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GETTING TO THE HEART OF CARDIAC AUTONOMIC BALANCE:

EXPLORING ANTECEDENTS OF HEALTH-PROMOTING AUTONOMIC FUNCTIONING AT AGE FIVE

A Dissertation in

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by

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ABSTRACT

Cardiac autonomic balance (CAB), which reflects joint influences of the sympathetic (SNS) and parasympathetic (PNS) nervous systems on the heart at rest, is a biomarker of pervasive public health problems in adulthood (Kemp & Quintana, 2013). Its components develop rapidly in infancy and stabilize by age five (Alkon et al., 2011). Individual differences in PNS functioning, which determines CAB in healthy adults (Cacioppo et al., 1994), have been linked with caregiving behaviors in infancy, including nutritive sucking, which may induce PNS reactivity and recovery (Quigley et al., 2017). Therefore, it is possible that early experiences lay the groundwork for later health by calibrating PNS components of CAB. In the present study, we sought to elucidate processes by which development of PNS tone in the first five years of life may give rise to health-promoting CAB at age five. Results indicated that, (H1) at age five, children who showed health-promoting low-SNS/high-PNS tones during recovery had shown relatively higher PNS tone beginning at four months and greater increases in PNS tone between 12 months and 4.5 years. From two weeks to four months, breastfed infants showed more PNS tone growth than non-breastfed infants. And, (H2), children who spent more time feeding at two weeks showed greater PNS recovery at five years than children who had spent less time feeding. Together, this suggests that feeding practices in the perinatal period may contribute to initiation of a developmental cascade: Establishment of high PNS tone prior to stabilization may afford space for PNS reactivity, limiting reliance on the more metabolically-costly SNS during self-regulatory development in early childhood (Kopp, 1982) and easing recovery. This developmental cascade may describe a process by which regulatory development in the first five years of life tunes the body and brain for physical and mental health in adulthood.

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Acknowledgments

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Introduction

Growing evidence suggests that children's early environments become biologically embedded in their regulatory physiology, with far-reaching implications for physical and mental health in adulthood (Del Giudice, Ellis, & Shirtcliff, 2011; Felitti & Anda, 1998; Shonkoff, Boyce, & McEwen, 2009). One possible biomarker of this embedding, cardiac autonomic balance (CAB)—which reflects the relative influences of the sympathetic (SNS) and parasympathetic (PNS) nervous systems on the heart at rest—underlies individuals' capacity to flexibly adapt during stress and social engagement. The SNS and PNS are central regulators of a variety of psychological and physical functions, including emotion regulation, the operation of most visceral organs, and systemic processes such as inflammation (Hall, 2015; Porges, 2007; Lim, Kim, Lee, & Namgung, 2016). Work has consistently found CAB to be a biomarker of disease and disorder that is detectable prior to symptom onset and that may mark the "final common pathway" linking mental and physical health (e.g., Kemp & Quintana, 2013; Thayer & Brosschot, 2005; Thayer & Lane, 2007).

Despite the clinical import of this construct, however, very little is known about its development. Existing work suggests that its components develop rapidly in infancy and stabilize by age five, concurrent with the emergence of social behavior and self-regulatory capacities (Alkon, Boyce, Davis, & Eskenazi, 2011; Calkins, 2011; Porges & Furman, 2011). Because the SNS and PNS are thought to be tuned by their use as children react to and recover from environmental demands, age-five CAB likely reflects biological embedding of earlier experiences (Berntson, Cacioppo, & Quigley, 1991; El-Sheikh, Kouros, Erath, Cummings, Keller, & Staton, 2009; Quigley & Moore, 2018).

In children growing up in low-risk, high-resource environments, age-five CAB may be determined primarily by PNS functioning. In one low-risk sample, resting heart rate was determined by the PNS and not by the SNS by age two (Buss, Goldsmith, & Davidson, 2005). By middle childhood, greater PNS than SNS influences on resting heart rate have been associated not only with greater capacity for behavioral self-regulation but also with mental and physical health (Beauchaine, 2001; Beauchaine & Thayer, 2015; Kemp & Quintana, 2013). Together, this work suggests that, to elucidate developmental antecedents of health-promoting CAB, it may be necessary to identify factors that contribute to this early-life PNS dominance.

The PNS may be particularly sensitive to environmental influences during its period of rapid development in the six months after birth (Massin & von Bernuth, 1997). During this time, normative increases in the PNS' regulatory capacities—likely promoted by parent influences on children's regulatory development (Field, Pickens, Fox, Nawrocki, & Gonzalez, 1995; Moore, Hill-Soderlund, Propper, Calkins, Mills-Koonce, & Cox, 2009; Propper et al., 2008; Quigley, Moore, Propper, Goldman, & Cox, 2017)—may initiate a developmental cascade (e.g., Masten & Cicchetti, 2010; Thelen, 2000): These increases in PNS tone, promoted by external regulatory resources, may confer expanded space for the PNS to react in response to environmental demands. This, in turn, may reduce reliance on more metabolically-costly SNS reactivity (Quigley & Moore, 2018; Wolff, Wadsworth, Wilhelm, & Mauss, 2012). While reliance on the SNS to respond to daily stressors and demands is associated with allostasis, ability to rely primarily on the PNS is thought to cultivate low-SNS/high-PNS CAB (Beauchaine & Thayer, 2015; Thayer & Brosschott, 2005). Therefore, in the absence of SNS-eliciting chronic or acute stress, infant-caregiver behaviors in the first months of life may initiate a health-promoting trajectory by tuning children's physiology to respond flexibly to and recovery efficiently from environmental demands relying primarily on the PNS.

Although a growing body of research has examined maturation of the SNS or PNS in isolation, as well as environmental correlates of SNS or PNS functioning (e.g., Bar-Haim, Marshall, & Fox, 2000; Bornstein & Suess, 2000; Oosterman, de Schipper, Fisher, Dozier, & Schuengel, 2010; Oosterman & Schuengel, 2007; for a review, see Propper & Holochwost, 2013), much less is known about factors shaping joint SNS-PNS functioning and, in particular, how development of one branch may influence not only its own later development but that of the other branch. Because the adult literature indicates that it is this *joint* functioning—apparent in CAB—which predicts risk and resilience, we took an initial step in the current study toward elucidating developmental processes that calibrate this dual-branch functioning. Using a longitudinal sample, we examined development of PNS tone from two weeks to 4.5 years, confirming and clarifying its longitudinal stability (Aim 1) and identifying periods of growth associated with joint SNS-PNS functioning at age 5.5 (Aim 2). We then sought to identify infant-caregiver behaviors that predicted those periods of PNS growth (Aim 3) or the SNS and PNS functioning thought to determine CAB at age 5.5 (Aim 4).

CAB as an outcome of joint SNS-PNS reactivity and recovery

To synthesize the diverse body of work on autonomic functioning and maintain clarity and consistency in the current paper, it is necessary to define three key constructs: tone, reactivity, and recovery. Levels of SNS or PNS activation at a given point in time are often referred to as SNS or PNS *tone*. While high SNS tone excites the heart (speeding heart rate), high PNS tone inhibits cardiac output (slowing heart rate). SNS and PNS tone when the organism is at rest—the measures contributing to CAB—reflect longer-term adaptations, or homeostasis. High PNS tone at rest is generally considered to be adaptive and may be an internal regulatory resource that confers ability to meet the particular demands of one's environment (e.g., Conradt, Measelle, & Ablow, 2013; Eisenberg et al., 2012; Sturge-Apple, Suor, Davies, Cicchetti, Skibo, & Rogosch, 2016; Thayer & Brosschot, 2005).

Consistent with the law of initial values, the resting tone of each branch determines that branch's capacity for *reactivity*, that is, the degree to which it can unilaterally excite or inhibit the heart (Hall, 2015). Reactivity, which reflects the difference between branch activation at rest (resting tone) and branch activation during an intra- or extra-individual perturbation (e.g., a somatic sensation, environmental stressor, or social demand), yields modulations in cardiac output characteristic of allostasis, or short-term adaptation to shifting conditions. Lastly, the degree to which a branch restores resting tone following perturbation is termed *recovery*. This reflects the difference between branch activation at rest and once the perturbation has passed. Patterns of SNS and PNS reactivity and recovery are thought to be perpetually modifying the resting SNS and PNS tones that jointly define CAB. Therefore, CAB is both the *product* of joint SNS-PNS reactivity and recovery and *sets the boundaries* of autonomic space within which each branch may react to demands (Fig. 1; Berntson et al., 1991).

The PNS is thought to have evolved in mammals to support the subtle, dynamic regulation necessary for social engagement (Porges, 2001), providing a sort of dimmer switch on the more metabolically costly fight-flight response of the SNS. Therefore, resting PNS tone is a regulatory resource that confers autonomic space to regulate via PNS reactivity; and reactivity patterns that involve PNS reactivity are likely to result in faster recovery of resting tones. Although some degree of SNS reactivity, in concert with PNS reactivity, is associated with strong emotion regulation in preschoolers (Stifter, Dollar, & Cipriano, 2011), relatively greater capacity for PNS reactivity has also been found to decrease individuals' reliance on the SNS to regulate (Wolff et al., 2012). Conversely, development of reactivity patterns that require the SNS to shoulder the regulatory burden may impede recovery and, over time, drive increases in resting SNS and decreases in resting PNS tones.

Through this process of reactivity and recovery, environmental conditions may become biologically embedded via SNS and PNS responses to the environment. In this way, CAB may reflect the ability to recover a calm state or protracted allostasis. Routinization of SNS and PNS reactivity patterns between six months and five years (Alkon et al., 2011) suggests that patterns of physiological regulation that are established in infancy and early childhood may have lasting effects on the functioning of regulatory physiology.

Clinical import and measurement of CAB

Autonomic balance has been defined and measured in a variety of ways by different fields and individual researchers, with some using single-branch or broad autonomic measures to speculate about dual branch functioning, others measuring SNS and PNS functioning via different organs, and still others examining CAB via dual branch cardiac measures (e.g., Abboud, 2010; Eppinger & Hess, 1915; Porges, 1976; Thayer & Brosschot, 2005; Wenger, 1941). The most consistent investigations of this construct have been conducted in the medical field, which defines autonomic balance as the relative influences of the SNS and PNS on the heart at rest (i.e., as CAB is defined in this project).

For the purposes of this project, we consulted existing work that has employed cardiac (rather than salivary or electrodermal) indices of SNS and PNS functioning. When referencing research that has measured the relative influence of the SNS and PNS on the heart at rest, we use the term "CAB." For accuracy and consistency, when referring to measures of the relative influences of the SNS and PNS on the heart under other conditions, we use the term “joint SNS-PNS functioning” or simply “joint functioning.”

Clinical import. CAB has been identified as a biomarker of ill health that precedes specific symptom development (Thayer & Lane, 2007) and therefore as a useful early screener for disease formation (Task Force of the European Society of Cardiology and the North American Society of Pacing Electrophysiology, 1996). In the adult literature, CAB has consistently been linked with mental and physical health outcomes, including pervasive and frequently comorbid public health problems such as depression and cardiovascular disease (e.g., Kemp & Quintana, 2013). While a host of diseases and disorders have been linked with high-SNS/low-PNS profiles of CAB (and some externalizing disorders with low-SNS/low-PNS CAB as well; Beauchaine, Gatzke-Kopp, & Mead, 2007), low-SNS/high-PNS CAB is consistently predictive of robust regulatory capacity and good health from middle-childhood through adulthood (for reviews, see Beauchaine, 2001; Thayer & Brosschot, 2005; Beauchaine & Thayer, 2017). This higher resting PNS than SNS tone is considered advantageous for two reasons: First, it reflects a high and appropriate degree of PNS inhibition of the heart in the absence of threat, facilitating regenerative processes and rest (Hall, 2015), and second, it theoretically provides the organism with space for adaptive PNS reactivity in response to intra- or extra-organismic demands (Thayer & Brosschot, 2005). In this way, high PNS tone can be thought of as an internal regulatory resource.

Measurement. Together, this work provides a strong basis for adoption of the adult medical field’s definition of CAB in developmental science. However, although developmental researchers have increasingly investigated SNS and PNS functioning in light of these systems’ putative roles in stress response, emotion regulation, social engagement, attention, and psychopathology (Beauchaine, 2001; Graziano & Derefinko, 2013; Porges, 2001; Porges & Furman, 2011), few studies articulate the medical field's definition of CAB and employ concurrent measurement of cardiac SNS and PNS tones. Work examining links among autonomic functioning, health, and mental health in adulthood has typically measured CAB via heart rate (reflecting combined effects of the SNS and PNS on cardiac output) or heart rate variability (reflecting primarily PNS influences on cardiac output). These methods are founded upon the finding that, in healthy adults, cardiac output at rest is influenced more strongly by the PNS than by the SNS (e.g., Cacioppo, Berntson, Binkley, Quigley, Uchino, & Fieldstone, 1994). Therefore, deviation from this normative balance (as indicated by a heart rate higher than 90 beats per minute or low heart rate variability; Thayer & Brosschot, 2005) is a useful metric for identifying autonomic dysregulation and disease processes. However, in light of normative changes in CAB across the lifespan (Korkushko, Shatilo, Plachinda, & Shatilo, 1991), this principle cannot necessarily be extended to early childhood. Understanding the emergence of stable CAB in childhood requires concurrent measurement of cardiac SNS and PNS functioning.

Cardiac SNS functioning is indexed most purely via pre-ejection period (PEP), with smaller values indicating higher SNS tone. Cardiac PNS functioning is indexed using measures of beat-to-beat variation in heart rate to compute respiratory sinus arrhythmia (RSA), with larger values indicating higher PNS tone. Most existing studies of cardiac autonomic functioning in early childhood have measured the PNS in isolation, used imprecise measures of SNS functioning (i.e., low-frequency heart rate variability; Cacioppo et al., 1994; Goldstein, Bentho, Park, & Sharabi, 2011), or examined SNS and PNS innervation of different organs, which may not provide comparable measures for mapping movement in autonomic space (El-Sheikh et al., 2009). Although work examining SNS and PNS functioning via different organs has yielded important insights to autonomic development, these authors have noted that these methods may not provide a metric of autonomic functioning comparable to those identified as clinically relevant later in life (e.g., El-Sheikh et al., 2009).

The gold standard for measuring CAB in early childhood requires concurrent collection of PEP and RSA and computation of their joint influence (e.g., using the formula developed by Berntson, Norman, Hawkley, & Cacioppo, 2008). Because this method involves concurrent measurement of cardiac SNS and PNS functioning, it provides the most precise index of the medical definition of CAB: the relative influences of the SNS and PNS on the heart at rest.

Maturation of PNS, SNS, and joint functioning in infancy and early childhood

Although little work has examined CAB maturation in the first five years directly, research on cardiac PNS and SNS development, separately, provides a tentative basis for understanding this specific construct. Examinations of normative maturation of PNS and SNS tones and of joint reactivity have generally converged on the findings that the SNS may mature early in gestation, while the PNS matures rapidly from the third trimester through infancy (Bornstein & Suess, 2000; DiPietro, Costigan, & Voegtline, 2015; Fracasso, Porges, Lamb, & Rosenberg, 1994; Porges & Furman, 2011), and coordinated SNS and PNS reactivity patterns only stabilize by age five (Alkon et al., 2011).

Stability. Although individual differences in PNS tone have been identified during gestation (DiPietro et al., 2004) and in healthy newborns (Stifter & Fox, 1990), they are unlikely to indicate lasting differences. PNS tone has been found to be stable from two months to five years (Bornstein & Suess, 2000). Other studies have likewise found moderate levels of stability from three to nine months (Izard et al., 1991), four months to four years (Bar-Haim et al., 2000), six months to five years (Alkon et al., 2011), nine months to three years (Porges, Doussard-

Roosevelt, Portales, & Suess, 1994), and 10 to 18 months (Stifter & Jain, 1996). In contrast, Fracasso and colleagues (1994) found PNS tone to be stable only over two- to five-month periods between five and 13 months; and Stifter and Jain (1996) found PNS tone to be unstable from five to 10 months. The one study that, to our knowledge, has initiated longitudinal collection of PNS tone prior to two months found instability from one to three months (Porter, Bryan, & Hsu, 1995). Together, this work suggests that individual differences in PNS tone at age five are unlikely to be detectable prior to two months but may emerge by two to four months. Five to 10 months may represent a period of instability; however, findings of moderate stability from two months to five years and four months to four years suggest that this may only reflect short-term reorganization.

Despite ongoing shifts in SNS and PNS tones through the lifespan (Kirjavainen, Ojala, Huhtala, Kirjavainen, & Kero, 2004; Korkushko et al., 1991; Massin & Bernouth, 1997), there is broad consensus that autonomic functioning stabilizes prior to middle childhood and likely reflects embedding of early experiences (Alkon et al., 2011; El-Sheikh et al., 2009). Therefore, the rapid organization of autonomic functioning that co-occurs with social and regulatory development from birth to five years (Kopp, 1982; Porges & Furman, 2011; Fig. 2) may render the system particularly sensitive to early positive and negative environmental conditions.

PNS tone growth. Parallel with behavioral immaturity in the perinatal period, the PNS appears to undergo a period of reorganization in the first postnatal month. PNS tone has been found to decrease from birth to one month of age (Schechtman, Harper, & Kluge, 1989), suggesting that PNS resources may be particularly low in the perinatal period. Healthy, full-term infants increased sharply in PNS tone (Schechtman et al., 1989) and decreased in heart rate (Galland, Hayman, Taylor, Bolton, Sayers, & Williams, 2000) from one to three months, and then showed shallower increases in PNS tone to six months (Schechtman et al., 1989), suggesting a re-initiation of the PNS maturation begun in gestation at one month of age. Consistent with theories that PNS tone supports social engagement (Porges, 2001) and adaptability to environmental conditions (Thayer & Brosschot, 2005), this maturation proceeds apace with increasing social behavior (e.g., emergence of social smiles and instrumental crying at three months; Ekman & Oster, 1979; Porges & Furman, 2011) and early emotion regulation (Fig. 2). Therefore, these PNS tone increases may support infants' attempts at engaging in social exchanges and at using social exchanges to regulate distress (Porges & Furman, 2011).

PNS tone has been found to continue to increase through late infancy (Bar-Haim et al., 2000; Patriquin, Lorenzi, Scarpa, & Bell, 2014; Schechtman et al., 1989), concurrent with reciprocal social exchanges, attachment formation, and early behavioral inhibition (Beebe, 2006; Kopp, 1982; Varin, Crugnola, Molina, & Ripamonti, 1996). It continues to increase to ages two and five (Bar-Haim et al., 2000; Bornstein & Suess, 2000), alongside formation of peer relationships, the ability to engage in cooperative play, increasingly accurate theory of mind, and self-regulation of behavior in accordance with social expectations (Gilliom, Shaw, Beck, Schonberg, & Lukon, 2002; Howes & Matheson, 1992; Kopp, 1982; Wellman, Cross, & Watson, 2001; Fig. 2). Although some degree of increase may continue to take place through childhood (Kazuma, Otsuka, Wakamatsu, Shirase, & Matsuoka, 2002; Massin & von Bernuth, 1997) and adolescence (Korushko et al., 1991), heart rate has been found to be determined by the PNS and not the SNS by age two in a low-risk sample (Buss et al., 2005); and levels of resting PNS tone are indistinguishable from adult levels by five years of age (Bornstein & Suess, 2000). Studies consistently find that the steepest PNS development occurs earlier in life, typically prior to one year (Korkushko et al., 1991; Massin & von Bernuth, 1997).

SNS tone growth. The earliest time point at which cardiac SNS data are currently available is six months. Cardiac SNS tone decreases from six to 60 months of age (Alkon et al., 2011) and through middle childhood (Hinnant, Elmore-Staton, & El-Sheikh, 2011) and adolescence (Allen & Matthews, 1997). In the one sample in which cardiac SNS and PNS tones have been collected longitudinally through infancy and early childhood, individual differences in resting SNS tones were moderately stable from six months to five years of age (Alkon et al., 2011). Although the authors did not compute CAB from these concurrent measures, this provides initial evidence for moderate stability in both SNS and PNS influences on cardiac functioning by six months. However, the ongoing instability in SNS and PNS reactivity patterns from six months to five years (Alkon et al., 2011; Bornstein & Suess, 2000; Quas, Bauer, & Boyce, 2004), suggests that the SNS and PNS remain open to calibration across early childhood as children develop physiological and behavioral strategies for responding to challenge.

Development of joint SNS-PNS reactivity. Consistent with theories that heightened reactivity confers sensitivity to context (Belsky & Pluess, 2009; Boyce & Ellis, 2005; Del Giudice et al., 2011), sensitive periods of CAB development may be marked by heightened SNS or PNS reactivity (Quigley & Moore, 2018). Therefore, although stabilization of SNS and PNS tones by six months might suggest that CAB is most plastic prior to that age, higher levels of reactivity in early childhood than middle childhood (Alkon, Goldstein, Smider, Essex, Kupfer, & Boyce, 2003) suggests that the preschool years may also represent a period of heightened sensitivity.

Furthermore, individual differences in SNS-PNS reactivity patterns—which reflect the degree to which an individual relies on the SNS, PNS, or both to regulate—stabilize at age five (Alkon, Lippert, Vujan, Rodriquez, Boyce, & Eskenazi, 2006; Alkon et al., 2011). Earlier instability may reflect children's shifting physiological responses as they are confronted with new demands, acquire new regulatory strategies, and internalize external regulatory resources in PNS tone. At age four to five, as in adulthood, reciprocal SNS reactivity (i.e., concurrent SNS increases and PNS decreases) appears to be the most common reactivity pattern (Alkon et al., 2011) and has been associated with strong emotion regulation (Stifter et al., 2011). Conversely, blunted SNS reactivity has been associated with externalizing behavior (Beauchaine et al., 2007), and blunted PNS reactivity has been shown to predict heightened SNS reactivity (Wolff et al., 2012), which has consistently been linked with adversity-driven allostatic processes (Calkins, Graziano, Berden, Keane, & Degnan, 2008; Oosterman et al., 2010; Oosterman & Schuengel, 2007). Together, this suggests that, between six months and five years, factors that support development of efficient SNS and PNS reactivity and recovery may cultivate emotion regulation and health-promoting low-SNS/high-PNS CAB. Given that CAB sets the boundaries of autonomic space within which each branch can react, low-SNS/high-PNS CAB is the profile that affords the greatest space for the reciprocal SNS reactivity pattern associated with emotion regulation (Fig. 3). Because routinization of reactivity patterns parallels development of increasing behavioral self-regulatory capacities and social competence (Fig. 2), and in light of associations between reactivity patterns and behavior (Beauchaine, 2001), particular patterns of physiological reactivity may differentially support patterns of behavioral regulation. In this way, children's acquisition of behavioral strategies for responding to challenge during this period may be apparent in joint SNS-PNS reactivity patterns and, therefore, CAB by age five.

In sum, normative trajectories of CAB across the first years of life are likely characterized by shifts towards PNS dominance (DiPietro et al., 2015; Kirjavainen et al., 2004; Korkushko et al., 1991; Massin & Bernouth, 1997). This suggests that normative autonomic maturity is marked by an increasingly robust capacity to regulate via the PNS (Hall, 2015; Porges & Furman, 2011) and an expansion of autonomic space (Fig. 3)—both of which heighten the system's adaptive flexibility. This is consistent with definitions, theory, and methodology in the adult medical literature and with established links between SNS dominance at rest and ill health later in life. And, shifting individual differences in joint SNS-PNS reactivity over the course of early childhood (Alkon et al., 2011) may indicate a sensitive period wherein the SNS and PNS are routinizing responses to environmental demands.

Relations between infant-caregiver regulation and PNS functioning

Dyadic navigation of responses to basic needs (e.g., hunger, fatigue, pain), emerging social processes (e.g., regulation of engagement and disengagement), and coordination of attention and movement (e.g., required in learning to feed oneself) afford opportunities for daily practice with regulating the PNS reactivity and recovery that support behavior and a return to a calm state (Armony & Vuilleumier, 2013; Rinaman & Koehnle, 2009). Throughout these daily tasks, external support from the caregiver expands the infant's limited regulatory resources (Gianino & Tronick, 1988). In doing so, this support promotes increasing self-regulatory competence by cultivating in the infant the internal regulatory resources necessary to evaluate affective stimuli, engage socially, form relationships, and respond to stress (Calkins, 2011). As discussed above, one of these internal regulatory resources—resting PNS tone—is thought to be continually modified by the degree to which individuals restore resting levels following response to environmental demands (Berntson et al., 1991). Therefore, parental support of reactivity and recovery during infancy may be a potent facilitator of the normative expansions of children's autonomic space reflected in increasing PNS tone and therefore high-PNS CAB.

Normative mammalian caregiving behaviors such as feeding and social soothing are thought to exercise the PNS, preparing it for future functioning (Calkins, 2011; Porges & Furman, 2011). If this is the case, adult CAB may bear the signature of early infant-caregiver regulatory exchanges. For example, the flexible PNS functioning found in breastfed infants (Quigley et al., 2017) and infants of more-sensitive mothers (Moore et al., 2009; Propper et al., 2008) may precede the low-SNS/high-PNS CAB associated with strong self-regulation (Thayer & Brosschot, 2005). Conversely, the constrained PNS functioning found in young children exposed to adversity (for a review, see Propper & Holochwost, 2013) limits the body's ability to restore calm following stress and may precede the high-SNS/low-PNS CAB characteristic of regulatory impairments, internalizing disorders, and cardiovascular disease later in life (for reviews, see Beauchaine, 2001; Kemp & Quintana, 2013). This may reflect a process in which caregivers themselves are over-taxed by environmental stressors (e.g., parental conflict), constraining the regulatory capacity of the dyadic system, which in turn constrains the regulatory development of the child (e.g., Busuito & Moore, 2017). Consistent with adaptive models of development (e.g., Belsky & Pluess, 2009; Blair & Raver, 2012; Boyce & Ellis, 2005; Del Giudice et al., 2011), therefore, PNS functioning appears to shape and be shaped by adaptations to proximal environments, including parental support for infant regulation, which may scaffold early PNS regulation.

Neuromuscular regulation: Infant feeding practices. Prototypical mammalian infant feeding behaviors co-evolved with and are regulated by the vagus nerve (a component of the PNS). In addition to its role in emotion regulation, the PNS governs a broad range of functions involved in feeding and digestion, including sucking, swallowing, and breathing (Porges & Furman, 2011). Because of this functional overlap, the gustatory-vagal hypothesis posits that nutritive sucking may be an early regulatory behavior that establishes the neurophysiological architecture necessary for socially-mediated regulation (Porges & Furman, 2011; Porges & Lipsitt, 1993). Several studies have found infants to experience decreases in PNS tone while sucking, indicating a sort of mechanically-, rather than cortically-, driven physiological mobilization (Lappi et al., 2007; Portales et al., 1997; Suess, Alpan, Dulkerian, Doussard-Roosevelt, Porges, & Gewolb, 2000).

Because of the distinctive neuromuscular action involved in breastfeeding (Brown, 2007), the infant vagus may be uniquely exercised by this form of sucking (relative to bottle-feeding and pacifier use). Breastfeeding requires organization of suck-swallow-breathe patterns not required by bottle-feeding (Goldfield, Richardson, Lee, & Margetts, 2006), and milk extraction requires a wave-like tongue movement that is thought to stimulate greater PNS reactivity than the straw-like sucking action involved in bottle-feeding (Moral et al., 2010; Quigley et al., 2017). Therefore, sucking in infancy—and breastfeeding in particular—may train the PNS for efficient reactivity and recovery during non-feeding social interactions. Consistent with this proposal, breastfed infants showed greater PNS reactivity than non-breastfed infants during a coregulatory episode with their mothers—suggesting active engagement in repairing the social interaction—and differences were independent of maternal sensitivity (Quigley et al., 2017). Breastfed infants' higher resting PNS tone (DiPietro, Larson, & Porges, 1987) and lower heart rate (Zeskind, Marshall, & Goff, 1992) indicates that sucking-induced PNS reactivity is followed by restoration of resting tone. This is apparent behaviorally in the calm, sedate state observed in infants following feeding and in breastfeeding's analgesic effects (Gray, Miller, Philipp, & Blass, 2002).

Importantly, however, relations between sucking and PNS functioning are apparent during other forms of nutritive and non-nutritive sucking as well: PNS tone has been shown to decrease during pacifier sucking; and six- to 18-week-old pacifier users had higher PNS tone at rest relative to non-pacifier users (i.e., during non-sucking periods of sleep; Franco, Chabanski, Scaillet, Groswasser, & Kahn, 2004). Furthermore, newborns who were breast- or bottle-fed following a heel lance showed smaller heart rate increases and greater recovery of resting PNS tone relative to newborns who were provided with no intervention, non-nutritive sucking, holding, or oral glucose (Weissman, Aranovitch, Blazer, & Zimmer, 2009). Therefore, while all forms of sucking may provide PNS-mediated regulatory support in early infancy, nutritive sucking may stimulate greater PNS reactivity and recovery than non-nutritive sucking, and breastfeeding may stimulate greater PNS reactivity and recovery than bottle-feeding.

Together, this work suggests that, in infancy, sucking is a behavior whose soothing function may operate by exercising flexible movement in parasympathetic space, including efficient mobilization and restoration of calm. This exercise may train the infant PNS to react and recover in the service of later social engagement or regulation of distress. However, although this exercise mechanism has been proposed in prior work (Quigley et al., 2017), to our knowledge no study to date has examined whether feeding longitudinally predicts PNS functioning in a dose-response manner, as would be expected if feeding calibrated the PNS by exercising it.

Social regulatory support in infancy and early childhood. In typically developing infants, concurrent with rapid increases in PNS tone from one to three months (Schechtman et al, 1989), there is a transition from reliance on neuromuscular (e.g., nutritive sucking) to increasingly social means of supporting infant regulation (Calkins, 2011; Feldman, 2006; Porges

& Furman, 2011). This transition is thought to be facilitated by development of increased cortical control of medullary nuclei, where the vagus originates (Porges, 2001; Porges & Furman, 2011). Although social support remains an important regulatory resource throughout life (Cohen & Wills, 1985), infancy—when autonomic space is rapidly expanding, reactivity levels are high, and patterns of joint SNS-PNS reactivity are stabilizing (Alkon et al., 2003; Alkon et al., 2011)—is the only period in which reliance on social support to regulate is normatively the primary strategy (Kopp, 1982). Therefore, qualities of and constraints on regulatory support provided by parents during this period may shape the child's later capacities for autonomic regulation.

Existing work has found normative increases in PNS tone from three to six months of age to be contingent upon maternal behavior: Infants of depressed mothers, who may be less able to provide regulatory support to their infants, did not show PNS tone increases between three and six months of age, while infants of non-depressed mothers did (Field et al., 1995). Likewise, at six months, infants in dyads that showed reciprocal coregulation during a free play had higher resting PNS tone than others (Porter, 2003). Although some of these effects are likely owed to genetics, molecular genetics research has found genetic effects on infants' PNS functioning to be moderated by maternal sensitivity between three and 12 months of age. In response to perturbation of a social interaction with their mothers at three and six months, infants with the *DRD2* allele (associated with risk for externalizing disorders) failed to show PNS reactivity regardless of maternal sensitivity level. However, by 12 months, infants with the risk allele who had highly sensitive mothers showed expected PNS reactivity, while infants of less-sensitive mothers did not (Propper et al., 2008), suggesting that supportive parenting may have recalibrated the infant PNS for more flexible functioning.

Increasingly, research is converging on the finding that caregiver behavior may shape PNS tone by scaffolding PNS reactivity and recovery. This is apparent by three months of age (Moore & Calkins, 2004) and can be observed in the PNS still-face effect (the Face-to-Face Still Face; Tronick, Als, Adamson, Wise, & Brazelton, 1978). This effect is marked by PNS reactivity (decreases in PNS tone) when the mother withdraws from social engagement, suggesting that, when regulatory support is withdrawn, infants increase their reliance on PNS-facilitated self-regulation. Infants' PNS reactivity during mothers' still-face, and their PNS recovery following the still-face, have been shown to be contingent upon the dyad's degree of synchrony and flexibility—indices of coregulation—respectively: Infants in dyads that were more-synchronous during the pre-still-face play episode showed PNS reactivity theorized to support efforts at self-regulation, while infants in less-synchronous dyads did not (Moore & Calkins, 2004). And, infants in dyads that showed high levels of affective flexibility during the reunion exhibited greater PNS recovery (Busuito & Moore, 2017).

Likewise, high levels of maternal sensitivity in the reunion episode predicted PNS recovery from the still-face to the reunion at five months (Conradt & Ablow, 2010). Conversely, high levels of maternal sensitivity measured in the *home* predicted greater infant PNS *reactivity* (i.e., PNS tone decreases) from the still-face to the reunion at six months (Moore et al., 2009). These apparently contradictory findings highlight the integration of social and parasympathetic systems and the way in which presence of external regulatory resources may decrease reliance on internal regulatory resources: While *prior experience* may have led the infants of more-sensitive mothers (Moore et al., 2009) to expect sensitive responding—such that PNS-supported social engagement to elicit these responses would be adaptive—*concurrent* maternal sensitivity

(Conradt & Ablow, 2010) likely provided regulatory support that decreased need for PNS reactivity.

Implications for SNS functioning. This inter-system buffering effect also appears to influence SNS functioning, such that availability of social support and capacity for PNS reactivity decreases reliance on the SNS to regulate. During a stressful task, four- to five-year-olds who had shown greater PNS reactivity during earlier stressors and were provided with concurrent social support showed the least SNS reactivity. Children with high PNS reactivity who were not provided with social support and children with low PNS reactivity, regardless of social support, showed higher SNS reactivity (Wolff et al., 2012). Therefore, the least SNS reactivity was exhibited by children with access to both internal (i.e., capacity for PNS reactivity) and external (i.e., social support) regulatory resources.

The same pattern has been identified in children who have experienced poor-quality relationships with their caregivers in infancy or early childhood: Multiple studies have shown low levels of PNS reactivity and high levels of SNS reactivity to challenge at five to seven years in children who have experienced abuse, neglect, foster involvement, or poor-quality caregiving (Calkins et al., 2008; Conradt et al., 2013; Eisenberg et al., 2012; Oosterman et al., 2010; Oosterman & Schuengel, 2007). This suggests that lack of access to social regulatory support in the first years of life may interrupt development of health-promoting PNS reactivity and recovery and heighten the regulatory burden on the SNS.

Implications for development of CAB. Taken together, this work suggests that neuromuscular regulation in the first three months of life, and provision of social regulatory support by the primary caregiver as early as three months, may shape infants' use of internal regulatory resources. Indicators of caregiver social support for infant regulation have been found to predict individual differences in PNS functioning characterized by relatively higher resting PNS tone (Field et al., 1995; Porter, 2003) and greater PNS reactivity during stress and social engagement (e.g., Moore & Calkins, 2004; Calkins et al., 2008; Oosterman et al., 2010) in more- versus less-supported children. And, at six months, breastfeeding and maternal sensitivity have been shown to exert independent effects on infants' PNS reactivity during social engagement, suggesting unique contributions of these two forms of parent-facilitated regulatory experiences (Quigley et al., 2017). Consistent with developmental cascade models (e.g., Masten & Cicchetti, 2010; Thelen, 2000), resources available in one system (i.e., social, PNS, and SNS) appear to influence the operation and development of others, and these inter-system influences are enduring.

Therefore, early regulatory exchanges, including neuromuscular regulation in the first three months of life and parental social support for infant regulation after three months, may promote the expansion of autonomic space—and of self-regulatory capacities (Gianino & Tronick, 1988)—by training the developing PNS to move flexibly through excitatory states and to restore calm. It is likely that neuromuscular means of regulating (e.g., breastfeeding) have the greatest impact on PNS development prior to the transition to increasingly social regulation around three to six months. Following this transition, while infants are developing the capacity to regulate emotion and form relationships (Fig. 2), increasingly social support for regulating distress is likely the greater influence on growth of PNS tone. If this is the case, these early regulatory experiences may calibrate PNS contributions to age five CAB, laying the groundwork for psychopathology and ill health or socioemotional and physical wellbeing.

The Current Study

Aim. Following a growing body of work suggesting that infancy and early childhood may be sensitive periods for PNS development and that regulatory experiences—including feeding and, later, social support during distress—may foster development of health-promoting CAB by scaffolding increases in PNS tone and capacity for efficient reactivity and recovery, the current study aimed to identify physiological and behavioral precursors to health-promoting CAB and autonomic functioning at age five. In doing so, we sought to elucidate developmental processes and normative early-life experiences (i.e., feeding, soothing) that may shape the joint SNS-PNS functioning that determines CAB at age five. Given theory and empirical work suggesting that CAB is determined by the degree to which each branch recovers resting tone following challenge (Fig. 1; Berntson et al., 1991; Linden, Earle, Gerin, & Christenfeld, 1997) and that, therefore, health-promoting low-SNS/high-PNS CAB results from the ability to restore physiological and emotional calm following distress (Quigley & Moore, 2018), we computed CAB from concurrent cardiac SNS and PNS tones during a recovery period that followed a series of lab tasks at age five.

Although CAB is jointly defined by SNS and PNS influences on the heart, development of PNS functioning is the focus of this project for two main reasons: First, in healthy individuals, CAB is marked by PNS dominance by middle childhood (Cacioppo et al., 1994; Korkushko et al., 1991), suggesting that the development of robust PNS tone may be critical to processes underlying regulation, health, and resilience (Thayer & Brosschot, 2005). And second, existing work suggests that PNS development may be calibrated by early, caregiver-facilitated regulation, while divergence from normative profiles of SNS functioning may emerge following chronic or acute exposure to stress (e.g., Porter, 2003; Lovallo, Farag, Sorocco, Cohoon, & Vincent, 2012).

Because the current study involved a low-risk sample, we were best equipped to examine autonomic development in the relative absence of chronic or acute stress. In this way, the study was designed to provide information about normative development that may inform understanding of developmental psychopathology and pathophysiology (Sroufe & Rutter, 1984). In doing so, we sought to address the first of a set of empirical questions necessary to understanding how early environments may become written into the brain and body, laying the groundwork for resilience or pathology (Quigley & Moore, 2018).

Hypotheses.

(H1) To identify physiological antecedents of health-promoting CAB, we first examined relations between changes in children's resting PNS tone from two weeks to 4.5 years and their age-five CAB. (To elucidate PNS and SNS contributors to that age-five CAB, we also examined relations between children's PNS tone growth and children's PNS and SNS tones during the recovery period separately.) To identify behavioral correlates of relevant periods of PNS tone growth, we investigated whether feeding practices (neuromuscular regulation) and non-oral soothing (social regulation) were associated with PNS tone change during each period examined. We expected:

(H1.1) relatively lower-SNS/higher-PNS age-five CAB to be related to greater PNS tone increases from two weeks to four months and from four to six months, but not to change from six to 12 months or 12 months to 4.5 years;

(H1.2) relatively higher age-five PNS tone to be related to greater PNS tone increases from two weeks to four months and from four to six months, but not to changes from six to 12 months or 12 months to 4.5 years; and

(H1.3) relatively lower age-five SNS tone to be associated with greater PNS tone increases from two weeks to four months and from four to six months.

Behaviorally, we expected:

(H1.4) two-week feeding practices but not two-month non-oral soothing to be associated with PNS tone change from two weeks to four months, such that more time feeding would be related to greater PNS tone increases; and

(H1.5) non-oral soothing, but not feeding practices, to be associated with PNS tone change from four to six and six to 12 months, such that infants who were effectively soothed by non-oral strategies following a routine inoculation at *two months* would show greater PNS tone increases from *four to six months* and those who were effectively soothed by non-oral strategies following routine inoculation at *six* months would show greater PNS tone increases from *six to 12 months*.

This would provide initial evidence that PNS tone development in the first six months may lay the groundwork for long-term PNS functioning and that early establishment of high PNS tone may confer capacity for PNS reactivity and recovery, decreasing reliance on SNS reactivity and allowing for development of low-SNS/high-PNS (health-promoting profiles of CAB. Furthermore, this would support proposals that such health-promoting PNS tone growth may be promoted by neuromuscular regulation in the first four to six months but by social regulation later in infancy.

(H2) We then examined whether perinatal feeding practices—which are thought to shape PNS tone in infancy—were associatd with age-five PNS functioning in a dose-response manner. We expected age-five PNS reactivity and recovery to be predicted by feeding practices at age two weeks, such that more time feeding at two weeks would be associated with greater PNS reactivity (PNS tone decreases) during tasks requiring interaction with a stranger (i.e., the research assistant) and with greater PNS tone recovery (PNS tone increases) during the recovery period. Infant feeding practices were expected to be unrelated to SNS reactivity or recovery.

Method

Data were drawn from a longitudinal study of emotion regulation development, the Emotional Beginnings Project (*PI C. Stifter*). Children were followed from two weeks of age to first grade. The current study used data from two week, four month, six month, 12 month, 4.5 year, and 5.5 year laboratory visits and from well-child visits at two and six months.

Participants

One hundred and fifty fully-term, healthy infants and their mothers and fathers were recruited through a community hospital in central Pennsylvania. The first visit took place when infants were two weeks old. At infant age two weeks, mothers ranged in age from 16 to 34 ($M = 29.68 \pm 5.50$) and had 10 to 26 years of education ($M = 15.59 \pm 2.70$). Most mothers (84%) were married. Participants were predominantly White (91.8%) and middle class. Fifty-two percent of infant participants were female, and 44.67% were firstborns. At infant age two weeks, 125 infants (74.4%) were breastfed exclusively or fed a combination of breastmilk and formula.

Between child ages 12 months and 4.5 years, an additional 18 families were recruited from another study whose demographic characteristics were comparable with those in the Emotional Beginnings Project. This was done to address attrition after additional time points were added.

Procedures

Infant inoculation. Infants and their mothers were videotaped following inoculations at two- and six-month well-child visits to assess infant reactivity and regulation in the presence of maternal soothing behaviors.

Physiological data collection. At two-week and four-, six-, and 12-month visits, following a warm-up period during which infants could become accustomed to the laboratory, disposable electrodes were placed on the infant's chest while the infant was seated in the parent's lap. The infant was then placed in a high chair while ECGs were recorded during an approximately five-minute baseline period in which the infant was quietly entertained by a research assistant. The 4.5-year baseline ECG recording was completed while children sat at a child-sized table and ranked toys to be used in a disappointment paradigm later in the visit. At the 5.5-year lab visit, ECGs and impedance cardiograms were placed following a series of introductory procedures (see *5.5-year laboratory tasks*, below).

Cardiac monitoring and data reduction. ECGs were collected using three electrodes placed in a triangular pattern on the lateral end of the right clavicle, lower left rib cage, and lower abdomen. Cardiac impedance was collected using a four-electrode configuration. These were placed on the back of the neck on the C4 vertebrae, at the top of the sternum, over the xiphisternal junction, and on the back over the thoracic spine (Allen, Fahrenberg, Kelsey, Lovallo, & van Doornen, 1990). The two current electrodes were approximately 2 cm above and below the recording electrodes. Basal thoracic impedance (Z_O), the first derivative of the change of thoracic impedance (dZ/ dt), and the ECG were measured using a Minnesota Impedance Cardiograph (Model 304B) connected to a laptop computer which was equipped with data collection hardware and software (Mindware Technologies, Westerville, OH).

To quantify heart rate data, the ECG and impedance signals were passed through an A/D converter with ECG and dZ/dt sampled at 1000 Hz and Z_O sampled at 500 Hz. Respiratory sinus arrhythmia (RSA), which measures heart rate variability occurring within the respiratory frequency, was derived from the interbeat interval series, and values were resampled at 25 milliseconds to create a stationary wave form. The integral of the power in the RSA band (.24-1.04 for young children) was extracted to remove heart rate variability outside of the respiratory band, and the natural logarithm of this measure was the RSA statistic, an index of PNS tone. Visual inspection of movement artifact was conducted, and data were edited manually by interpolating artificial heart beats to retain the time series. Pre-ejection period (PEP), a measure of SNS-mediated cardiac output, was derived by taking the time between the onset of the ECG Q wave and dZ/dt B point (indicating the beginning of the ejection).

5.5-year laboratory tasks. Following introductory procedures (explanation of a point-based economy system in which the child could earn tickets for completing certain tasks, explanation that the research assistant was taking care of a friend's baby down the hall, placement of electrocardiograms (ECGs) and impedance cardiograms, and completion of a non-contingent reward-punishment task and a sensation-seeking scale), mothers were asked to leave the room. Mothers remained out of the room while children completed the following tasks:

Emotion interview. Children received the following prompts from a trained research assistant: "Now I am going to ask you some questions about your feelings, and I want you to think carefully about some situations that made you happy, mad, sad, and scared. Can you tell me about a time when you felt mad?" and "When you felt mad and you didn't want anyone to know, what did you do?" These questions were repeated, substituting sad, happy, and scared. Additional prompts were given if the child had difficulty thinking of a situation (e.g., "Did you ever feel scared when you heard a noise in the middle of the night?").

Movie. Children were told that they would watch a short movie about a girl "about your age who gets burned in a fire and has to go to the hospital and how her friends react to her." Before starting the film, the research assistant left the room and shut out the lights. The movie, which was designed to assess empathy, lasted for six minutes, during which the child remained alone in the room.

Movie interview. When the movie ended, the research assistant returned, turned the lights back on, and asked how much the child liked the movie and how they felt about it (i.e., "Did you feel down or bad?").

Verbal fluency. The Verbal Fluency subtest of the McCarthy Scales of Children's Abilities (McCarthy, 1972) was administered as a cognitive challenge task requiring children to generate as many words as possible that fit a given category (e.g., things to eat, animals, things to wear) in a limited amount of time. In addition to calling on children's verbal abilities, the time limit on this word generation task required children to process instructions and retrieve semantic information quickly.

Story recall. The Story Recall subtest of the McCarthy Scales of Children's Abilities (McCarthy, 1972) provided a second cognitive challenge. Children listened to a short story, read by a research assistant, and then were asked to tell the story back as accurately as possible immediately afterwards. This required children to maintain attention to the story, to hold key elements in memory, and then to recall those elements either verbatim or in their own words.

Baby Cry, Response, and Recovery Period. Immediately following the story recall task, a second research assistant knocked on the door, and the first research assistant informed the child that they would return after checking on something in the booth. Children were then left alone in the room. After 30 seconds, a tape of infant crying was played for one minute. Following the end of the tape, the research assistant remained out of the room for an additional 30 seconds.

The research assistant then returned to the room and began to clean up. If the child did not mention a baby crying, the research assistant provided prompts: "Did anything happen while I was gone?" And then, if the child still did not mention the baby crying, "Did the baby cry? The baby did not cry while I was gone? Are you sure?" The research assistant then told the child that they were going to check on the baby.

The research assistant remained out of the room for one minute before returning and saying, "The baby is hungry. I left the bottle in here somewhere." If the child did not point out the bottle, the research assistant asked, "Have you seen the baby's bottle?" Whether or not the child pointed out the bottle, the research assistant then said, "Oh, there it is! I'll be right back. I have to go and give the baby the bottle," before leaving the room again.

Given the distinct demands of the various stages of this task, which may have differentially elicited SNS and PNS responding (Porges, 2007), it was divided into three episodes: the initial two minutes in which the child was alone in the room listening to the cry tape (*baby cry*), the subsequent three minutes in which the research assistant had returned to the room and was asking the child questions about what had happened while they were gone (*response*), and the final two minutes, which involved time alone and a brief helping task (*recovery period*). The baby cry episode of this task may have elicited some emotional response from children but did not require social engagement, while the response episode involved no emotion elicitation but did pull for some social engagement. The recovery period episode involved neither infant cry nor social engagement for the first minute and then a brief helping task (requiring no verbal communication) in the second; therefore, it was theorized that this episode would require minimal SNS or PNS activation.

Measures

A complete list of measures collected at each time point is presented in Table 1.

Demographics. Demographic data were collected at infant age two weeks. Mothers reported on infant sex and mother age, education (years), and marital status.

Feeding practices.

Breastfeeding status. During an interview at the two-week lab visit, mothers reported on infant feeding method (i.e., breastfeeding, formula feeding, or a combination of these). Responses were coded as “any breastfeeding” (1) or “no breastfeeding” (-1).

Feeding time. At infant age two weeks, mothers completed feeding diaries. Mothers recorded feeding practices (i.e., breastfeeding, formula feeding, other feeding method-unknown, or no feeding-left blank) in five-minute increments for four days. Because neuromuscular regulation is thought to affect PNS functioning in a dose-response manner (Porges & Lipsitt, 1993) total feeding time was calculated as the sum of time spent feeding during the four-day diary period.

Soothing practices. Infants and mothers were observed following routine inoculation, as noted above. Infant and mother behavior were coded (Jahromi, Putnam, & Stifter, 2004), and codes were analyzed using Hidden Markov Modeling (HMM; Rabiner & Juang, 1986; Stifter & Rovine, 2015) to extract trajectories of dyadic states. These trajectories were then used to identify distinct typologies of dyadic regulation (Backer, Quigley, & Stifter, 2018), which were consolidated into two categories at each age for use in the current study.

Coding infant and mother behavior. Following extraction of the last needle, each five-second interval of infant behavior was coded as (0) no vocalization, (1) fussing or whining, (2) low intensity crying, or (3) high intensity crying. Interrater reliability was strong, Cohen’s $\kappa = 0.92$ for 10% of cases across two- and six-month visits.

Concurrently, each five-second interval of mother behavior was coded as (1) displays of affection, such as kissing and hugging, (2) other touching, such as patting and stroking, (3) holding with or without rocking, (4) vocalizations, including talking and singing, (5) caretaking activity, such as dressing and diaper changing, (6) attempts to distract the infant, (7) face-to-face interaction, and (8) feeding or pacifying via bottle, nursing, or pacifier. Codes were not mutually exclusive. Interrater reliability for mothers' behaviors ranged from Cohen's κ = 0.78 - 0.98 for 10% of cases across two- and six-month visits.

Computing infant-mother soothing trajectories. Trajectories of infant-mother soothing were then computed using HMM, which probabilistically identified dyadic states (i.e., level of infant distress and concurrent mother soothing behavior) across the period in which infants showed distress. A four-state model provided the best fit for the two-month data, and a six-state model provided the best fit for the six-month data (see Stifter & Rovine, 2015 for details):

At two months, the best-fitting HMM model identified four dyadic states as follows:

(1) High infant reactivity; mother caretaking
(2) High/moderate infant reactivity, mother holding, rocking, vocalizing, affection
(3) Low/low infant reactivity; mother holding, rocking, vocalizing, affection
(4) Any level of infant reactivity; mother feeding/pacifying, holding, vocalizing, distraction, face-to-face

At six months, the best-fitting HMM model identified six dyadic states as follows:

(1) High infant reactivity; mother holding, rocking, vocalizing
(2) Moderate infant reactivity; mother holding, rocking, vocalizing
(3) Low/no infant reactivity; mother holding, rocking, vocalizing
(4) Any infant reactivity; mother feeding/pacifying
(5) Low/no infant reactivity; mother feeding/pacifying
(6) Any infant reactivity; mother caretaking

Identifying typologies of dyadic emotion regulation. To identify individual differences in patterns of dyadic regulation following inoculation, cluster analyses were used to identify groups of dyads whose posterior state trajectories were maximally similar within group and maximally dissimilar between groups (Backer et al., 2018). Modeling was conducted in R Studio (R Core Team, 2015) using the "TraMiner" (Gabadinho, Ritschard, Müller, & Studer, 2011; Gabadinho, Studer, Müller, Buergin, & Ritschard, 2016; Studer & Ritschard, 2016), 'cluster' (Maechler et al., 2016), and 'fpc' (Hennig, 2015) packages. Pairwise dissimilarities between trajectories were computed using optimal matching to identify edit distances, which indicate minimal costs for exchanging one state for another state (Gabadinho, et al., 2011; Lesnard, 2006). A hierarchical clustering algorithm was applied to the pairwise dissimilarities, iteratively merging minimally-dissimilar clusters, based on edit distance, until a single cluster including all trajectories was formed. Cluster solutions were selected following (a) visual inspection of the dendogram generated by the iterative merging process, (b) comparison of fit indices for different cluster solutions, and (c) consideration of theory (Kaufman & Rousseeuw, 1990; Maechler et al., 2016). Using this method, four clusters were identified at two months and five clusters at six months. Clusters were validated by examining infant and mother correlates of cluster membership. Visual inspection of each cluster's trajectory recommended the following group descriptions. Two-month clusters and their descriptions are as follows:

(1) *Well-regulated* (*N* = 46): Attainment and maintenance of low/no infant reactivity, coupled with mother holding, rocking, vocalizing, affection (HMM State 3).

(2) *Poorly regulated* (*N* = 61): Failure to reach or maintain a calm state, often transitioning to and maintaining high/moderate infant reactivity, coupled with mother holding, rocking, vocalizing, affection (HMM State 2).

(3) *Disorganized* (*N* = 21): Maintenance of high infant reactivity, coupled with mother caretaking (HMM State 1) despite many dyads achieving brief periods of calm (HMM State 3). Many dyads quickly transitioned from feeding to caretaking.

(4) *Feeding/pacifying* (*N* = 13): Large durations in feeding/pacifying (HMM State 4) with moderate time in highly reactive states (HMM States 1 and 2) and little or no time in calm states (HMM State 3).

Six-month clusters and their descriptions are as follows (Backer et al., 2018):

(1) *Well-regulated* (*N* = 27): Diminishing infant reactivity coupled with mother holding, rocking, or vocalizing.

(2) *Effective use of food to soothe* (*N* = 22): Achievement of calm via feeding or pacifying, with more time spent in a low/no distress feeding state than a moderate/high distress feeding state.

(3) *Less-effective use of food to soothe* (*N* = 17): Long durations of infant fussiness (HMM State 5) coupled with feeding/pacifying; frequent failure to restore calm.

(4) *Poorly regulated* (*N* = 52): Long durations of high/moderate infant reactivity, coupled with a variety of mother soothing strategies; frequent failure to restore calm.

(5) *Moderately well-regulated* (*N* = 13): Diminishing infant reactivity coupled with mother holding, rocking, or vocalizing, but longer durations in fussy states relative to Cluster 1 (HMM State 3).

More detailed descriptions of the creation of soothing trajectories (i.e., HMMs) and of six-month typologies of dyadic regulation (i.e., clusters) are reported by Stifter & Rovine (2015) and by Backer and colleagues (2018), respectively.

Categorizing dyads according to their non-oral soothing success. To test the hypotheses that use of non-oral regulatory strategies would predict growth in PNS tone only after four months, clusters at each timepoint were categorized according to whether infants successfully soothed in the presence of non-oral regulatory strategies (e.g., holding, rocking, vocalizing). At two months, Cluster 1 ("Well-Regulated") was categorized as "effective non-oral soothing" (*N* = 46), and Clusters 2 ("Poorly Regulated"), 3 ("Disorganized"), and 4 ("Feeding/pacifying") were coded as "oral soothing or ineffective non-oral soothing" (*N* = 95). At six months, Clusters 1 ("Well-Regulated") and 5 ("Moderately Well-Regulated") were coded as "effective non-oral soothing" (*N* = 39) and Clusters 2 ("Effective Food to Soothe"), 3 ("Moderately Effective Food to Soothe"), and 4 ("Poorly Regulated") were coded as "oral soothing or ineffective non-oral soothing" (*N* = 92). Category membership was not stable across time.

Physiological Measures.

RSA & PEP. Child RSA, an index of PNS tone, was derived from heart rate recordings collected during baseline procedures at child ages two weeks, four months, six months, 12 months, and 4.5 years.

RSA and PEP, an index of SNS tone, were derived from heart rate and cardiac impedance recordings during a series of tasks in the laboratory at 5.5 years. Mean RSA and PEP were calculated for each minute of cardiac monitoring during the 5.5-year visit. Higher values of RSA indicated higher PNS tone. Lower values of PEP (i.e., shorter time between onset of the ECG Q wave and dZ/dt B point) indicated higher SNS tone, while higher values of PEP indicated longer periods and lower SNS tone.

CAB. Because ECG and impedance cardiogram recording at the 5.5-year visit were initiated following a series of potentially stressful procedures, including a non-contingent reward/punishment task and mothers' departure from the room, baseline measures of RSA and PEP were not available. Therefore, in the absence of initial resting measures, we computed CAB during the recovery period. Because CAB is thought to be continually renegotiated through *recovery* of SNS and PNS tones (Berntson et al., 1991), examination of concurrent PEP and RSA after challenges had ended provided a useful approximation of the construct of interest.

Berntson and colleagues' (2008) method was used to compute CAB during the recovery period. This value, which Berntson and colleagues call CAB regardless of context (i.e., during rest, perturbation, or recovery), was quantified as the standardized value of PNS tone minus the standardized value of SNS tone. (Note that PEP values must be multiplied by -1, because smaller PEP values indicate higher SNS tone.):

$$z\text{RSA} - (-z\text{PEP})$$

Higher values indicate greater PNS and lessor SNS influences on cardiac output.

In the current study, values of Berntson's CAB tended to increase across the 5.5-year lab visit and were highest during the recovery period, supporting our proposition that joint SNS-PNS functioning during the recovery period reflected some degree of recovery from prior stressors and therefore was a reasonable indicator of children's (resting) CAB.

Missing data

Sample size varied over the course of the study and across measures, as some families moved out of town, were otherwise unavailable for follow-up, or refused study components. This resulted in different sample sizes in different sets of analyses.

Questionnaire-based feeding data (i.e., mothers' reports on breastfeeding status) were available for all 150 infants at two weeks. A subsample ($N = 60$) of two-week feeding diary data were available for use in the current study.

Soothing practices following two sets of routine inoculations were available for 141 dyads (75 female infants; *M* age = 2.1 months, range = 1.5-3.5 months) at two months and 133 dyads (66 female infants; *M* age = 6.3 months, range = 4.9-8.8 months) at six months. Observations were missing due to families moving out of town or refusing to have inoculation procedures videotaped.

Baseline RSA data were available for 144 infants at two weeks, 143 infants at four months, 140 infants at six months, 136 infants at twelve months, and 81 children at 4.5 years (Table 2). At the 5.5-year visit, when both RSA and PEP were collected, data were missing differently by measure. Computations of joint SNS-PNS functioning during the recovery period were available for 52 children. Frequencies by measure and task are reported in Table 3. Physiological data were missing due to ECG or impedance cardiogram equipment problems or, at 4.5- and 5.5-year visits, to children refusing electrode placement. Data from the two- and six-month inoculation visits and from the two-week, four-, six-, and 12-month, and 4.5-year lab visits were not missing as a function of demographic characteristics, breastfeeding status, or infant physiology.

However, PEP (and therefore joint SNS-PNS functioning) data during the recovery period at age 5.5 were not missing at random: Relative to children who had complete PEP data, children with missing data had marginally lower RSA during the movie interview (*M* = 5.29 ± .99 vs. 5.74 ± 1.12), story recall (*M* = 4.91 ± .85 vs. 5.43 ± 1.16), baby cry (*M* = 5.71 ± 1.04 vs 6.23 ± 1.20), and recovery period (*M* = 5.52 ± 1.01 vs. 6.03 ± 1.19) procedures, indicating that children who were experiencing a greater need to regulate during these tasks were more likely to have incomplete PEP data during the final task. Children with missing PEP data in the recovery period also had younger mothers (*M* age = 28.79 ± 5.66 vs. 32.02 ± 4.31 years) and were more likely to have mothers who were not married at infant age two weeks, X^2 (1, N = 150) = 10.75, p = .00, than children with complete data. These factors may have contributed to decreased variability in values of joint SNS-PNS functioning at the end of the 5.5-year lab visit, making it more difficult to detect predictors of individual differences. Data were not missing as a function of two-week feeding practices or two-week to 4.5-year RSA.

Analytic Plan

Preliminary analyses. Relations among main study variables (i.e., feeding practices, soothing practices, and child physiology) and between main study variables and candidate covariates (i.e., demographic factors and infant sex, selected based on their associations with main study variables in prior research) were examined using SPSS Version 25. Correlations were also computed among baseline (two weeks, four months, six months, 12 months, and 4.5 years) and recovery period (5.5 years) values of child RSA (Table 4) to examine PNS tone stability from two months to five years.

Tests of hypotheses.

(H1.1-3) To identify periods of PNS growth associated with age-5.5 CAB, PNS tone, and SNS tone during the recovery period, three repeated measures generalized linear models (GLMs) were examined using SPSS Version 25. Each model included RSA at two weeks, four months, six months, 12 months, and 4.5 years as the within-subjects factor and either *(H1.1)* CAB, *(H1.2)* RSA, or *(H1.3)* PEP during the 5.5-year recovery period as a covariate (conceptually, a between-subjects factor). Within-subjects repeated contrasts were used to identify periods of RSA change associated with age-5.5 physiology.

To determine whether RSA differed as a function of age-5.5 physiology at individual time points, post hoc one-way analyses of variance (one-way ANOVAs) were conducted with child RSA at two weeks, four months, six months, 12 months, or 4.5 years as the dependent variable and a median split of child RSA or PEP during the age-5.5 recovery period as the between-subjects factor.

(H1.4-5) Using the PROC REG procedure in SAS software Version 9.5 of the SAS System for Windows (SAS Institute Inc., 2012), linear regression was employed to identify behavioral correlates of RSA growth during each time period. The dependent variable was RSA change (calculated as the difference between RSA at the later age and RSA at the earlier age), and predictor variables in each model were: breastfeeding status at two weeks (yes/no), feeding time at two weeks, and effective non-oral soothing at two or six months (i.e., membership in *two*-month cluster 1 vs. clusters 2, 3, or 4; or membership in *six*-month clusters 1 or 5 vs. clusters 2, 3, or 4), controlling for infant sex, maternal education, and RSA at the beginning of the growth period being examined.

Regressions were used to test these hypotheses instead of repeated measures GLMs because the latter deletes cases listwise, resulting in loss of the full case if a child was missing data for any of the five time points under consideration. When overlaid with available feeding diary data, $N = 60$, this would have resulted in an analytic sample of $N = 23$ prior to addition of covariates.

(H2) To examine whether early feeding and soothing practices predicted age-5.5 PNS or SNS reactivity or recovery, two models were estimated using the PROC MIXED procedure in SAS software Version 9.5 of the SAS System for Windows (SAS Institute Inc., 2012). This data analytic method is appropriate for repeated measures designs (Little & Rubin, 1987) and dealing with missing data (Schafer & Graham, 2002). Restricted maximum likelihood (REML) was used in reporting model parameters, and degrees of freedom were estimated using the between-within method.

Separate models were conducted for RSA and PEP. The dependent variable was child RSA or PEP during each of the 5.5-year lab tasks. Each model (RSA and PEP) included intercept (emotion interview, which was the first task in which physiological data were recorded); lab procedure (movie, movie interview, verbal fluency, story recall, baby cry, response, and recovery period) as the repeated factor; breastfeeding status at two weeks; feeding time at two weeks; effective non-oral soothing at six months; the interactions of lab task by feeding time (terms multiplied), which tested the effect of feeding time on change in RSA or PEP from the emotion interview to each task; and maternal education and infant sex as covariates. A breastfeeding by feeding time term was included in both RSA and PEP models to detect moderating effects of one variable on the other. Binary variables were effect coded as -1 and 1: breastfeeding status was coded as -1 for non-breastfed and 1 for breastfed; effective non-oral soothing was coded as -1 for "oral soothing or ineffective non-oral soothing" and 1 for "effective non-oral soothing;" and infant sex was coded as -1 for male and 1 for female.

Results

Preliminary analyses

Physiology.

Two-week to 4.5-year RSA. Descriptive statistics for two-week to 5.5-year RSA and for two-week to 5.5-year RSA as a function of breastfeeding status are presented in Table 2. (Statistics are presented for age-5.5 RSA in the recovery period.) Infants who were breastfed at all at two weeks ($M = 3.20 \pm .76$) had higher four-month RSA than infants who were not breastfed ($M = 2.79 \pm .80$), $F(1, 141) = 5.46$, $p < .05$. Two-week to 4.5-month RSA did not differ as a function of two-week feeding time, two- or six-month effective non-oral soothing, or mothers' marital status, education, or age. Male infants ($M = 3.34 \pm .64$) had higher four-month RSA than female infants ($M = 2.96 \pm .85$), $F(1, 141) = 8.97$, $p < .01$.

RSA, PEP, and CAB at 5.5 years. Descriptive statistics for child RSA, PEP, and CAB during the 5.5-year lab visit are presented in Table 3.

RSA in each task, PEP in each task, and CAB in the recovery period did not differ as a function of two-week breastfeeding status, two- or six-month effective non-oral soothing, mothers' marital status, or infant sex. Children of older mothers had lower RSA during the verbal fluency task at age 5.5, $r(61) = -.33$, $p < .01$, but did not differ in other tasks. Children of mothers who had more years of formal education had significantly lower PEP (higher SNS tone) in each task of the 5.5-year lab visit, *r*s ranging from -.38 (movie interview) to -.48 (baby cry).

Although two-week feeding time was not associated with RSA or PEP in any task or with CAB in the recovery period at 5.5 years, it was associated with RSA and CAB *change scores*, which were employed to examine candidate variables for inclusion in (H2) analyses. Infants who spent more time feeding at two weeks showed greater RSA recovery (computed as RSA in the recovery period minus RSA in the initial, emotion interview, task), $r(21) = .45, p < .05$, and greater CAB recovery (computed as CAB in the recovery period minus CAB in the emotion interview), $r(14) = .71, p < .01$, relative to children who spent less time feeding at two weeks. Likewise, infants who were breastfed at all at two weeks (*M* RSA recovery = .51 ± .73; *M* CAB recovery = .19 ± .93) showed greater RSA recovery, $F(1, 55) = 5.02, p < .05$, and CAB recovery, $F(1, 36) = 7.66, p < .01$, during the 5.5-year lab visit relative to non-breastfed infants (*M* RSA recovery = -.03 ± .71; *M* CAB recovery = -.78 ± .61). PEP recovery did not differ as a function of two-week feeding practices (i.e., feeding time or breastfeeding status), and no recovery scores differed as a function of two- or six-month effective non-oral soothing or of demographic variables.

RSA Stability. Consistent with prior work, by four months, baseline RSA was moderately stable through 4.5 years (*r*s = .28-.49). To examine the validity of using joint SNS-PNS functioning in the recovery period as an approximation of age-5.5 CAB, correlations between age-5.5 RSA during the recovery period and RSA at each previous time point were examined. With the exception of six-month RSA, which was marginally correlated with 5.5-year recovery period RSA ($r = .22$), four-month to 4.5-year RSA was moderately stable with 5.5-year recovery period RSA (*r*s = .27-.57). Two-week baseline RSA was correlated with four-, six-, and 12-month baseline RSA but not with 4.5-year baseline RSA or 5.5-year recovery period RSA (Table 4).

Feeding practices. At infant age two weeks, 125 infants were exclusively breastfed or combination fed, and 25 infants were not breastfed. Total time spent feeding over the course of four days, as reported in the two-week feeding diaries, ranged from 320 minutes (5.33 hours) to 2,160 minutes (36 hours; *M* = 16.04 ± 6.31 hours).

Infants who were breastfed at all at two weeks (*M* = 16.83 ± 6.66 hours) spent more time feeding at two weeks relative to infants who were not breastfed (*M* = 12.51 ± 2.36 hours), *F*(1, 58) = 4.46, $p < .05$. Mothers who breastfed at all at infant age two weeks were more highly educated (*M* = 15.96 ± 2.68 years) than mothers who did not (*M* = 13.76 ± 1.93 years), *F*(1, 148) = 15.15, $p = .00$. Married mothers were more likely than unmarried mothers to breastfeed at all at two weeks, X^2 (1, *N* = 150) = 5.71, $p < .05$. Breastfeeding status did not differ as a function of two- or six-month effective non-oral soothing, mother age, or infant sex. Two-week feeding time did not differ as a function of two- or six-month effective non-oral soothing; maternal age, education, or marital status; or infant sex.

Soothing practices. Two- and six-month effective non-oral soothing groups did not differ as a function of maternal age, education, or marital status or of infant sex.

Covariates to be included in main analyses. Because of their relations with variables of interest in existing research and in preliminary analyses reported above, maternal education and infant sex were included in main analyses of H1.4-5 and H2. In addition to their relations with infant physiology and feeding practices in the current study, prior work has also found relations among maternal education, breastfeeding status, and maternal sensitivity (Quigley et al., 2017) and between infant sex and PNS tone (Tibu, Hill, Sharp, Marshall, Glover, & Pickles, 2014). Because marital status was related to maternal education, *F*(1, 148) = 35.71, $p = .00$, such that married mothers had more years of education than unmarried mothers (16.11 ± 2.57 vs. 12.88 ± 1.51 years), and because maternal education was related to both feeding status and child physiology, maternal education was retained as a covariate in main analyses and marital status was not.

Tests of hypotheses

(H1) Physiological and behavioral predictors of health-promoting autonomic functioning.

(H1.1) Periods of RSA growth associated with CAB during the recovery period at age 5.5. A main effect of Berntson's CAB during the recovery period, $F(1, 32) = 5.27$, $p < .05$, $\eta^2 = .14$, showed that children with relatively lower-SNS/higher-PNS profiles had shown higher RSA from two weeks to 4.5 years. Contrary to expectations, an age by Berntson's CAB interaction, $F(4, 29) = 3.74$, $p < .05$, $\eta^2 = .34$, showed that children with relatively lower-SNS/higher-PNS profiles during the recovery period had shown greater RSA increases from 12 months to 4.5 years, $F(1, 32) = 10.56$, $p < .01$, $\eta^2 = .25$ (Fig. 4).

(H1.2) Periods of RSA growth associated with RSA during the recovery period at age 5.5. A main effect of RSA during the recovery period showed that children with higher RSA during the recovery period had shown higher RSA across early childhood, $F(1, 49) = 14.44$, $p < .001$, $\eta^2 = .23$ (Fig. 5). However, post hoc one-way ANOVAs examining RSA at each time point as a function of RSA during the 5.5-year recovery period (median split) showed that, although four-month, six-month, and 4.5-year RSA differed as a function of 5.5-year RSA, two-week RSA did not; and differences in 12-month RSA were marginal (Table 5).

Because the assumption of sphericity was not met, the Greenhouse-Geisser test of within-subjects effects was interpreted and showed a significant age by age-5.5 RSA interaction, $F(3.37, 165.22) = 5.65$, $p = .001$, $\eta^2 = .10$. However, within-subjects contrasts revealed only that children who had higher RSA during the recovery period had shown marginally greater RSA increases between 12 months and 4.5 years, $F(1, 49) = 3.43$, $p < .10$, $\eta^2 = .07$. Although this was unexpected, it should be noted that (a) the within-subjects repeated contrast was only marginally significant, and (b) there was likely insufficient power to detect effects of RSA change during growth periods hypothesized to be related to age-5.5 RSA, as observed power was .31 for the two-week to four-month period and .11 for the four- to six-month period (Cohen, 1988).

(H1.3) Periods of RSA growth associated with PEP during the recovery period at age 5.5. A marginal age by age-5.5 PEP interaction, $F(4, 29) = 2.17, p < .10, \eta^2 = .23$, suggested that change in children's RSA between time points differed as a function of their age-5.5 PEP during the recovery period. Due to the low power to detect effects (observed power = .57; Cohen, 1988) and the approaching-large effect size, within-subjects repeated contrasts were examined despite the marginal multivariate test. These showed that children with higher PEP (lower SNS tone) during the recovery period had experienced greater increases in RSA (greater increases in PNS tone) between 12 months and 4.5 years, $F(1, 32) = 7.19, p < .05, \eta^2 = .18$, relative to children with lower recovery period PEP (higher SNS tone; Fig. 5). Post hoc one-way ANOVAs revealed no differences in RSA at any earlier time point as a function of recovery period PEP (median split).

(H1.4) Correlates of two-week to four-month RSA change. A linear regression, Adjusted $R^2 = .55, p < .001$, predicted two-week to four-month RSA growth from breastfeeding status at two weeks (yes/no), feeding time at two weeks, and effective non-oral soothing at two months, controlling for infant sex, maternal education, and two-week RSA. Contrary to expectations, feeding time was not associated with two-week to four-month RSA change. However, greater two-week to four-month increases were predicted by breastfeeding status, $B = .31$, $p < .05$, such that infants who had been breastfed at two weeks showed greater RSA increases from two weeks to four months. Greater RSA increases were also predicted by two-week RSA, $B = -.78, p < .001$, such that infants with lower two-week RSA showed greater increases from two weeks to four months. As expected, two-month effective non-oral soothing did not predict RSA change.

(H1.5) Correlates of four- to six-month and six- to 12-month RSA change. A linear regression, Adjusted $R^2 = .17, p < .05$, predicted four- to six-month RSA growth again from breastfeeding status at two weeks (yes/no), feeding time at two weeks, and effective non-oral soothing at two months, controlling for infant sex, maternal education, and four-month RSA. However, contrary to expectations, only four-month RSA was significant, $B = -.50, p < .001$, such that infants with lower four-month RSA showed greater increases from four- to six-months.

A linear regression, Adjusted $R^2 = .24, p < .01$, predicted six- to 12-month RSA growth from breastfeeding status at two weeks (yes/no), feeding time at two weeks, and effective non-oral soothing at *six* months, controlling for infant sex, maternal education, and six-month RSA. Again, contrary to expectations, only six-month RSA was significant, $B = -.71, p < .001$, such that infants with lower six-month RSA showed greater increases from six to 12 months.

In light of relations with age-5.5 physiology, predictors of 12-month to 4.5-year RSA growth were also examined. A linear regression predicted 12-month to 4.5-year RSA growth, again from breastfeeding status at two weeks (yes/no), feeding time at two weeks, and effective non-oral soothing at six months, controlling for infant sex, maternal education, and 12-month RSA. Although, consistent with earlier models, infants with lower 12-month RSA showed greater 12-month to 4.5-year RSA increases, $B = -.91, p < .05$, the overall model was not significant. Results are presented in Table 6.

(H2) Predictors of age-5.5 RSA and PEP reactivity and recovery. Two general mixed linear models (MLMs) were used to examine children's RSA and PEP during the 5.5-year laboratory visit in relation to two-week feeding practices (breastfeeding status and feeding time) and effective non-oral soothing at six months, controlling for maternal education and infant sex. Because effective non-oral soothing at six months was not significant in either model, correlated with age-5.5 RSA or PEP in any task, predictive of RSA growth in (H1), or related to other variables of interest in preliminary analyses, it was trimmed from both models. Results presented below therefore reflect children's RSA and PEP as a function of two-week feeding practices (breastfeeding status and standardized time spent feeding), controlling for standardized maternal education and infant sex.

Because *reactivity* and *recovery* are operationalized as the difference between a branch's tone during (reactivity) or after (recovery) challenge and a baseline, a reference cell coding was employed such that positive within-subjects effects (i.e., task or task by feeding time interactions) indicated RSA or PEP values higher than during the first task during which cardiac monitoring was completed (emotion interview). In the RSA model, higher values indicate *increases* in PNS tone relative to the emotion interview. In the PEP model, higher values indicate *decreases* in SNS tone relative to the emotion interview.

RSA. Results are presented in Table 7. Children's RSA was higher during the movie, $B = .49$, $p = .001$, $f2 = .06$, baby cry, $B = .65$, $p < .0001$, $f2 = .10$, cry response, $B = .39$, $p < .05$, $f2 = .03$, and recovery period, $B = .57$, $p < .001$, $f2 = .07$, relative to the (earlier) emotion interview. A main effect of maternal education indicated that children of more-highly educated mothers showed lower RSA across the visit, $B = -.17$, $p < .05$, $f2 = .00$. A marginal main effect of feeding time suggested that infants who were fed for more time at two weeks may have shown higher RSA across the visit, $B = .01$, $p < .10$, $f2 = .00$. In partial accordance with (H2), a breastfeeding status by feeding time interaction, $B = -.02$, $p < .05$, $f2 = .00$, revealed that RSA only differed as a function of breastfeeding status for *low* feeding time babies (Fig. 6). In accordance with (H2), children who were fed for more time at two weeks showed greater RSA recovery (i.e., increases relative to the emotion interview procedure) during the recovery period, $B = .004$, $p < .05$, $f2 = .02$, relative to children who were fed for less time (Fig. 7). However, contrary to expectations, feeding practices did not significantly predict RSA reactivity in any task.

PEP. A marginal main effect of maternal education indicated that children of more-highly educated mothers showed marginally lower PEP (higher SNS tone) across the visit, $B = -3.94$, $p < .10$, $f2 = .00$. In accordance with (H2), breastfeeding status and feeding time at two weeks did not predict PEP reactivity or recovery. Children's PEP did not differ from levels of PEP in the emotion interview in any task.

Discussion

Causal pathways from early childhood experiences to adult health are likely complex. Developmental trajectories toward risk or resilience are explained not only by traditional risk factors such as smoking and physical activity, but by regulatory capacities and their inscription in the body and brain (e.g., Chen, Langer, Raphaelson, & Matthews, 2004; Dong et al., 2004; Thayer & Brosschot, 2005; Thayer & Lane, 2007). Cardiac autonomic balance (CAB) has emerged as a candidate biomarker of these pathways because it indicates the capacity of the SNS and PNS to regulate a diverse set of psychological and physiological functions. The SNS, PNS, and joint SNS-PNS determinants of CAB develop rapidly in infancy and early childhood, stabilizing by age five (Alkon et al., 2011; Bornstein & Suess, 2000); and the same profiles of SNS and PNS functioning associated with risk in childhood predict ill-health in adulthood (see Quigley & Moore, 2018 for a review). Despite the potential clinical import of this biomarker, however, little work has examined biobehavioral processes contributing to its development in the first five years.

With the current study, we took an initial step towards describing these processes, which may, particularly in low-risk settings, be best characterized using a developmental cascades model (for reviews, see Cox, Mills-Koonce, Propper, & Gariepy, 2010; Masten & Cicchetti, 2010; Thelen, 2000). According to this model, transactions among systems (e.g., parasympathetic, dyadic) alter developmental trajectories within, between, and among other systems, with far-reaching consequences for functioning in a broad range of domains. Although findings in the current study are descriptive rather than predictive, they provide initial evidence consistent with this perspective: Factors that promote PNS tone growth in the first four months may initiate a health-promoting cascade in which high PNS tone may elicit and be bolstered by external regulatory resources across time. This capacity for PNS regulation has been shown to decrease reliance on SNS reactivity, further easing recovery and keeping resting SNS tone low (Wolff et al., 2012). In this way, common caregiving behaviors in the first postnatal weeks and months may initiate a cascade of biobehavioral transactions whose consequences are evident in children's regulatory physiology five years later.

Stability of PNS tone and implications for CAB

Because CAB is determined primarily by the PNS in healthy adults (Cacioppo et al., 1994), we sought to better understand factors that foster health-promoting high PNS tone in infancy and early childhood. Longitudinal examinations of PNS tone across infancy and early childhood suggest that it stabilizes early—perhaps by two or four months of age (Bar-Haim et al., 2000; Bornstein & Suess, 2000); PNS tone has been found to be moderately stable from two months to five years ($r = .30$; Bornstein & Suess, 2000) and from four months to four years ($r = .46$, Bar-Haim et al., 2000), but not from one to three months ($r = .12$; Porter et al., 1995). In accordance with most of this prior work (Alkon et al., 2011; Bar-Haim et al., 2000; Bornstein & Suess, 2000; Izard et al., 1991; Porges et al., 1994; Porter et al., 1995; cf. Fracasso et al., 1994; Stifter & Jain, 1996), preliminary analyses on the current sample found that, by four months—but not two weeks—PNS tone was moderately stable through 5.5 years ($r = .27$). Resolution of this apparent perinatal instability into stable individual differences may be driven by genetic (i.e., "pre-programmed" differences that emerge over time) and environmental (i.e., calibration by experiences) factors and their interaction. One likely environmental factor (i.e., perinatal feeding practices) was examined in the current study and is discussed below. These results add to a growing literature indicating that the perinatal period is marked by shifting individual differences in PNS tone. In this way, the first postnatal month appears to be a window of PNS reorganization that proceeds alongside organization of biorhythms and acquisition of basic abilities (e.g., feeding, eliciting the caregiver; Feldman, 2007; Quigley & Moore, 2018; Schechtman et al., 1989). Although PNS determinants of age-five CAB are unlikely to be evident at birth, they may be detectable by four months of age.

While this period of instability may recommend the first four months after birth as a sensitive period for PNS development, normative decreases in PNS tone from birth to one month (Schechtman et al., 1989) may also reflect a protective mechanism by which lessor capacity for PNS reactivity decreases sensitivity to context as the individual undergoes the transition from womb to world. These two possibilities may reflect competing hypotheses or may operate sequentially, such that PNS buffering in the first month of life is followed by PNS sensitivity to context prior to stabilization at two to four months.

Pathways to health-promoting CAB at age five

High stability between age-4.5 baseline and age-five recovery period PNS tones ($r = .57$) suggested that recovery period PNS tone did, as proposed, provide an appropriate approximation of resting levels. Furthermore, relations between age-five recovery period PNS tone and earlier, baseline, measures were similar in magnitude to relations between age-4.5 baseline PNS tone and earlier measures. Together, these findings lend empirical support to our proposal that examination of physiological functioning in the recovery period would offer insight to children's CAB.

Children who showed health-promoting low-SNS/high-PNS CAB at age five had shown higher PNS tone across infancy and early childhood and greater PNS tone increases between 12 months and 4.5 years relative to their high-SNS/low-PNS peers (Fig. 4). To identify periods of PNS tone growth associated with PNS and SNS contributions to this profile—and to examine whether PNS and SNS determinants of CAB emerged from distinct developmental processes—we examined PNS antecedents of PNS and SNS tones during the recovery period individually.

Developmental antecedents of PNS determinants of CAB. Children with higher PNS tone during the recovery period at age five had shown higher PNS tone across infancy and early childhood, suggesting that lasting differences in PNS tone are detectable early in the first year of life. However, post hoc analyses revealed that, although children's PNS tones at four months, six months, and 4.5 years differed (and PNS tone at 12 months differed marginally) as a function of age-five PNS tone during the recovery period, two-week PNS tone did not. Visual inspection of Figure 5, together with findings that PNS tone was stable from four months to 5.5 years but not from two weeks to 5.5 years, also indicates that PNS tone trajectories had diverged by four months but had not at two weeks (Table 4). Therefore, factors that promote increases in PNS tone prior to four months of age may have lasting influences on PNS functioning. Age-five PNS tone during the recovery period—which is thought to determine PNS components of CAB (Berntson et al., 1991)—may bear the signature of these factors.

Two such factors were identified as predicting this salient period of PNS tone growth. First, infants with lower initial (two-week) PNS tone showed greater PNS tone increases than infants with higher initial PNS tone. This finding was common to all time periods examined (Table 6), likely because lower initial PNS tone allows for greater autonomic space to increase (Berntson et al., 1991). However, with the exception of PNS tone at four months (which was higher in male infants and in infants who had been breastfed at two weeks relative to female and non-breastfed infants, respectively), correlates of these individual differences in initial PNS tone were not identified in the current study.

Second, greater two-week to four-month PNS tone increases were observed in infants who were breastfed at two weeks, relative to infants who were not. This is consistent with the gustatory-vagal hypothesis that nutritive sucking induces PNS reactivity and recovery prior to acquisition of social regulatory abilities (Porges & Furman, 2011) and with proposals that the unique neuromuscular action of breastfeeding involve more strenuous exercise of the PNS than bottle-feeding (Quigley et al., 2017). Therefore, this early, daily PNS exercise may promote some degree of the PNS tone growth observed in breastfed infants between two weeks and four months. That two-week PNS tone did not differ as a function of breastfeeding status or age-five PNS tone during the recovery period indicates that these two growth-associated factors (i.e., lower initial PNS tone and breastfeeding) reflect two independent predictors of PNS tone growth rather than an elicitation of caregiving behavior by infant physiology.

An important competing hypothesis is that factors associated with breastfeeding status may have driven these effects on PNS tone growth. In the current sample, married and more highly-educated mothers were disproportionately likely to breastfeed at two weeks; and resources associated with these socioeconomic indicators have also been associated with individual differences in PNS functioning (e.g., Suurland et al., 2017). Although effects of breastfeeding on two-week to four-month PNS tone growth were independent of maternal education, statistical relations between breastfeeding and maternal education in the current sample make it impossible to truly disentangle their independent effects. These results will need to be replicated in a sample in which breastfeeding and socioeconomic status are less confounded.

Developmental antecedents of SNS determinants. SNS determinants of joint functioning during the recovery period at age five were associated with a different pattern of

PNS tone growth than were PNS determinants: Health-promoting low SNS tone was preceded by larger increases in PNS tone between 12 months and 4.5 years specifically, whereas health-impairing high SNS tone was preceded by smaller increases during this period (Fig. 5). Although we were unable to identify environmental correlates of these growth differences, prior research provides a framework for interpreting this pattern.

The low-SNS-associated surge in PNS tone between 12 months and 4.5 years accompanies acquisition of physiological and behavioral strategies for navigating new social-emotional demands. Between 12 months and 4.5 years, children develop self-regulatory abilities such as compliance and effortful inhibition (Thompson, 1991); increasing social reciprocity (Howes & Matheson, 1992); and capabilities in other domains that have been linked with emotional changes (e.g., autonomous movement; Pemberton Roben et al., 2012). These abilities require new strategies for regulating arousal and elicit new regulatory support from the environment, and their development proceeds alongside routinization of joint SNS-PNS reactivity patterns (Alkon et al., 2011), which may reflect a period of heightened cross-system influence. Therefore, quick growth in PNS tone during this period may reflect two mutually-influential processes: First, it suggests establishment of reactivity patterns characterized by relatively greater PNS than SNS reactivity, which facilitate PNS recovery and therefore heighten PNS tone over time. Second, by conferring expanding autonomic space for PNS reactivity, these PNS tone increases may shift the regulatory burden increasingly onto the PNS and off of the more metabolically-costly SNS (Berntson et al., 1991; Wolff et al., 2012). In this way, the surge in PNS tone growth observed in children with low SNS tone at age five may reflect routinization of PNS-reliant reactivity and recovery patterns that decrease dependence on the SNS. Consistent with McEwen's (1998) description of the process by which allostatic load accumulates or is avoided, this limited reliance on fight-or-flight responding in the face of mild, daily challenges is likely to maintain health-promoting low-SNS/high-PNS CAB.

This putative development of PNS-reliant reactivity and recovery patterns is likely shaped by support from external regulatory resources (Calkins et al., 2008; Oosterman et al., 2010; Oosterman & Schuengel, 2007). These effects were not detected in the current study, perhaps due to the measure used, a lack of concurrent measurement (e.g., of parenting practices at 12 months or during the preschool period), or to other factors (see *Null findings*, below). However, prior work indicates that regulatory supports in the environment scaffold PNS recovery in infancy and early childhood (Busuito & Moore, 2017; Conradt & Ablow, 2010). As these external resources become internalized in increasing PNS tone, which is associated with prosocial behavior in low-risk contexts by early childhood (Beauchaine, 2001; Conradt et al., 2013; Eisenberg et al., 2012; Sturge-Apple et al., 2016), the latter may support elicitation of positive engagement from their caregivers and peers (Kennedy, Rubin, Hastings, & Maisel, 2004). In this way, PNS growth between 12 months and 4.5 years may facilitate the "upward spiral" identified in adults in which higher PNS tone supports social connection, and social connection, in turn, leads to higher PNS tone, even independent of earlier PNS tone (Kok & Fredrickson, 2010). Consistent with Wolff and colleagues' (2012) findings that children who had shown greater PNS reactivity and had access to concurrent social support showed the least SNS reactivity in response to stress induction, this upward spiral may buffer the SNS from over-taxation by allowing reliance on the PNS *and* external resources to regulate. In this way, internal (PNS) and external (caregiver or other social support) regulatory resources may exert multiplicative, rather than additive, influences on children's development of regulatory physiology, as heightened capacity in one system may heighten capacity in others.

The fact that this putative "upward spiral" begins after infancy makes sense in light of developmental changes in behavioral correlates of PNS tone: Although high resting PNS tone is associated with prosocial behavior in low-risk contexts by toddlerhood (Beauchaine, 2001; Conradt et al., 2013; Eisenberg et al., 2012; Sturge-Apple et al., 2016), it is associated with greater positive *and* negative behavioral reactivity in infancy (e.g., Fox, 1989; Porges et al., 1994; Stifter & Fox, 1990; Stifter, Fox, & Porges, 1986). This is likely owing to infants' limited repertoires for communicating their needs, such that social engagement-facilitating high PNS tone in infancy may support both positive and negative approach-oriented behaviors (Beauchaine, 2001). Therefore, high-PNS-tone-supported behavior in infancy may not elicit positive responding from caregivers as reliably as would high-PNS-tone-supported behavior in early childhood.

In sum, these findings may point to a second window of opportunity for calibrating health-promoting CAB, perhaps specifically by protecting the SNS from over-taxation. Routinization of reactivity patterns between six months and five years, together with increasing abilities to elicit a range of caregiver responses to distress, may render sympathetic, parasympathetic, and social systems susceptible to cross-system influence during this period.

Effects of early feeding practices on PNS and SNS functioning at age five

Consistent with the gustatory-vagal hypothesis, early feeding practices predicted PNS, but not SNS, functioning at age five in a dose-response manner: More time spent feeding at two weeks of age predicted greater PNS, but not SNS, recovery following a series of mild stressors at age five (Fig. 7). This lends additional support to the theory that early feeding practices train the PNS for efficient reactivity and recovery in non-feeding situations and that effects of this PNS exercise are lasting (Porges & Furman, 2011; Quigley et al., 2017). To our knowledge, this is the first study that has identified a dose-response pattern between perinatal feeding practices and PNS functioning in a non-feeding context in the preschool period.

Contrary to expectations, feeding practices did not predict PNS *reactivity* (i.e., decreases in PNS tone) during the age-five lab visit. Although this is initially perplexing in light of associations between breastfeeding and PNS reactivity in infancy (Quigley et al., 2017) and between regulatory supports more broadly and PNS reactivity in the preschool and early elementary periods (Calkins et al., 2008; Oosterman & Schuengel, 2007; Oosterman et al., 2010), this may have been because the task against which reactivity was measured (the emotion interview) did not reflect a true baseline. Rather, children's PNS tones during the emotion interview seem to have reflected PNS reactivity that had already occurred (perhaps in response to coming to the lab, interacting with a new person, completing a non-contingent reward-punishment task, and having their mother leave the room). Consistent with this hypothesis, PNS tone tended to increase, on average, over the course of the lab visit (Table 3), suggesting movement toward recovery. Also in accordance with this proposal—and consistent with Porges' (2001) theory that the PNS evolved to support social engagement in mammals—the tasks in which children's PNS tone differed from the emotion interview involved little or no engagement with the research assistant. In these tasks (i.e., the movie, baby cry, response, and recovery period), children showed *higher* PNS tone than they had in the emotion interview. In interactive tasks (i.e., the movie interview, verbal fluency, and story recall), children's PNS tone did not differ significantly from that in the emotion interview, another interactive task. Given the emotional valence of both the movie and the baby cry tasks, these differences are not likely owed to differences in the degree of stress involved in the *task* but in the degree of stress involved in engaging with a new person.

It is also possible that, by age five, perinatal feeding practices predict PNS recovery only, and not reactivity. In accordance with this interpretation, children who were fed for more time at two weeks showed marginally higher PNS tone across the age-five lab visit than children who were fed for less time. This may have indicated faster movement toward recovery and/or higher resting PNS tone in these children, in which case they may have had higher PNS tone than others even when showing the same degree of reactivity. Of note, however, effects of feeding time on PNS tone across the visit differed for breastfed versus non-breastfed children: Breastfeeding only predicted distinct levels of PNS tone for children who were fed for low amounts of time at two weeks, such that *breastfed*, low-feed-time children showed *high* PNS tone and *non-breastfed*, low-feed-time children showed *low* PNS tone (Fig. 6). Although this was not hypothesized, it is consistent with proposals that nutritive sucking exercises the infant vagus prior to acquisition of social soothing abilities and that more exercise may yield greater benefits for PNS functioning. For children who were fed for moderate amounts of time, feeding method had no effect on PNS tone. However, for children who experienced less sucking-induced exercise (i.e., low amounts of feeding time), breastfeeding may have been required to produce heightened PNS tone. Because breastfeeding, which requires organization of suck-swallow-breathe patterns and involves distinct tongue movements from bottle feeding (Brown, 2007; Goldfield et al., 2006; Moral et al., 2010), may induce particularly strenuous exercise of the infant vagus (Quigley et al., 2017), infants may gain PNS benefits even with small amounts of breastfeeding time. Of note, however, only a subsample of two-week feeding diaries was available for analysis in the current study; results should be replicated in the full sample. As hypothesized, and consistent with the gustatory-vagal hypothesis that nutritive sucking operates specifically on the PNS, there were no feeding effects on age-five SNS functioning.

Effects of maternal education on PNS and SNS functioning at age five. Maternal education also exerted effects on children's physiological functioning, such that children of more-educated mothers showed lower PNS tone and marginally higher SNS tone across the visit. In this relatively low-risk sample, this may have reflected greater induction of stress or anxiety by (and greater need to regulate in response to) lab tasks in children of more-educated mothers. Prior research has found that children from affluent backgrounds may experience higher levels of anxiety than children in at-risk samples, perhaps owing to a "culture of affluence" marked by pressure to perform (Luthar, 2003). Additional research is needed to better understand these effects of maternal education on PNS and SNS functioning. Specifically, future work should examine whether relations between maternal education and child physiology are curvilinear, such that children of the most- and least-educated mothers show the most SNS and PNS reactivity in response to mild stressors.

Notably, effects of feeding practices and maternal education on PNS functioning in the current study were independent. Because more highly-educated mothers are more likely to breastfeed than less-educated mothers, it has been suggested that apparent breastfeeding benefits may be owed to mothers' IQ or socioeconomic status (Der, Batty, & Deary, 2006; Horta & Victora, 2013; Thulier & Mercer, 2009). Our findings of dose-response feeding time effects on children's PNS recovery, independent of maternal education, provide new evidence that feeding-associated benefits do not operate solely through breastfeeding *or* associated socioeconomic factors, particularly as feeding time was unrelated to demographic characteristics. This does not provide counter-evidence for breastfeeding or socioeconomic effects. Rather, the current study provides some evidence to suggest that socioeconomic status and perinatal feeding practices get under the skin via distinct mechanisms. And, importantly, feeding-associated benefits are not exclusive to breastfeeding: More time breast- *or* bottle-feeding at two weeks may confer psychological and physical benefits by bolstering the internal regulatory capacities conferred by quick PNS recovery.

Null findings

Contrary to expectations, effective non-oral soothing following inoculation did not predict PNS tone growth during any time period or PNS or SNS functioning at age five. This was in contrast to large bodies of existing research that have found associations between mothers' parenting behavior in infancy and children's PNS functioning (e.g., Busuito & Moore, 2017; Conradt & Ablow, 2010; Moore et al., 2009; Propper et al., 2008; for a review, see Propper & Holochwost, 2013) and between infant temperament and PNS functioning (e.g., Calkins, 1997; Huffman et al., 1998; Stifter & Corey, 2001; Stifter & Fox, 1990; Stifter & Jain, 1996). Null findings in the current study, therefore, may have been due to the measure of infant-mother soothing used, to the timing of these measures, or to other factors.

The measure used in the current study was quite different from those used in prior work, which has typically measured maternal behavior via sensitivity or attachment (e.g., Conradt & Ablow, 2010; Izard et al., 1991; Moore et al., 2009; Oosterman et al., 2010) or dyadic behavior via synchrony or flexibility (e.g., Busuito & Moore, 2017; Busuito & Quigley et al., 2019; Moore & Calkins, 2004). Our measure of effective non-oral soothing was computed from a set of maternal behavior and infant reactivity following inoculation (Jahromi et al., 2004). Unlike most other measures of dyadic behavior, this one distinguished among soothing *strategies* rather than measuring the degree of supportive behavior observed. Therefore, it may be that the means by which mothers soothe their infants has less of a lasting effect on children's autonomic functioning than whether or not that soothing takes place, and at the necessary time. Consistent with the concept of "good enough" parenting (Winnicott, 1965), successful internalization of external regulatory resources may simply require that those external resources—whether they are presented as holding and rocking, talking or singing, affection or distraction—be *available* in times of distress. In other words, the metric of caregiving quality that matters for development of regulatory physiology may be the degree to which caregiver behavior responds to the child's needs, rather than the precise form that that takes.

Conversely, it is also possible that the variable used in the current study was *insufficiently* sensitive. Although the trajectories of infant-mother soothing and typologies of dyadic regulation from which our variable was computed included fine-grained, temporally-situated information about dyads' regulation, we combined these typologies into just two groups ("effective non-oral soothing" and "oral soothing or ineffective non-oral soothing"). This was done to address specific questions in the current study as well as attrition between 12 months and 4.5 years that led to small cell sizes in age-five analyses. However, this may have cost us ability to detect effects of salient qualities of the dyad following distress. Of note however, preliminary analyses (not reported herein) using the original four- (at two months) and five- (at six months) typology clusters did not reveal relations with demographic factors, feeding practices, or physiology, suggesting that null findings are not owed entirely to the consolidation of the measure or to attrition prior to five years.

Another possibility is that the relevant factor is the infant's latency to soothe—which may be shortened in the presence of caregiver support. Children who are able to show quick behavioral recovery from distress are theoretically likely to show corresponding physiological recovery that cultivates health-promoting low-SNS/high-PNS CAB; and caregiver support has been shown to facilitate this recovery (Busuito & Moore, 2017; Conradt & Ablow, 2010).

Therefore, future work could examine whether a “latency to soothe” variable predicted subsequent physiological functioning and, specifically, latency to PNS recovery.

Lastly, in light of speculations (presented above) about factors that may promote the low-SNS-associated PNS tone surge between 12 months and 4.5 years, it may be that parenting behaviors need to be measured in this later period. Future research should examine whether, consistent with proposals above, PNS tone growth from 12 months to 4.5 years is contingent upon presence of new or heightened caregiver support in early childhood (i.e., controlling for caregiver behavior in infancy). This work should examine concurrent child PNS tone, child behavior, and caregiver behavior to test the “upward spiral” hypothesis (Kok & Fredrickson, 2010).

Limitations and Future Directions

It is necessary to note several limitations of the current study. First, multiple factors contributed to small analytic samples in certain analyses. Due the subsample of feeding diary data available at two weeks, attrition between 12 months and 4.5 years, and normative rates of physiological data loss at five years, some analyses may have lacked power to detect effects. Relatedly, disproportionate loss of PEP data for low-RSA infants and infants of less-educated mothers likely decreased variability in the sample. This may have made it harder to detect predictors of age-five SNS functioning. Therefore, these findings should be replicated in larger samples, and null findings in the current study should be interpreted cautiously. Specifically, relations between perinatal feeding practices and age-five PNS and SNS reactivity and recovery should be replicated using the full sample of two-week diary data.

Secondly, future work should corroborate these findings using a "true baseline" measure of CAB. Challenges with collecting baseline data in the lab have been noted by other researchers (Gunnar & Talge, 2007; Jessop & Turner-Cobb, 2008), leading to the development of physiological data collection methods that can be carried out in more naturalistic settings. Although the large correlations between children's 4.5-year baseline PNS tones and 5.5-year recovery period PNS tones (Table 4)—together with increases in PNS tone across the lab visit—support the use of CAB during the recovery period as an indicator of CAB at rest, future work should replicate these findings using a measure of CAB collected in a more naturalistic baseline setting.

Third, the current study did not include measures of SNS tone at two weeks, four months, six months, or twelve months, limiting our ability to examine early-life SNS contributors to joint functioning at age five. Now that methods have been developed to collect PEP in children as young as six months (Alkon et al., 2006), corresponding investigations of early cardiac SNS development should be pursued.

Fourth, the current study provides descriptive findings to guide future research. Future work, however, should employ analytic methods better equipped to test predictive and causal relationships. This will require larger sample sizes than were available in the current study.

Lastly, the current sample provides initial information about developmental antecedents of joint SNS-PNS functioning in a low-risk sample. In accordance with principles of developmental psychopathology, which hold that knowledge about normative developmental processes can inform understanding of pathological processes (Sroufe & Rutter, 1984), this is intended to lay the groundwork for future inquiries. Future research is now needed to investigate how early caregiving behaviors and PNS tone development across infancy and early childhood may predict later CAB in high-risk samples. For example, potential buffering effects of feeding practices or caregiving behaviors on PNS and SNS determinants of CAB should be explored. The examinations of SNS functioning in infancy discussed above will also be important in these higher-risk samples. This work might also elucidate whether CAB stabilizes at age five under all or only particular (e.g., e.g., low-risk, high-resource environments) conditions.

Conclusions

Calibration of health-promoting low-SNS/high-PNS CAB may begin in the first weeks of life. In low-risk settings, feeding practices in the perinatal period may be part of a developmental cascade in which establishment of high PNS tone confers autonomic space for the PNS to bear the regulatory burden, decreasing reliance on the SNS. As an internal regulatory resource, this high PNS tone may aid social engagement, eliciting additional support from caregivers and facilitating prosocial behavior with adults and peers alike (Kennedy et al., 2004; Porges, 2007). In this way, high PNS tone may initiate an “upward spiral” (Kok & Fredrickson, 2010) in which internal and external regulatory resources compound over time. Effects of this compounding between 12 months and 4.5 years may protect the SNS from over-taxation, yielding low SNS tone by age five. Furthermore, dose-response effects of perinatal feeding on age-five PNS recovery lend new evidence that this primitive soothing behavior may train the PNS for quick recovery even in non-feeding contexts years later. This efficient recovery may drive maintenance of health-promoting CAB. Taken together, results of the current study begin to describe a developmental process by which physiological profiles of risk or resilience may arise in the first five years of life.

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Tables & Figures

Table 1

Measures available at each age

Age	Measures		
	Physiology	*Feeding*	*Soothing*
2 wks	Baseline RSA	Breastfeeding status Feeding diary	
2 mos			Effective non-oral soothing
4 mos	Baseline RSA		
6 mos	Baseline RSA		Effective non-oral soothing
12 mos	Baseline RSA		
4.5 yrs	Baseline RSA		
5.5 yrs	RSA, PEP during lab tasks and recovery period		

Note. RSA = respiratory sinus arrhythmia. PEP = pre-ejection period.

Table 2

Descriptive statistics for two-week to 5.5-year RSA

	Full Sample		Breastfed at 2 weeks		Non-Breastfed at 2 weeks	
	N	*M (SD)*	*N*	*M (SD)*	*N*	*M (SD)*
2-wk RSA	144	2.87 (.95)	120	2.68 (.92)	24	2.91 (.95)
4-mo RSA	143	3.14 (.77)	121	3.20 (.76)*	22	2.79 (.80)*
6-mo RSA	140	3.06 (.75)	116	3.07 (.75)	24	3.01 (.79)
12-mo RSA	136	3.81 (.91)	113	3.77 (.86)	23	3.99 (1.16)
4.5-yr RSA	81	5.54 (.97)	57	5.52 (1.01)	10	5.53 (1.01)
5.5-yr *RP* RSA	73	5.88 (1.16)	48	6.07 (1.17)	11	5.85 (.98)

Note. *N*s for breastfed and non-breastfed children at ages 4.5 and 5.5 do not sum to the total *N* because of participants added between 12 months and 4.5 years. RSA = respiratory sinus arrhythmia. RP = recovery period. *Significant difference, $p < .05$.

Table 3

Descriptive statistics for child physiology during the 5.5-year laboratory visit

Measure	Task	*N*	Min	Max	*M*	*SD*
RSA	Emotion Interview	79	2.28	7.70	5.45	1.09
	Movie	81	3.14	8.80	6.13	1.21
	Movie Interview	79	2.75	7.73	5.58	1.09
	Verbal Fluency	78	3.22	7.87	5.53	1.07
	Story Recall	76	2.62	7.45	5.27	1.09
	Baby Cry	77	3.43	8.36	6.06	1.17
	Response	76	2.95	8.32	5.81	1.20
	Recovery Period	73	3.41	8.72	5.88	1.16
PEP	Emotion Interview	55	62.94	152.67	110.67	14.81
	Movie	57	59.04	156.19	111.10	17.80
	Movie Interview	57	70.05	150.32	112.57	15.51
	Verbal Fluency	56	63.86	142.00	112.58	13.94
	Story Recall	56	62.71	144.72	113.46	15.34
	Baby Cry	55	64.17	147.10	111.56	15.71
	Response	55	67.32	152.00	112.00	15.75
	Recovery Period	52	68.32	151.25	113.45	15.98
Berntson's CAB	Recovery Period	52	-3.42	3.14	.12	1.37

Note. RSA = respiratory sinus arrhythmia. PEP = pre-ejection period. Berntson's CAB = *z*RSA-(-*z*PEP), a computation of joint SNS-PNS functioning.

Table 4

Correlations among child RSA from two weeks to 5.5 years

Variable	2-wk RSA	4-mo RSA	6-mo RSA	12-mo RSA	4.5-yr RSA
2-wk RSA (Baseline)	--				
4-mo RSA (Baseline)	.29**	--			
6-mo RSA (Baseline)	.38**	.49**	--		
12-mo RSA (Baseline)	.28**	.28**	.35**	--	
4.5-yr RSA (Baseline)	.19	.33**	.32**	.45**	--
5.5-yr RSA (Recovery Period)	-.01	.27*	.22†	.33*	.57**

Note. RSA = respiratory sinus arrhythmia. $^{\dagger}p < .10$. $^{*}p < .05$. $^{**}p < .01$.

Table 5

Child RSA at two weeks, four months, six months, 12 months, and 4.5 years as a function of child RSA during the recovery period at 5.5 years

Age	Recovery Period RSA	*M*	*SD*	One-way ANOVA
2 weeks	Low	3.24	1.44	$F(1, 30) = .34, p = .56$
	High	3.51	1.17	
4 months	Low	3.07	.53	$F(1, 55) = 4.52, p < .05$
	High	3.43	.74	
6 months	Low	2.91	.59	$F(1, 57) = 4.18, p < .05$
	High	3.28	.76	
12 months	Low	3.61	.84	$F(1, 56) = 3.22, p < .10$
	High	4.00	.81	
4.5 years	Low	5.05	.82	$F(1, 63) = 26.43, p < .001$
	High	6.04	.73	

Note. Means, standard deviations, and ANOVA results are based on one-way analysis of variance tests in which child RSA at two weeks, four months, six months, 12 months, or 4.5 years was the dependent variable and a median split of child RSA during the recovery period at the 5.5-year lab visit was the between-subjects factor. RSA = respiratory sinus arrhythmia.

Table 6

Predictors of RSA growth in each period examined (H1.4 & 5)

	2 wks – 4 mos			*4 mos – 6 mos*			*6 mos – 12 mos*			*12 mos – 4.5 yrs*		
Variable	*B*	*t*	*p*	*B*	*t*	*p*	*B*	*t*	*p*	*B*	*t*	*p*
Intercept	**2.26**	**3.71**	**.00**	**2.17**	**3.22**	**.00**	**3.64**	**3.71**	**.00**	**7.46**	**3.68**	**.00**
Initial timepoint RSA	**-.78**	**-7.95**	**.00**	**-.50**	**-3.70**	**.00**	**-.71**	**-3.96**	**.00**	**-.91**	**-2.65**	**.02**
Infant Sex	-.07	-.71	.48	.05	.46	.65	.01	.09	.93	.21	.76	.46
Mother Education	.01	.21	.83	-.03	-.99	.33	-.05	-1.10	.28	-.17	-1.79	.10
Breastfeeding Status at 2wks	**.31**	**2.16**	**.04**	.17	1.12	.27	.06	.29	.77	.45	1.02	.32
Feeding Time at 2wks	.00	-.50	.62	.00	-.94	.35	.00	-.07	.94	.00	-.28	.79
Effective Non-Oral Soothing	.10	.97	.33	.07	.64	.53	-.09	-.54	.59	-.13	-.34	.74
R^2		**.60**			**.26**			**.34**			.44	
Adjusted R^2		**.55**			**.17**			**.24**			.20	
F		**12.05**	**.00**		**2.85**	**.02**		**3.32**	**.01**		1.84	.16

Note. “Initial timepoint RSA” is the infant’s RSA at the beginning of the growth period being predicted (e.g., two-week RSA for the two-week to four-month period; four-week RSA for the four- to six-month period). RSA = respiratory sinus arrhythmia. Significant terms are bolded.

Table 7

Child RSA as a function of 5.5-year lab tasks and perinatal feeding practices (H2)

	Coefficient	SE	*T*	*df*	*p*	*f2*
Baseline-Intercept	6.03	.44	13.73	19	.00	
Infant Sex	-.16	.15	-1.07	19	.30	
Mother Education	**-.17**	**.07**	**-2.61**	**19**	**.02**	**.00**
Movie Task	**.49**	**.15**	**3.21**	**149**	**.00**	**.06**
Movie Interview Task	.07	.16	.44	149	.66	
Verbal Fluency Task	.12	.16	.78	149	.43	
Story Recall Task	-.04	.16	-.24	149	.81	
Baby Cry Task	**.65**	**.16**	**4.16**	**149**	**.00**	**.10**
Cry Response Task	**.39**	**.16**	**2.49**	**149**	**.01**	**.03**
Recovery Period	**.57**	**.16**	**3.51**	**149**	**.00**	**.07**
Breastfeeding Status at 2 wks	-.23	.43	-.55	19	.59	
Feeding Time at 2 wks	.01	.01	1.74	19	.10	.00
Breastfeeding x Feeding Time	**-.02**	**.01**	**-2.34**	**19**	**.03**	**.00**
Movie * Feeding Time	.00	.00	1.40	149	.16	
Movie Interview * Feeding Time	.00	.00	1.80	149	.07	
Verbal * Feeding Time	.00	.00	1.82	149	.07	
Story * Feeding Time	.00	.00	1.04	149	.30	
Baby Cry * Feeding Time	.00	.00	1.11	149	.27	
Response * Feeding Time	.00	.00	.77	149	.44	
Recovery Period * Feeding Time	**.00**	**.00**	**2.00**	**149**	**.04**	**.02**

Note. Significant coefficients are bolded.

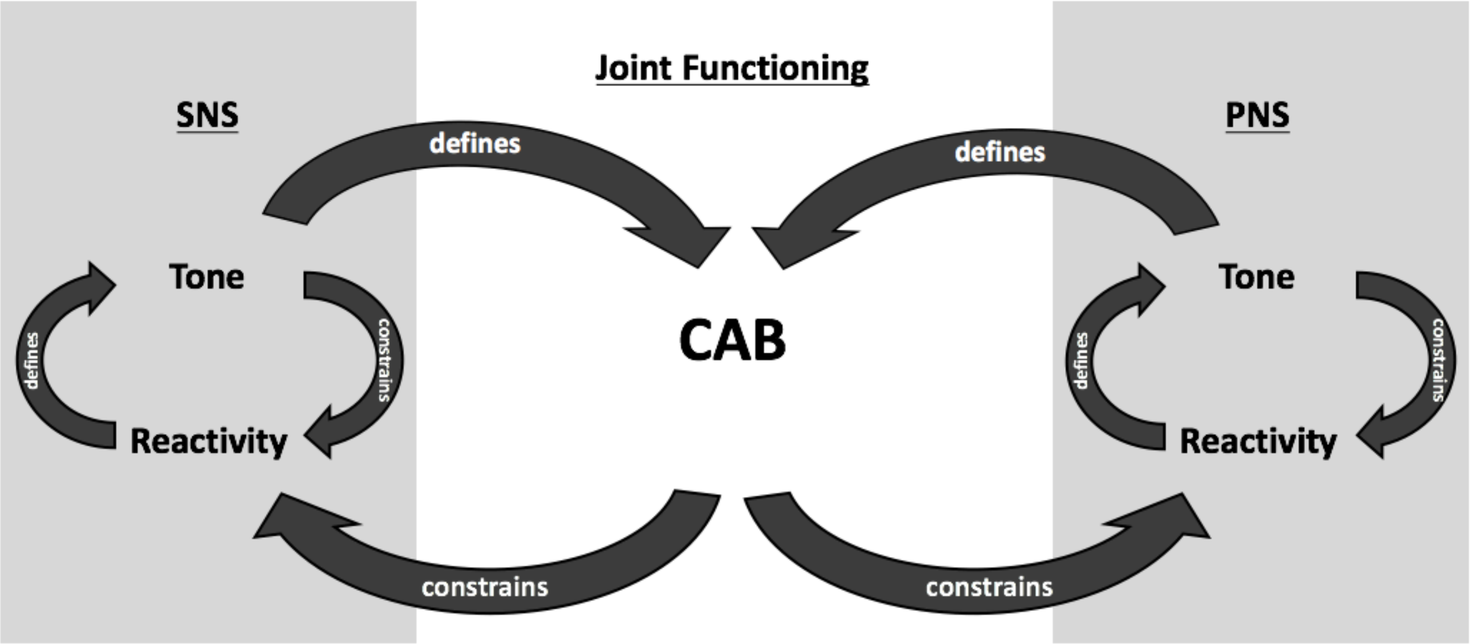
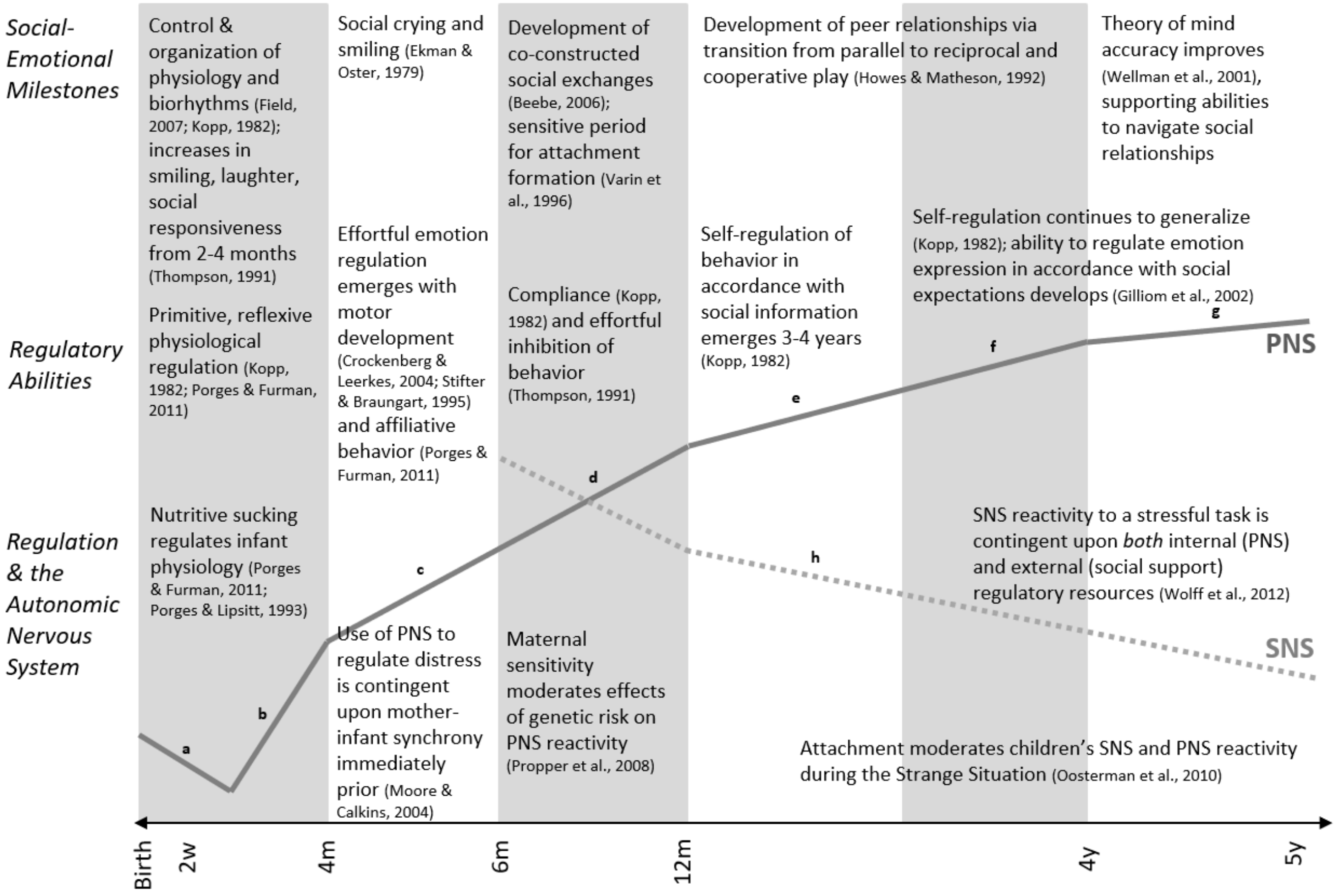


Figure 1. CAB constrains autonomic space for and is perpetually modified by SNS and PNS reactivity and recovery**.**

Reprinted from Quigley & Moore, 2018.



[a] Izard, 1991; Schechtman et al., 1989 [b] Bar-Haim et al., 2000; Izard, 1991; Schechtman et al., 1989 [c] Bar-Haim et al., 2000; Fracasso et al., 1994; Izard, 1991; Stifter, Fox, & Porges, 1989 [d] Bar-Haim et al., 2000; Porges et al., 1994; Stifter & Jain, 1996 [h] Alkon et al., 2011

Figure 2. Social, emotional, and regulatory development parallel maturation of SNS and PNS tones.

Reprinted from Quigley & Moore, 2018.

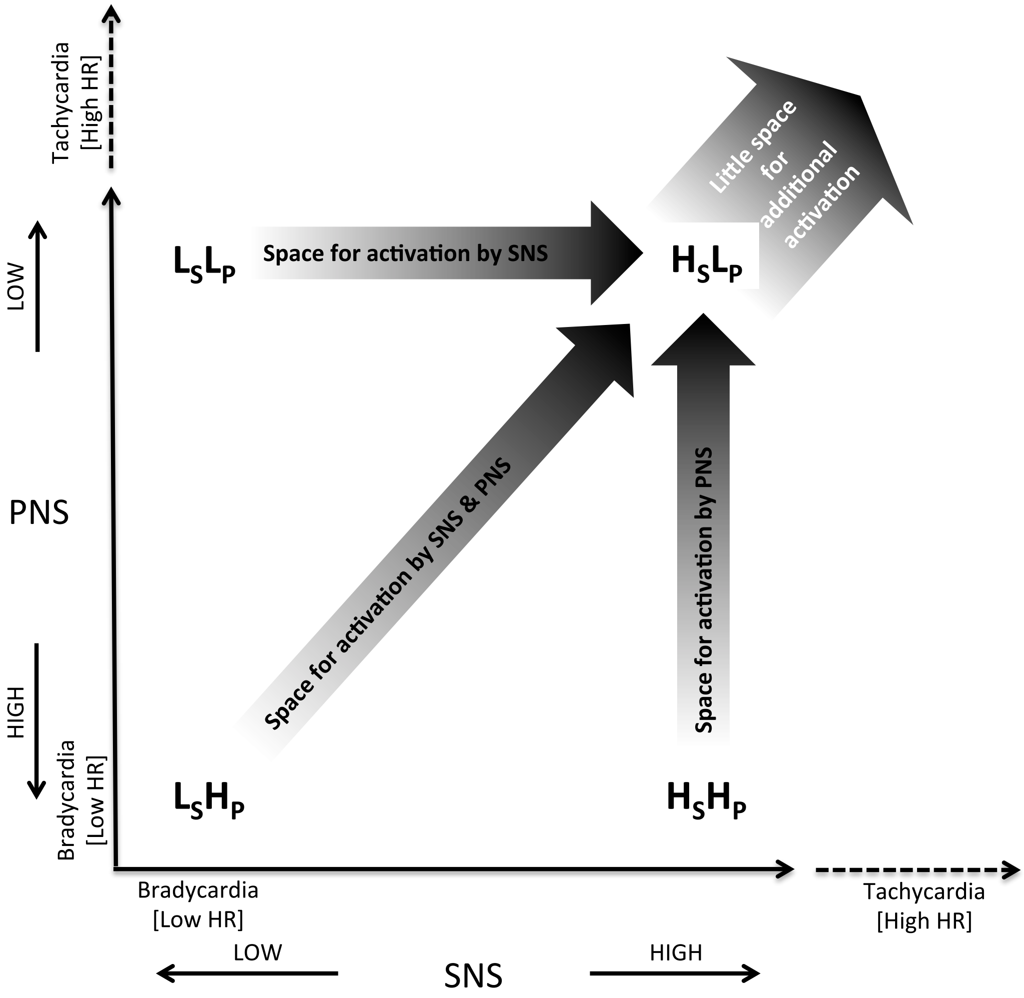


Figure 3. Cardiac autonomic balance constrains movement in autonomic space.

Points in space represent possible profiles of cardiac autonomic balance (CAB). (L = Low, H = High. Subscript S = SNS, subscript P = PNS.) Note that CAB is a continuous measure and may fall anywhere in this plane; however, the four points are used to illustrate space for adaptation conferred by CAB at different locations in autonomic space. Reprinted from Quigley & Moore, 2018.

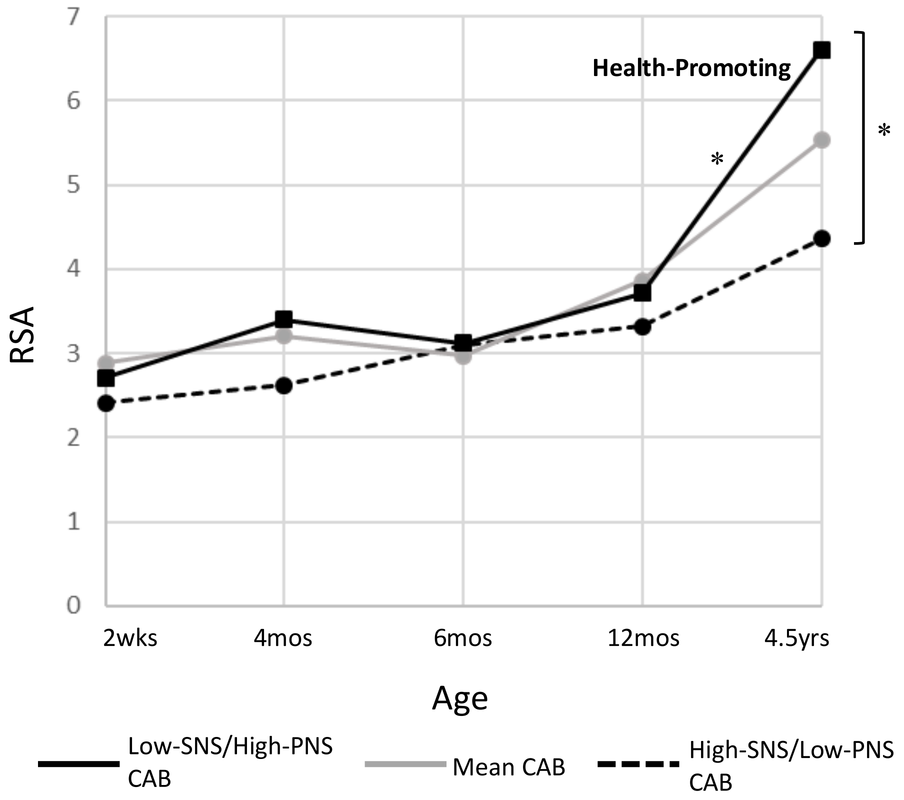


Figure 4. RSA growth from two weeks to 4.5 years as a function of CAB during the recovery period at age 5.5 *(H1.1)*.

A main effect of CAB, $F(1, 32) = 5.27$, $p < .05$, $\eta^2 = .14$, showed that children with relatively lower-SNS/higher-PNS profiles had shown higher RSA at each time point across infancy and early childhood. An age by CAB interaction, $F(4, 29) = 3.74$, $p < .05$, $\eta^2 = .34$, showed that children with relatively lower-SNS/higher-PNS profiles during the recovery period had shown greater RSA increases from 12 months to 4.5 years, $F(1, 32) = 10.56$, $p < .01$, $\eta^2 = .25$. “Low-SNS/High-PNS CAB” reflects CAB values greater than zero. “High-SNS/Low-PNS CAB” reflects CAB values less than zero. “Mean CAB” reflects mean values for the sample. RSA = respiratory sinus arrhythmia; CAB = zRSA-(-zPEP) (Berntson et al., 2008).

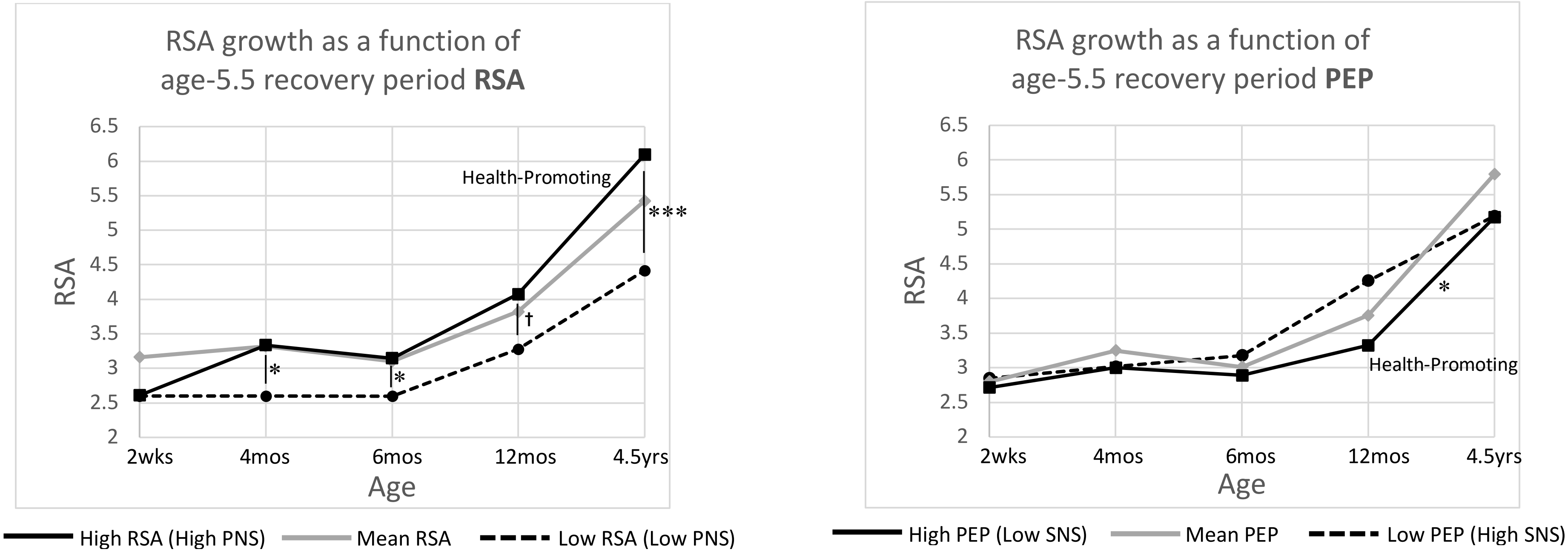


Figure 5. RSA growth from two weeks to 4.5 years as a function of RSA and PEP during the recovery period at age 5.5 *(H1.2 & 3)*.
A main effect of age-5.5 RSA showed that children with higher RSA during the recovery period had shown higher RSA across early childhood, $F(1, 49) = 14.44$, $p < .001$, $\eta^2 = .23$. However, post hoc one-way ANOVAs showed no significant differences at two weeks (Table 5). Children with higher age-5.5 PEP (health-promoting lower SNS tone) had shown greater RSA increases between 12 months and 4.5 years, $F(1, 32) = 7.19$, $p < .05$, $\eta^2 = .18$, relative to children with lower age-5.5 PEP (higher SNS tone). Low and high RSA and PEP lines reflect values 1 *SD* below or above the mean, respectively. Mean RSA and PEP lines reflect mean values. RSA = respiratory sinus arrhythmia; PEP = pre-ejection period.
†$p < .10$. *$p < .05$. ***$p < .001$.

Figure 6. Age-5.5 RSA only differs by breastfeeding status for children who spent low amounts of time feeding at two weeks.

"Low" feed time RSA values were calculated for feeding times ≤ 1 *SD* below the mean. "Mean" feed time RSA values were calculated for feeding times between -1 and 1 *SD* around the mean. High feed time RSA values were calculated for feeding times ≥ 1 *SD* above the mean; however, no non-breastfed babies fell into this category. Mean RSA for breastfed babies in the high feed time category was 5.74. RSA = respiratory sinus arrhythmia. *$p < .05$.

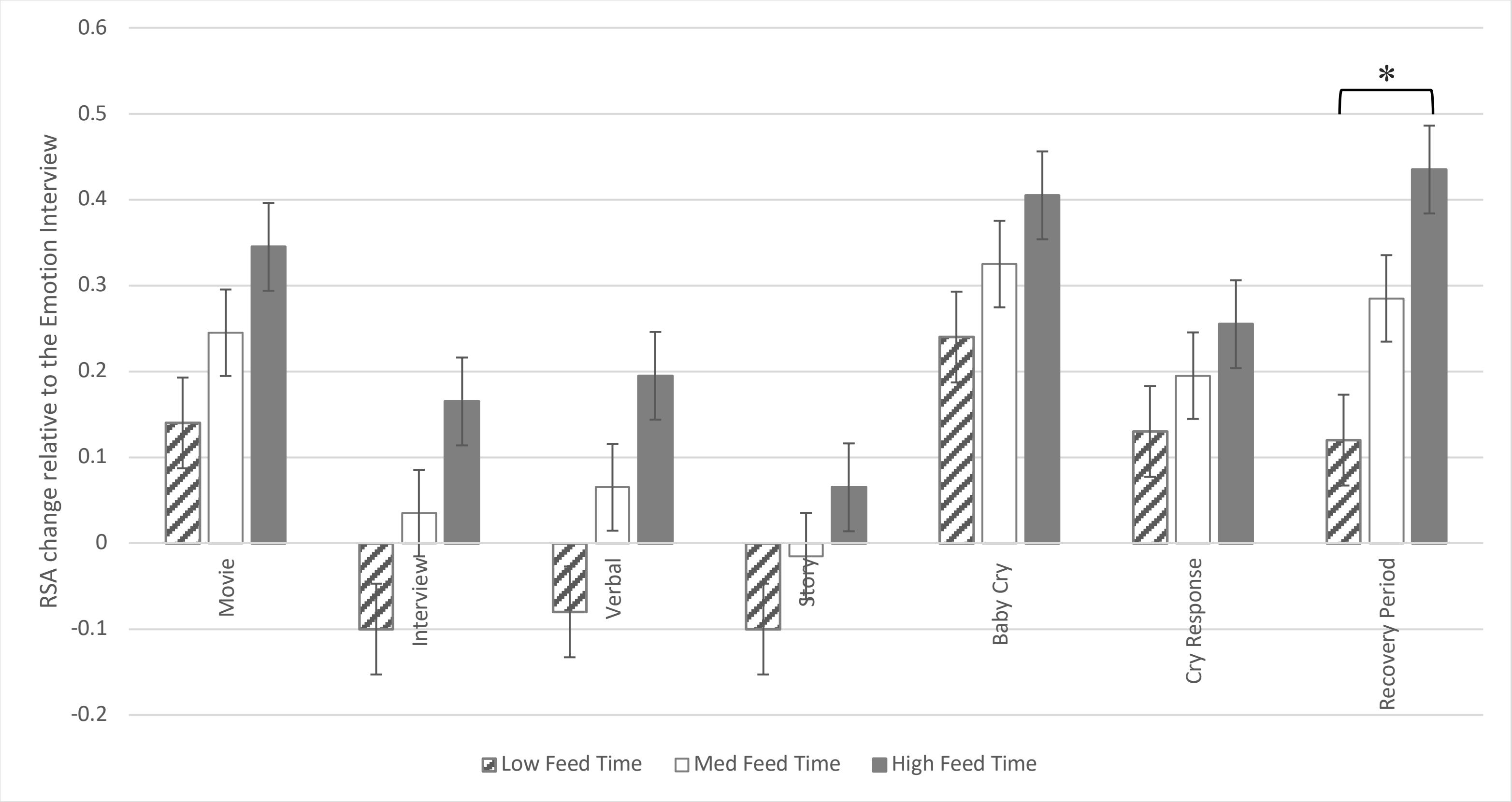


Figure 7. RSA reactivity or recovery in each task of the age-5.5 lab visit as a function of two-week feeding time *(H2)*. More time feeding at two weeks predicted greater RSA recovery during the recovery period at five years, $B = .004$, $p < .05$, $f2 = .02$. Error bars reflect standard errors. “Low feed time” reflects RSA change values for feeding times 1 *SD* below the mean. “Med feed time” reflects RSA change values for mean feeding time. “High feed time” reflects RSA change values for feeding times 1 *SD* above the mean. RSA = respiratory sinus arrhythmia. *$p < .05$.

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Education

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University Graduate Fellow, The Pennsylvania State University
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Human Rights Essay Prize, Harvard University
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Selected Papers

Busuito, A.* & **Quigley, K.***, Moore, G., Voegtline, K., & DiPietro, J. (2019). In Sync: Physiological Correlates of Behavioral Synchrony in Infants and Mothers. *Developmental Psychology, 55*(5), 1034-1045.
*These authors contributed equally to the manuscript. Author order was determined alphabetically.

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Cohen, J., Oser, C., & **Quigley, K.** (2013). Igniting the Policy Conversation: Bringing a Trauma-Informed Approach to Early Childhood System Building. *Zero to Three Journal, 34*(2), 24-33.

Melmed, M. & **Quigley, K.** (2012). Foreword. In Zigler, Muenchow & Ruhm, *Time Off with Baby: The Case for Paid Care Leave.* Washington, DC: ZERO TO THREE Press.

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