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Autonomic Regulation, Polyvagal Theory, and Children's Prosocial Development

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A team of linguists recently identified a small set of words, around two dozen, that have survived from their origins in an early Eurasiatic language that dates to some 15,000 years ago (Pagel, Atkinson, Calude, & Meade, 2013). That language might have given rise to more than 700 distinct known languages across the expanse of Asia and Europe. That these few "ultraconserved" words have weathered the millennia and appear in almost unchanged forms across disparate tongues in far-flung lands speaks to their essential, core function for the most enduring common elements of human communication.

Included in the list is the verb "to give."

Perhaps more than any other social mammalian species, the survival of humans has relied on our abilities to cooperate, trust, and help one another. Without question, humans can be selfish, untrustworthy, manipulative, and violent. Yet antisocial drives are not the sole motivators of human behavior, and in the history of our species these divisive impulses have been counteracted by prosocial motivations. We want to comfort and care for others, to share our efforts and belongings, and to know that others likewise will act prosocially toward us. To paraphrase Walt Whitman (1855, in Greenspan, 2005), "we are large, we contain multitudes." This complexity has bedeviled some evolutionary scientists who have focused singularly on the drive for survival of the individual organism, or individual gene. Yet, numerous sociobiologists have proposed models and presented data demonstrating that cooperative and altruistic acts can enhance the survival of social species (for review, see Hastings, Miller, Kahle, & Zahn-Waxler, 2014). In parents nurturing their young, in peers facilitating each other's play, and in neighbors sharing their tools, labor, and products, our ability to engage in harmonious social interactions has allowed us to endure and thrive.

Empathy is recognized as one of the primary, proximal motivations for engaging in cooperative, helpful, compassionate, and altruistic activities—in short, for giving of ourselves to benefit others. More than 200 years ago, Adam Smith (1759) proposed that our capacity to feel empathy for another's emotional circumstances was embodied in our own visceral responses. Modern evolutionary and functional theories of emotion continue this perspective, as emotional experiences involve changes in somatic and autonomic activity that prepare one to respond appropriately to the stimuli that evoke the emotions (Damasio, 2000; Hastings & Guyer, in press). Developmental scientists recognize that these approaches need to be ontological, accounting for the development of physiology, emotion, and behavior as children mature within the social spheres of their families, neighborhoods, and culture. Thus, an essential aspect of understanding the multidimensionality of prosocial development is examining how psychophysiological regulation underlies and contributes to children's emotional and behavioral responses to the needs and well-being of others.

Much of the research on the links between autonomic physiology and empathy or prosocial behavior in children and adults has been pursued outside of a particular theory or model. Yet, having such an overarching framework, based on current evolutionary and neurobiological knowledge, could provide structure and coherence for the complicated observations that have been made and could guide further efforts to understand the psychophysiology of prosocial development. In this chapter we propose that the polyvagal theory (Porges, 1985, 1995, 2007, 2011) can serve this purpose. Briefly, the polyvagal theory is a framework for understanding the evolution and regulatory functioning of the mammalian parasympathetic nervous system (PNS) through the influence of the 10th cranial nerve, or vagus nerve, on cardiac activity. Over more than 30 years of work, Porges has developed, refined, and validated his proposals that activity of the vagus nerve contributes to the self-regulation of attention, emotion, and social behavior. Empathy and prosocial behavior are included in—indeed, are central to—that set of adaptive competencies.

We begin by reviewing some of the basic neuroanatomy of the autonomic nervous system (ANS) and examine how this knowledge informed the early psychophysiological research on the development of empathy and prosocial behavior. We then expand on the polyvagal theory and how it places the vagus nerve at the center of a "social engagement system" that coordinates mammalian interactions and, in particular, supports the capacity for empathic, cooperative, and prosocial activities. The few recent studies on polyvagal theory and prosocial functioning are then considered, followed by our own recent research on parasympathetic regulation of emotion and children's empathic and prosocial development. We conclude with our reflections on the psychophysiological preparedness of children—and adults—to care, to help, and to give.

Autonomic Nervous System

The ANS is the rapid communication system between the central nervous system and the organs and smooth muscle tissues of the body, transmitting signals bidirectionally along its two primary branches, the sympathetic nervous system (SNS) and the parasympathetic nervous system (PNS) (Berntson, Quigley, & Lozano, 2007; Dawson, Schell, & Fillion, 2007). The SNS and PNS differ structurally and neurochemically in their modes of activity, but jointly function to prepare the body for quick responses to salient stimuli. Antagonistic models of homeostatic regulation suggest that the SNS and PNS work as oppositional forces, with sympathetic activity eliciting increases in autonomic arousal and preparedness for active coping (excitatory; "fight-or-flight") and parasympathetic activity reducing arousal and supporting vegetative states (inhibitory; "rest-and-digest"). These opposing influences serve to return arousal to some optimal set-point after an evocative stimulus has perturbed the system.

The SNS is part of the sympathetic adrenomedullary system, one of the body's primary stress-response systems. In response to perceived threats or challenges, the SNS triggers the release of epinephrine and norepinephrine from the adrenal medulla, which contributes to the fight-or-flight response of many tissues. The activity of the PNS is principally "down-regulatory," serving to soothe or slow respiration, heart rate, and similar functions. Thus, a withdrawal or reduction of parasympathetic innervations in the presence of an evocative stimulus can help to release resources for active coping. After the challenge has been met, increased influence of the PNS terminates the sympathetically induced somatic arousal and facilitates recovery, returning the body to a calm state.

Although there are times at which the ANS functions according to the homeostatic principle, and homeostasis has served as the basis for a strong history of psychophysiological research, many researchers now regard this antagonistic model as too simplistic a portrayal of the complex and dynamic ways in which the SNS and PNS control somatic arousal. For example, the alldynamic control model (Berntson & Cacioppo, 2007) recognizes that we are constantly facing changing stimuli throughout our daily activities that require modifications to arousal levels. Hence, a system of autonomic regulation that continually exerted effort to return one toward a single set-point of arousal would be inefficient. From this perspective, the two branches of the ANS work in reciprocal, independent, and cooperative ways to continually adjust the activity levels of our physiological states in order to support adaptive functioning. In effect, being physiologically well regulated entails being flexible and responsive to both external cues and internal needs.

MEASURING AUTONOMIC NERVOUS SYSTEM ACTIVITY

Most organs are innervated by both branches of the ANS, which exert varying degrees of dominant influence. Some widely used measures of arousal do not

allow researchers to draw precise inferences about the underlying causes of physiological change, because they are subject to both sympathetic and parasympathetic control. For example, general arousal can be assessed through increases in heart rate or blood pressure, but one cannot be certain of the extent to which these changes are due to greater sympathetic influence, to lessened parasympathetic influence, or to some interaction between the SNS and PNS. Fortunately, psychophysiologicalists have identified a set of noninvasive biological measures that can be attributed to the influence of one of the two branches.

More such measures exist for the SNS, and the first to be identified and still most widely used is the electrodermal response (EDR) or skin conductance levels (Dawson et al., 2007). The eccrine sweat glands are purely under the control of the SNS. Increased perspiration lowers the impedance of a weak electrical current between two electrodes applied to the skin, and measurement of that transmission provides an easy index of sympathetic arousal. Another measure gaining popularity is cardiac pre-ejection period (PEP), which is the duration of a brief component of a heartbeat called the electrical systole. Increases in sympathetic innervation shorten the PEP, which contributes to a faster beating of the heart (Berntson et al., 2007). Two more recently identified measures garnering the attention of developmental psychophysiologicalists are salivary levels of the enzyme alpha-amylase and pupillary dilation (changes in pupil size), although these are not exclusively influenced by the SNS.

To date, there is only one widely accepted, noninvasive measure of the PNS. The vagus nerve exerts a strong chronotropic influence on heart rate, affecting variations in the speed at which the heart beats, through its controlling influence on the sinoatrial node, the "pacemaker" of the heart (Berntson et al., 2007; Porges, 2011).¹ Although many factors affect heart rate variability (HRV), the specific component called *respiratory sinus arrhythmia* (RSA), or *cardiac vagal tone*, is recognized as an effective index of PNS influence on cardiac activity. Via the vagus nerve, the PNS establishes a coupling of the respiratory cycle and heart rate, with the interval between beats of the heart shortening slightly during inhalation and lengthening slightly during exhalation. Various statistical algorithms exist for isolating the specific frequency of HRV that corresponds to this coupled process, with the quantification of that frequency being called RSA. Increased parasympathetic influence is reflected in greater RSA, which usually (but not always) is associated with slower heart rate.

¹ Some developmental researchers have used a more global index of *heart rate variability* (HRV) as a measure of PNS regulation (e.g., Fabes et al., 1993, 1994). There are other contributors to HRV than the vagus nerve and coupling with the respiratory cycle, however, such that HRV cannot be treated as a precise and specific index of parasympathetic influence over cardiac activity. These studies have not been included in this review.

BASAL VERSUS REACTIVE PHYSIOLOGY

Activity of the ANS can be measured when people are in a quiescent state, in the absence of evocative stimuli. These basal or baseline measures often are characterized as individuals' typical levels of arousal, reflective of SNS and PNS activity in a calm waking state. Measures of reactive physiology consider arousal levels in response to salient cues or task demands. Usually, researchers are interested in knowing not only the level of SNS or PNS activity within the evocative context, but how the levels of activity have changed from the basal to the reactive state. Examining reactive change scores is thought to reveal how individuals are applying their sympathetic and parasympathetic regulation of arousal. Most developmental studies of reactive physiology have used fairly simple and static change scores, such as the arithmetic difference between measures of a given physiological index in the basal state and in an evocative context (Burt & Obradović, 2013). As we will discuss, these have increasingly been recognized as too simplistic for understanding the dynamic processes of physiological regulation (Hastings, Kahle, & Han, 2014).

Early Examinations of the Autonomic Nervous System and Prosocial Development

Because increased somatic arousal could support a motivation to withdraw from an aversive stimulus, some developmental researchers have argued that increased SNS activity in response to others' sadness, pain, or fear could reflect personal distress, which would interfere with other-oriented, prosocial engagement (Eisenberg, Fabes, Schaller, Carlo, & Miller, 1991). Conversely, it also has been proposed that orienting, attending, and responding to the needs of others could require mobilization of resources, such that increased SNS activity would support prosocial responding (Zahn-Waxler, Cole, Welsh, & Fox, 1995). There have been similarly opposing hypotheses put forward for the role of the PNS in empathic and prosocial responses (Hastings, Zahn-Waxler, Robinson, Usher, & Bridges, 2000). On the one hand, because effective prosocial behavior involves responding calmly to the needs of others, more "down-regulatory" parasympathetic activity, as indexed through higher RSA, could support such well-regulated, other-oriented actions. On the other hand, the distress or needs of another must be noticed for a prosocial response to be mounted, and reduced PNS activity, commonly called vagal suppression, might facilitate orienting or attending to those cues.

Findings reported in the developmental literature on the psychophysiology of empathy and prosocial behavior from the late 1980s through 2000 offered some support for all of these divergent predictions (Hastings, Zahn-Waxler, & McShane, 2006), though when considered collectively some patterns begin to emerge. A small majority of studies on heart rate and heart rate change suggested that

more prosocial children had lower basal heart rates or more slowing of heart rate when observing sadness, distress, or pain in others (e.g., Eisenberg, Fabes, Miller, et al., 1989; Fabes, Eisenberg, & Miller, 1990). But higher basal heart rate (e.g., Zahn-Waxler et al., 1995) or heart rate acceleration in response to stimuli (e.g., Holmgren, Eisenberg, & Fabes, 1998) also were linked with prosocial indices in some studies. Conversely, studies of the specifically SNS index of skin conductance were more consistent in showing that stronger basal conductance and greater EDR were associated with more distressed responses or less prosocial behavior (e.g., Eisenberg et al., 1991; Fabes, Eisenberg, & Eisenbud, 1993). Considered together, then, these early studies provided moderately consistent evidence that strong SNS activity could interfere with children's empathic and prosocial responses to the needs of others.

With regard to parasympathetic regulation, between 1993 and 2000 there were four studies of children's empathy, sympathy, prosocial behavior and personal distress responses that included measures of basal RSA or RSA during exposure to emotional distress in others (Eisenberg, Fabes, Karbon, et al., 1996; Eisenberg, Fabes, Murphy, et al., 1996; Hastings et al., 2000; Zahn-Waxler et al., 1995). All of these included multiple measures of children's emotions and behaviors, and all found that the majority of relations between RSA and children's emotions and behaviors were nonsignificant. Of the significant associations, children with greater basal RSA were characterized as less empathic or prosocial in two studies (Eisenberg, Fabes, Karbon, et al., 1996; Zahn-Waxler et al., 1995). Children with greater RSA during exposure to evocative stimuli were sometimes found to be more empathic or prosocial (Eisenberg, Fabes, Murphy, et al., 1996) and sometimes found to be less so (Eisenberg, Fabes, Murphy, et al., 1996; Hastings et al., 2000). Overall, the early research provided little evidence that parasympathetic control of cardiac activity was an important contributor to children's prosocial development.

So why have we continued to study RSA?

Polyvagal Theory in Social Mammals

Porges (2007, 2011) has constructed the polyvagal theory around the evolutionary needs of mammals to both control their metabolically costly and sympathetically driven high heart rates, and, in response to nonthreatening cues from conspecifics, to inhibit fight-or-flight responses that would interfere with social cohesion and cooperative action. Let's unpack those tenets.

More primitive and evolutionarily older species, such as reptiles, do not show evidence of RSA (Porges, 2011). They have lower cardiac demands when at rest, and their behavioral responses to evocative cues are limited to orienting, freezing, defensive posturing, and fleeing. Reptiles do not prolong their attention to gather further information, express emotions, or attempt vocal communication.

Conversely, warm-blooded mammals have high-capacity cardiac muscles that, if left unchecked, would beat very quickly (Porges, 2011). This rapid heart rate is driven by the sinoatrial node, which functions as the heart's pacemaker and attempts to drive a level of cardiac activity that is considerably above what we would consider to be typical resting heart rates. Consequently, unregulated cardiac activity would rapidly consume energy stores. Despite this, mammals also have a broader and more flexible range of behavioral responses to evocative cues, including prolonged attention, affective expression, and vocalization.

The polyvagal theory accounts for these biological and behavioral differences between species by the fact that, in mammals, the vagus is actually a family of nerves that originate in adjacent but distinct parts of the brainstem and that serve different metabolic and behavioral functions (Porges, 2007). Shared across reptilian and mammalian species is the mostly unmyelinated vagus nerve that descends from the dorsal motor nucleus of the vagus (DMNX) and contributes to orienting and freezing responses. It is also responsible for involuntary vegetative functions, such as digestion. Unique to mammals is the myelinated vagus that descends from the nucleus ambiguus (NA) and persistently inhibits the sinoatrial node; hence, it is the "vagal brake" on cardiac activity. The quantification of that chronotropic control, RSA, is solely the product of the myelinated vagus (Porges, 2011). This branch of the vagus system also is associated with other cranial nerves that originate in the NA, such as the facial and trigeminal nerves, that control head orienting, facial expressions, and activity of the throat and larynx—in other words, muscles that are essential for emotional and vocal communication and over which mammals can exert voluntary control.

Thus, Porges (2011) has theorized that the regulatory activity of the myelinated vagus serves as both a check on cardiac activity that allows mammals to be in calm states and as part of the mechanism for expressing or communicating that calm and nonthreatening state to others. Further, because it is solely the product of the myelinated vagus that descends from the NA, RSA provides an index of both of those regulatory functions. When a salient or evocative stimulus is detected, orientation and attention are needed, and some suppression of RSA (or "release of the vagal brake") can be expected in support of that orienting response. If the stimulus is perceived to be threatening or challenging, such that resources might need to be mobilized in support of active coping responses, then greater or prolonged RSA suppression would be expected. If the stimulus is perceived to be nonthreatening or safe, however, then RSA augmentation (or "applying the vagal brake") would support calm engagement with this context.

These evaluations of threat or safety can occur extremely quickly and without conscious awareness. Porges (2007) has proposed the term "neuroception" for the activity of neural circuits in the primitive parts of the brain that rapidly distinguish safe versus threatening situations or people and then trigger prosocial versus defensive motor action patterns, respectively. Cooperative social species cannot rely only on fight, flight, or freeze responses. Porges (2011) argues that "to create

relationships, humans must subdue these defensive reactions (in order) to engage, attach, and form lasting social bonds," and that "'Playing nice' comes naturally when our neuroception detects safety and promotes physiological states that support social behavior" (p. 12).

IMPLICATIONS OF POLYVAGAL THEORY FOR PROSOCIAL BEHAVIOR

Responding in caring and helpful ways toward another who is experiencing distress requires that one remain relatively calm rather than becoming distressed and focused on oneself. Calm and sociable engagement with others is supported by greater down-regulation of cardiac activity by the myelinated vagus. This parasympathetic regulation is reflected in higher RSA. Thus, maintaining relatively higher RSA when witnessing another in distress should be expected to support one's preparedness to respond to that distress in prosocial ways.

This is not to say that RSA suppression is reflective of poor parasympathetic self-regulation. Developmental studies have shown that children manifest RSA suppression in response to many stimuli and contexts, including films, puzzles, and social interaction tasks. Typically, RSA suppression has been measured using arithmetic or residualized change scores, and modest RSA suppression has been interpreted as a physiological index of effective emotion regulation (e.g., Katz & Rigterink, 2012). Indeed, a recent meta-analysis showed that children with more externalizing and internalizing problems tended to show less RSA suppression than children with fewer problems (Graziano & Derefinko, 2013). Intriguingly, though, the magnitude of RSA suppression was not reliably associated with indices of children's positive social functioning, such as peer relations, social competence, and prosocial behavior.

Inherent to the polyvagal theory is the proposal that there is not likely to be a simple linear association between emotion regulation and the magnitude of RSA change in response to stimuli (Beauchaine, 2012; Porges, 2011). Whether stronger RSA suppression, weaker RSA suppression, or RSA augmentation is reflective of effective parasympathetic regulation that supports adaptive behavior will depend on multiple factors (Hastings, Kahle, & Han, 2014). These include the nature of the social context or eliciting stimulus; different behavioral responses would be appropriate when encountering someone who is sad, versus scared, versus in pain, versus happy and friendly, and therefore different patterns of parasympathetic reactivity might be expected in these contexts. Analogously, distinct patterns of PNS regulation might be expected to support such prosocial behavioral responses as attentiveness and information processing, sympathy and compassion, or helpfulness and efforts to cheer someone up (Light & Zahn-Waxler, 2011). In addition, there are likely to be developmental changes in parasympathetic regulation; as children's emotional, cognitive, and social competencies mature, so too might there be changes in PNS activity that supports these competencies.

Finally, recognizing that emotional processes unfold over time, parasympathetic regulation needs to be considered as a dynamic process, rather than a simple difference between discrete states as suggested by static measures such as arithmetic or residual change scores (Brooker & Buss, 2010; Burt & Obradović, 2013). What is the shape of parasympathetic change over the course of an empathic episode? What is the magnitude of change at different points in time during empathy, rather than on average across an empathic experience? One might expect both RSA suppression and augmentation, perhaps occurring at different points during an empathic episode, to underlie children's ability to mount an appropriate prosocial response.

Our Recent Implementations of Polyvagal Theory

This perspective on the polyvagal theory grew out of our careful consideration of Porges's (2007, 2011) writings, but also from noticing in our own studies and in the wider literature findings that ran counter to the prevailing zeitgeist in developmental psychophysiology that more RSA suppression necessarily reflects better regulation (e.g., Marcovitch et al., 2010). Four recent studies of RSA change and displays of sympathy or prosocial behavior again produced divergent findings, but with a glimmer of a consistent pattern beginning to emerge (Hastings, Miller, et al., 2014). In two studies, more RSA augmentation (or less suppression) in response to empathy-eliciting stimuli was associated with greater sympathetic concern or compassion (Gill & Calkins, 2003; Oveis, Cohen et al., 2009). In two other studies, more RSA suppression (or less augmentation) to a challenging puzzle (Graziano, Keane, & Calkins, 2007) or an examiner feigning distress (Liew et al., 2011) predicted more prosocial behaviors like sharing and helping. Thus, mobilization of resources by the withdrawal of parasympathetic influence (RSA suppression) appeared to be associated with instrumental prosocial actions, whereas preparedness for calm social engagement by application of the vagal brake (RSA augmentation) was linked with positive, other-oriented emotional responses.

Our studies of RSA and emotion regulation also pointed to potentially beneficial roles of RSA augmentation. In an examination of the social engagement system, we examined preschoolers' parasympathetic activity during a brief play period with unfamiliar peers (Hastings, Nuselovici et al., 2008). Almost as many children displayed RSA augmentation relative to basal RSA as showed RSA suppression. In accord with Porges's (2007) concept of neuroception, we hypothesized that children who displayed RSA augmentation perceived the novel social context as safe for social engagement, whereas those who displayed RSA suppression saw it as an unsafe or intimidating situation. Supporting this, we found that RSA augmentation was associated with mothers' reports of children having better behavioral self-regulation and fewer internalizing and externalizing problems. Clearly,

taking context into consideration is important for understanding how PNS activity is related to adjustment.

We next tackled the issue of timing: How could we examine the chronometry of parasympathetic regulation as it unfolded over an emotional event? We decided to use latent growth curve (LGC) modeling (Bollen & Curran, 2006) to examine the slope of RSA change in response to emotion inductions (Miller, Chochol, et al., 2013). Examining repeated measures of RSA over a 60-second anger story that involved four narrated pictures, each presented for 15 seconds, we found that children exhibited RSA suppression from (1) the neutral introduction to (2) the initiation of anger, followed by RSA augmentation (or recovery) in (3) the intensification of anger and stable RSA through (4) the mildly positive resolution. The LGC analysis showed that the latent slope of nonlinear change was a better fit to the RSA data than were linear or quadratic slope models, with the changes over time reflecting an initial "release of the vagal brake" (RSA suppression, perhaps in support of an orienting response) as the angry content of the story was presented, followed by "applying the vagal brake" (RSA augmentation, which could support calm attention) while children watched the story unfold. That this overall pattern reflected effective parasympathetic regulation of emotion was evident in the fact that the latent, nonlinear slope predicted children's behavioral self-control, as assessed through their reports of not responding aggressively to peer provocations. Conversely, neither the individual RSA suppression nor RSA augmentation components were uniquely associated with control of aggression (Miller et al., 2013). Therefore, children's effective self-regulation of anger was captured in their capacity to dynamically and flexibly modulate their levels of PNS activity.

To directly test whether this approach to measuring parasympathetic regulation might inform our understanding of children's empathy and prosocial behavior, we recently applied these techniques in an examination of children's RSA in a typical empathy-induction paradigm: while they watched a sad film (Miller, Nuselovici, Chochol, & Hastings, 2013). During the empathy-induction film, children saw two 90-second stories, which both progressed from affectively neutral to depicting sadness strongly and then were resolved and returned to neutral content (Zahn-Waxler et al., 1995). The normative pattern of RSA change was nonlinear in shape, and very similar to what we had observed for RSA response to the angry story (Miller, Chochol et al., 2013). On average, children showed RSA suppression during the initial introduction of sadness followed by RSA recovery and augmentation during the intensification of sadness, and RSA at the (affectively neutral) end of the stories was not different from what it had been at the (neutral) start. LGC modeling again showed that a latent slope of nonlinear change was an excellent fit to the data and provided a picture of parasympathetic regulation that is more closely analogous to theoretical depictions of emotions as dynamic processes that correspond with rapidly changing events in the environment (Cole, Martin, & Dennis, 2004; Dennis, Buss, & Hastings, 2012).

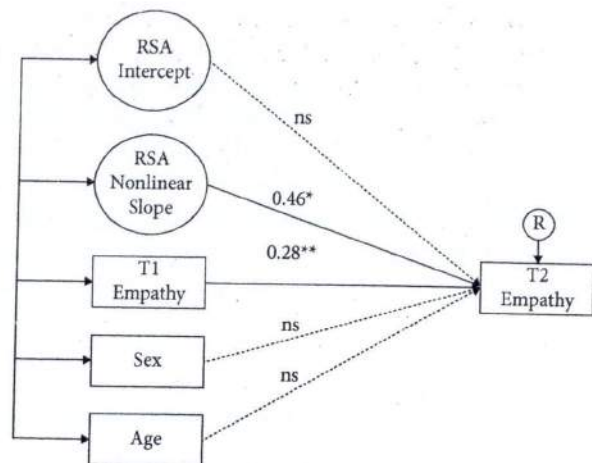


FIGURE 6.1 Latent slope of nonlinear RSA change during an empathy induction video predicts the development of empathic concern two years later.

Note: RSA = Respiratory Sinus Arrhythmia. * $p < .05$, ** $p < .01$, two tailed. Standardized path coefficients.

This was a longitudinal investigation. We observed children's behavior on the same day we measured their RSA and again 2 years later, when they returned to the lab. In both lab visits, the commonly used accident simulation paradigm (Van Hulle et al., 2013; Zahn-Waxler et al., 1995) was implemented to assess children's sympathetic and prosocial responses to distress in others, which were aggregated into a single measure of empathic concern (Hastings et al., 2000). Surprisingly, the latent slope of nonlinear RSA change was not associated with children's concurrent displays of empathic concern (nor were the separate measures of RSA suppression or augmentation). However, the latent slope significantly predicted the development of empathic concern over time. Controlling for children's initial empathic concern, children who showed more dynamic change in RSA (more suppression followed by more augmentation) displayed significantly more empathic concern in response to the accident simulations 2 years later (see Figure 6.1).

This finding suggests that flexible disengagement and reengagement of the PNS during empathy supports children's development of prosocial and sympathetic responding to the distress of others. During empathic experiences, initial RSA suppression may support orienting to the distress of others as an emotionally salient event, as well as helping to initiate related coping efforts. Subsequent RSA augmentation then may be important for reinstating a calm but socially engaged state that supports other-oriented rather than self-oriented responding. Thus, this dynamic measure of RSA could help to resolve the discrepancies in the past literature by illustrating that both RSA suppression and RSA augmentation,

albeit at different points during an emotional episode, are important for children's empathic concern.

As a final example, we examined the autonomic regulation of preschoolers' propensities for altruistic giving (Miller, Kahle, Lopez, & Hastings, 2013). Altruism is a form of prosocial behavior that requires sacrificing something of personal value for the benefit of others (Grusec, Hastings, & Almas, 2011). In this study, throughout a lab visit children were given tokens that could be traded in for a prize at the end. Before receiving the prize, children were given an opportunity to donate some, none, or all of their prize tokens to anonymous sick children so they also could get prizes. Children's PNS and SNS activity were assessed by recording RSA and PEP, respectively, while they received information about the opportunity to give to others in need, while they completed the altruism task, and afterward, while the examiner put away materials while chatting casually. There was, overall, very little change in sympathetic activity over the task, and children's PEP was unrelated to their altruistic giving. Conversely, children's parasympathetic activity was closely linked to altruism. Modeling analyses showed that children with greater parasympathetic activity (higher RSA) during the instruction period gave away significantly more of their tokens. While they were completing the altruism task itself, though, children who experienced greater RSA suppression also gave away more tokens. Finally, there was recovery of RSA during the concluding period, and children who had given away the most tokens also showed the most RSA augmentation.

This pattern closely parallels the aggregate picture from the four recent studies on RSA change and prosocial responding summarized at the start of this section (and see Hastings, Miller, et al., 2014), as well as the predictions of polyvagal theory (Porges, 2011). First, calm social engagement while learning about the opportunity to help others, as conferred by higher RSA, predicted more altruistic giving. Second, prosocial behavior was facilitated through preparedness for active but nondefensive coping, as RSA suppression released cardiac resources without requiring increased sympathetic activity (which would drive fight-or-flight responses). Third, having helped others in turn contributed to reestablishing a state of positive social connection, as reflected in RSA augmentation. Overall, children's willingness to give of themselves in order to help others was intricately linked to their capacity for flexible parasympathetic regulation.

Conclusions and Future Directions

The polyvagal theory is a powerful conceptual framework for organizing our observations of, and expectations for, the psychophysiological basis of prosocial development. An initial perception of inconsistency in the relations between PNS activity and children's empathy, sympathy, helpfulness, and altruism observed in

past research belies a deeper pattern of complex yet meaningful parasympathetic regulation. Flexible increases and decreases in the inhibitory influence of the myelinated vagus nerve on cardiac activity, as revealed by augmentations and suppressions of cardiac RSA, support children's calm attentiveness toward the needs of others and their ability to act on this empathic engagement in order to provide assistance. The magnitude and timing of these dynamic changes in parasympathetic influence are likely to be dependent on context, social partners, and specific cues, but the social engagement system is finely tailored to be adaptive to our complex social and sociable world.

There is still, of course, much to be learned about the psychophysiology of empathy and prosocial behavior. As developmental scientists, we are very concerned with understanding the origins and maturational course of autonomic regulation of emotional and social processes. Although facial expressions of sympathy in response to others can be detected in infancy (Roth-Hanania, Davidov, & Zahn-Waxler, 2011), we do not yet know how early in development parasympathetic activity begins to influence young children's empathic engagement with others. As well, recognizing the multidimensionality of prosocial development, it will be important to examine how PNS regulation becomes involved in regulating the cognitive, affective, and behavioral aspects of children's positive responses to others. Although the research of Eisenberg and colleagues (e.g., Eisenberg, Fabes, Murphy, et al., 1996) and others (see Hastings, Miller, et al., 2014; Hastings et al., 2006) has identified links between RSA and sympathy and prosocial behavior in children of varying ages, there has not yet been a comprehensive, developmental investigation of how the PNS comes to regulate the multidimensional aspects of prosociality.

Neurobiological regulation also is complex and multidimensional. The PNS is one branch of the ANS, which itself is one system within our complex neurobiology. Although most affective and developmental psychophysiologicalists examine distinct systems in isolation, we know that our genes, brains, hormones, ANS, and other neurobiological processes must function in integrated and interactive ways to support our emotional, cognitive, behavioral, and social functioning (Hastings, Miller, et al., 2014). Further, our close relationships, surrounding community, and cultural structures both affect the development of these neurobiological systems and modulate how physiological activity contributes to psychosocial activity (Hastings, Kahle, & Han, 2014).

Scientists are beginning to embark on such integrative, multilevel examinations of empathy and prosocial behavior (e.g., Feldman, 2012), and this research holds great promise for our future understanding of our capacities to be compassionately engaged with others. The polyvagal theory can play a key role in guiding these investigations, because the PNS clearly is one of the systems that has been shaped by evolutionary forces to support our capacity to be a cooperative social species. When we give, our heart is in the right place.

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