies (e.g., Blandon, Calkins, Keane, & O'Brien, 2008; Calkins & Keane, 2004; Davis, Quiñones-Camacho, & Buss, 2016).

Hastings, Kahle, and Han (2014) provide an excellent review and synthesis of this literature with regard to how ANS physiology relates to children's emotional functioning and development. Some of the most exciting new work in developmental ANS physiology has centered on leveraging this noninvasive technique to clarify children's active emotion *regulation* processes (e.g., Buss et al., 2017; Hastings et al., 2008; Morales, Beekman, Blandon, Stifter, & Buss, 2014). For example, Davis et al. (2016) showed that RSA reactivity in the form of increased parasympathetic influence was detected among 5–6 year olds while they actively implemented emotion regulation strategies to regulate evoked sadness and fear, relative to children in a control group. In the context of an active emotion regulation challenge, thus, RSA reactivity characterized by augmentation was the more adaptive pattern (i.e., the pattern corresponding to active regulatory attempts). Buss et al. (2017) demonstrated that dysregulated fear, a form of temperamental fearfulness characterized by context-inappropriate fear (e.g., high fear in low-threat contexts; Buss, 2011; Buss et al., 2013), was associated with a distinct pattern of ANS physiology in fear contexts in toddlerhood and prospectively predicted later social wariness and withdrawal. This suggests that the neurobiological and psychophysiological underpinnings of dysregulated fear manifest in faulty emotion regulation processes that have been linked to the development of social anxiety symptoms—particularly when children encounter low-threat novelty and are actively trying to manage their outsized negative emotions.

Building on this and other ANS investigations that have revealed the connections between faulty emotion regulation and psychopathology, recent work has linked resting RSA and the repertoire of adaptive discrete emotion regulation strategies children know to distinct types of psychopathological symptoms in late childhood (Quiñones-Camacho & Davis, 2018). In this study, resting RSA was examined in relation to symptoms of externalizing, anxiety, and depression. Children's repertoires of adaptive discrete emotion regulation strategies (e.g., the number of different adaptive strategies they described to manage anger, fear, and sadness) were coded from their open-ended responses to an interview about their emotional experiences. Resting RSA interacted with child age to predict externalizing symptoms, such that lower resting RSA was associated with more externalizing problems for the younger children in the sample (7–8 year olds). The relation between resting RSA and anxiety, in contrast, was qualified by both child age and the repertoire of adaptive emotion regulation strategies children knew they could use to manage *fear*, specifically. Higher resting RSA was associated with fewer anxiety symptoms, but only for older children (10–11 year olds) with a larger repertoire of adaptive strategies they could draw upon to regulate fear. Of note, the studies described here represent an important new focus of empirical attention, as they share the goal of examining active emotion regulatory processes in real time, rather than mapping psychophysiological patterns to survey reports of general emotion regulation skill or children's strategy use tendencies.

Another promising direction for empirical investigations of emotional development using the ANS is to examine recovery processes in addition to initial resting baseline and reactivity measures. Kahle, Miller, Lopez, and Hastings (2016) examined children's sympathetic recovery from an anger provocation. The preschoolers in this study showed a general pattern of increased sympathetic activation in the form of pre-ejection period (PEP) reactivity to the provocation. The extended pattern of physiological change into the repair phase of the task, however, revealed considerable variability in children's recovery from the affective perturbation. PEP lengthening (indicative of decreasing sympathetic activation, an adaptive pattern of SNS function in the repair phase of the task) was positively associated with parent report of emotion regulatory abilities. This paper is one of the few investigations of ANS physiology that has directly examined sympathetic rather than parasympathetic processes and is notable for its focus on characterizing the *recovery* phase of the experience. Recovery processes may be especially important to understand for a complete picture of children's emotion regulation capabilities (see also Obradović, 2016), and much remains to be done with this avenue of inquiry.

5 | THE PSYCHOBIOLOGY OF EMOTIONAL DEVELOPMENT IS EMBEDDED WITHIN SOCIOCULTURAL CONTEXT

Importantly, laboratory-based paradigms like those discussed above may not always fully capture the complex processes involved in children's emotional reactions to everyday experiences, because these experiences are embedded in sociocultural contexts that are frequently not considered in the design of such paradigms. For instance, as every parent of a young toddler will attest, emotional competence has to be socialized (Eisenberg, Cumberland, & Spinrad, 1998) and norms about optimal emotional reactions vary, depending on the cultural desirability of each emotion (Kitayama, Mesquita, & Karasawa, 2006); socialization of emotional competence involves teaching children to align their emotional reactions with those norms (Tsai, 2007). Thus, sociocultural processes inevitably interact with biological factors such as brain maturation to shape emotional responses across development. Cultural neuroscience research builds on the foundations of affective neuroscience discussed above to acknowledge this interrelation of culture and biology, creating tasks that emphasize neurobiological phenomena across cultural contexts (Chiao et al., 2008; Moriguchi et al., 2005). This work has the potential to speak not only to the neural processes involved in the development of emotional responding but also to how cultural meanings, values, and norms might shape these processes. Next, we review recent empirical evidence of cultural variation in the neurobiological mechanisms underlying emotion reactivity and regulation, arguing that integrating the knowledge of cultural contexts into experimental research can provide more critical insights into the development of emotional states.

Developmental science has long recognized the need to situate our understanding of emotional processes and development within the sociocultural contexts of children's lives (e.g., Raver, 2004; Rogoff et al., 1993), and recent work has underscored the importance of considering cultural influences on children's emotional development (Chen, Zhou, Main, & Lee, 2015; Cole & Jacobs, 2018; Liew, Kwok, Chang, Chang, & Yeh, 2014). Despite these insights, research designed to clarify the impact of sociocultural processes on the psychobiology of emotional development has been scant.

Social experiences calibrate or "tune" the child's developing emotion reactivity and regulatory systems. For example, close relationships are implicated in interpersonal outcomes across the lifespan, from mother–infant emotional and biological synchrony (Feldman, 2007) to physical health concordance in long-married couples (Meyler, Stimpson, & Peek, 2007). Parents have notable influence on children's regulatory physiology, as documented in both animal and human models (e.g., Feldman, 2012, 2015 ; Parent et al., 2005). Parents' physiological states generally underlie their positive engagement with children, which supports children's physiological regulation (Moore et al., 2009). Through repeated interactions, parents and other social partners may socialize an adaptive style of physiological responsiveness in children. But, the social experiences that children have as they develop are likely to vary across cultural contexts, and variation in cultural expectations for caregiving affect when, how, and how often children are physically soothed, the way parents talk about and react to children's emotions, and the emotion regulation strategies that parents use, model, or endorse (e.g., Cole & Jacobs, 2018; Grabell et al., 2014).

Ensuring that scientific understanding of development generalizes to children residing in different sociocultural strata is the crucial next step for work in this area. To this end, we join other scholars of affective science in calling for greater attention to cultural processes in models of psychobiology, emotion, and development (e.g., Kim & Sasaki, 2014; Matsumoto & Hwang, 2012). Khan, Schmidt, and Chen (2017) recently articulated a developmental framework of the cultural neuroscience of emotion, adapted from Matsumoto and Hwang (2012) that provides a useful starting point to guide future research. In this review, they describe genetic and (where available) psychophysiological indices of cross-cultural emotion processes including shyness, aggression, and interpersonal emotion. These authors' focus on the three selected behavioral phenotypes of emotion processes and biological factors like temperament, genetics, and resting physiology provide insight into the trait-like or dispositional aspects of emotional reactions that are informed by culture and biology. Our review is a timely complement to this perspective, as our focus on different psychobiological techniques and different aspects of emotional development (i.e., reactivity and regulation) instead emphasizes the state-like aspects of emotional responding and their measurement. Both reviews point out the relative paucity of research into cultural or cross-cultural processes and call for specific integration of developmental considerations (e.g., age or developmental phase) to investigations of and reasoning about interactions between culture and biology. Thus, a clear direction for the next decades of research and theorizing about the psychobiology of children's emotional development is to carefully consider cultural processes that constrain, temper, or promote different patterns of reactivity and regulation.

6 | NEUROPHYSIOLOGY AND CULTURE

While affective neuroscience has significantly advanced our understanding of the neural systems involved in the development of emotion reactivity and regulation, there has been limited neuroscience research that has situated emotional experiences within a cultural context—particularly during childhood. This gap in knowledge is unfortunate, as cultural neuroscience can provide critical insight into the neural underpinnings (and downstream physiological correlates) of emotion reactivity and regulation. Specifically, culturally situated beliefs, values, and practices may influence how children experience, interpret, express, and control their emotions, shaping neurobiology, and behavior. Given that the neural systems underlying emotion can vary between cultures (Chiao et al., 2008; Hot, Saito, Mandai, Kobayashi, & Sequeira, 2006; Moriguchi et al., 2005) and that cultural values and norms can shape the regulation of emotions in behavioral and psychophysiological domains (Butler, 2011, 2015 ; Davis, Greenberger, Charles, & Chen, 2012; Grabell et al., 2014), the complex interplay between biological and cultural influences may not be fully represented in our current understanding of the neural bases of emotion reactivity and regulation.

As highly social beings, our lives are inherently intertwined with other people's, and culturally embedded situations that provide opportunity for social interaction shape the ways in which we experience and express our emotions toward others. Ethnographic accounts illustrate that there is substantial cultural variation in children's emotional environments across different populations (Lancy, 2015). From birth, caregivers interact with children in diverse ways across cultures: There is variability in both the degree and frequency to which emotions (Matsumoto, 1990) and arousal (Tsai, 2007) are displayed, and in the types of cues, caregivers use to respond to bids for attention (Kärtner et al., 2008; Kärtner, Keller, & Yovsi, 2010; Little, Carver, & Legare, 2016). Different interactional styles may reflect distinct child socialization goals (Steinberg, 2001; Tobin, Hsueh, & Karasawa, 2009). For instance, children respond differently to group consensus based on socialization practices that emphasize attention to social conformity versus individuality (Corriveau & Harris, 2010). Thus, implicit and explicit cultural messages strongly shape the way we learn to experience, express, and regulate emotion.

Cultural variation in neurobiological mechanisms may exist even in the absence of cultural variation at the behavioral level. In other words, people living in different cultural environments may develop distinct neural mechanisms that underlie the same observable behavior or recruit the same neural mechanism to varying extents during a task (Chiao et al., 2008). Recent neuroimaging work focusing on the role of culture in the experience of emotion makes the compelling argument that people learn the strength of their feelings based on the cultural messages they learn about expressing emotion (Immordino-Yang & Yang, 2017; Immordino-Yang, Yang, & Damasio, 2014, 2016). These messages about the display of emotion in turn putatively shape the actual embodied experience and expression of that feeling. In a series of experiments conducted with Chinese young adults in Beijing and American participants in Los Angeles, Immordino-Yang, Yang, and Damasio (2014), Immordino-Yang, Yang, and Damasio (2016) presented social stories meant to induce a range of emotional states of admiration or compassion inside an fMRI scanner, while concurrently collecting subjective reports of feeling strength and physiological recordings. While no group differences emerged in the strength of subjectively reported feelings or the magnitude of brain activation, the correspondence between them exhibited culture-specific patterns in dissociable portions of the anterior insular cortex (AIC), involved in proprioceptive awareness and embodied cognition (see Section 1). Specifically, in Chinese participants, the strength of their subjective feelings tracked response magnitude in the ventral portion of the AIC, whereas among American participants, subjectively reported feeling strength tracked fluctuations in the dorsal portion. Because of their dissociable afferent and efferent connections, ventral and dorsal portions of AIC support separable functions related to emotional processing: Ventral AIC subserves autonomic regulatory processes, whereas dorsal AIC subserves somatosensory processes. In other words, cultures that value greater emotional restraint, like China, differentially activate regions associated with regulating autonomic activity (ventral AIC) relative to cultures that value greater emotional expressiveness, like the United States (dorsal AIC). Of note, variation in activity in these subregions was not correlated with fluctuations in physiological activity, indicating that culture specifically influences the subjective construction of emotions.

Taken together, these data suggest that cultural differences in behavioral expressiveness norms may lead to variations in the subjective experience of emotions themselves, mediated by lower level emotion processing regions like the AIC. Though the expression of emotions is typically assumed to be a consequence of subjective emotional experiences, the relation between emotional experience and expression is most likely bidirectional. Given that emotional expressions can serve as feedback for emotional experience, cultural display rules may moderate response in brain regions associated with emotional experience. As a result, when encountering stimuli that induce admiration, compassion, or fear, members of cultures with adherence to strict display rules may exhibit differentiated reactivity in regions that process such emotional stimuli. These research findings are provocative in that they suggest that how our emotions are embodied critically pivots on cultural norms. They also raise the important question of how the construction of emotions unfolds during development, highlighting the need for future research to consider whether and to what extent cultural processes interact with age and developmental stage to shape children's psychobiological functioning.

7 | NEXT STEPS

We make two prospective recommendations for research into the psychobiology of children's emotion reactivity and regulation: integrate the cultural and developmental affective neuroscience perspectives, and strive to create a representative and generalizable knowledge base.

First, to consider the dynamic interaction of brain and culture across the lifespan, developmental researchers will need to consider trajectories of change and how development is implicated in the neurobiological embedding of culture (Hyde, Tompson, Creswell, & Falk, 2015). For instance, at what ages do different types of cultural experiences play a role in emotional learning and brain development and in what ways might the influence of cultural norms, practices and values be more or less plastic over time? Evidence from behavioral work has demonstrated that understanding of concepts like culture, race, and ethnic identity varies across development (Baron & Banaji, 2006; Rogers et al., 2012). Language acquisition is one prominent example of the role of development in the effects of culture and the brain (Kuhl, 2010). Another example, later in development, is the increased emotional sensitivity to social context in early adolescence. During this period, a new social phase emerges which is characterized by strong desire for integration with peer groups (Nelson, Jarcho, & Guyer, 2016; Nelson, Leibenluft, McClure, & Pine, 2005). Emotions, cognitions, and behaviors all shift from relatively nonspecific (e.g., not targeted toward individuals) play, toward peers and peer group acceptance. This tends to happen during early adolescence soon after puberty has begun (Blakemore, 2012; Blakemore & Mills, 2014; Crone & Dahl, 2012; Larson, Richards, Moneta, Holmbeck, & Duckett, 1996). Adolescents become highly sensitive to social cues (Nelson, 2017), and as a result, adolescent reward systems may be sensitized in the presence of peers (Chein, Albert, O'Brien, Uckert, & Steinberg, 2011), with peers, rather than parents, engendering distinct subcultural influences. Thus, in adolescence, peers may be a particularly salient cultural influence, especially as this is a period of greater brain maturation in the reward system (Hyde et al., 2015). Incorporating a developmental perspective to cultural and affective neuroscience would result in exciting new avenues of research inquiry and thinking. We call for carefully designed, prospective longitudinal research studies that follow individuals as they develop to better characterize whether and when cultural norms become embodied in children's affective psychobiological functioning.

Second, we see a need for researchers to make thoughtful choices about the inherent characteristics of the increasingly diverse populations they choose to study (e.g., Are participants bicultural, newly acculturated, born and raised in a minority culture?). Overlooking the heterogeneity of individuals' backgrounds and experiences as we consider psychobiological processes may obscure meaningful differences not only in risk profiles, but also in sources of yet-untapped or unrecognized strength. We encourage researchers to more thoroughly describe sample characteristics and report information about the emotional and psychobiological variables in their studies for different ethnic/cultural groups, to facilitate larger scale and aggregate (i.e., meta-analytic) approaches and accelerate understanding of these differences.

One shortcoming of the current cultural neuroscience work is that research to date has been limited largely to comparisons between East Asians and European Americans. While there is increasing recognition that non-Western interdependent culture is far from homogenous (Kitayama, Duffy, Kawamura, & Larsen, 2003; Kitayama, Ishii, Imada, Takemura, & Ramaswamy, 2006), this diversity has yet to be fully understood empirically in investigations of children's developing psychobiology and socioemotional functioning. It is necessary to begin to broaden knowledge beyond WEIRD (Western, Educated, Industrialized, Rich, and Democratic) samples of Western/American participants (Heinrich, Heine, & Norenzayan, 2010), and it is also important to be thoughtful about how best to isolate the cultural effects and processes of potential interest (e.g., Gatzke-Kopp, 2016).

As a first step toward establishing a complete, representative, and generalizable understanding of the developmental psychobiology of emotion reactivity and regulation, we suggest focusing research efforts on Latinx populations in the United States. The reasons for this recommendation are rooted in the changing demographics of the United States, the logistics of cultural assimilation pressures that Latinx families face (Kitayama & Salvador, 2017), and what we view as the transformative opportunities to identify emotional resilience processes that may be unique to this population (and that would be illustrated most effectively by combining behavioral and psychobiological techniques).

First, the Latinx population is the most rapidly growing today in the United States, but these children lag behind non-Latinx counterparts in education, mental health, and physical health without clear explanations as to why this is the case. This gap in our understanding of child development will only widen as the Latinx population continues to comprise a greater proportion of the US population. Second, emotion reactivity and regulation processes among Latinx children would be influenced by socialization of unique cultural norms including *respeto* (respect for elders), *familism* (importance of family), *simpatia* (agreeableness), and *personalismo* (valuing personal relationships; Campos & Kim, 2017; Carlo & de Guzman, 2009). These norms have particular implications for emotional functioning, as they emphasize expressive displays of personal charm, affability, and generosity as imperative within this group (Sanchez-Burks, Nisbett, & Ybarra, 2000). This indicates a putative culturally specific pathway to emotional resilience and adaptive functioning that has received very little attention and is not yet fully understood. Emerging research supports this endeavor, illustrating that among Mexican American adolescents, strong family values serve as a potential buffer of neurobiological risk for stress-related pathology (Fuligni & Telzer, 2013; Telzer, Fuligni, Lieberman, & Galván, 2013; Telzer, Masten, Berkman, Lieberman, & Fuligni, 2011). More broadly, understanding cultural influences on emotion neurobiology requires probing their connections with individuals' subjective experiences (Rogers et al., 2012).

Kitayama and Uskul (2011) have noted that through socialization, neural networks are plastically formed and modified through various rewards and reinforcements over time and become patterned after cultural beliefs, values, and practices. The emphasis on emotion expressivity that Latinx cultural norms encourage may be due in part to historically high levels of ethnic diversity in many Latin cultures (Rychlowska et al., 2015), which may have novel consequences for children's developmental trajectories as members of a particular cultural orientation (e.g., Rogoff et al., 1993; Rogoff, 2016). Measures of psychobiological functioning are particularly well suited to clarify whether, when, and how Latinx cultural norms mechanistically shape general healthy functioning (e.g., Ruiz, Sbarra, & Steffen, 2018) and emotion reactivity and regulation processes specifically. Our understanding of Latinx children's emotional development is still scant and preliminary, and is a pressing concern for future research endeavors within developmental psychobiology. Thus, we call for programmatic research on potential sources of psychological resilience, including family, peer, and cultural contexts.

8 | CONCLUSIONS

Our goal in this review was to illuminate both the unique opportunities and inherent limitations of taking a developmental psychobiological approach to the study of emotion reactivity and regulation. We believe that psychophysiology and neuroimaging provide a valuable complementary level of analysis to behavioral approaches to understanding emotional development. These techniques provide the unique opportunity to assess situational experience directly, in real time, and to potentially identify mechanistic overlap between psychological processes typically considered distinct. We see the opportunity for many exciting advances in knowledge that are just on the horizon. An interdisciplinary, developmental perspective on the psychobiology of children's emotion reactivity and regulation will forward scientific understanding by enabling the creation of innovative research protocols that align psychobiological measures with techniques for documenting subjective experiences, social relationships, and cultural contexts.

CONFLICT OF INTEREST

No conflicts declared.

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