

# The Neurobiology and Physiology of Emotions: A Developmental Perspective

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## Abstract

This essay discusses the physiological and neural activity associated with emotion processes, with a focus on the development of this activity in children. We review some conceptual issues about the distinctions between the components of emotion, including the physiology associated with emotions themselves, attempts to regulate emotions, and trait or state patterns of responding. Foundational work examining autonomic nervous system activity is summarized, and we highlight recent work that attempts to investigate emotion processes in multiple systems. We then suggest that two fruitful avenues of future research include the examination of the neurobiology and physiology of social emotions, and further investigation into the temporal dynamics of emotion processes.

## INTRODUCTION

Research on the neurobiology of emotional processes has largely proceeded along two lines. Basic emotion perspectives drive the search for dedicated circuits for specific and discrete emotions in the brain, body, and behavior, whereas psychological constructionist perspectives seek shared underlying components or dimensions of activity in the brain and body that come together during the experience of many emotions. Common to these perspectives is the recognition that physiological activity is a critical component of emotion and that examining physiology offers a deeper understanding of emotion processes. Importantly, there appear to be typical responses of the brain and body that are specific to, or differentiate between, certain emotions, but also great individual variation in physiological responses to emotions that have implications for regulation, behavior, and adjustment.

In our work, we have focused on examining the development of the physiological aspects of emotion (Hastings, Kahle, & Han, 2014). A developmental

approach explicitly acknowledges that the etiology and ontology of adult functioning cannot be fully understood without identifying the origins and trajectories of emotions in childhood. In this chapter, we focus extensively on the activity of the autonomic nervous system (ANS) and how it is associated with two other core aspects of emotions and neurobiology: the brain and the hypothalamic-pituitary-adrenocortical (HPA) axis. We highlight the importance of multimethod research designs that integrate activity across multiple physiological systems, and we touch on some of the cutting-edge work in this area. We then put forth two areas of future work that we think would have exciting implications for our understanding of emotion in children—the physiology of social emotions, such as guilt and pride, and the temporal dynamics of emotion physiology. Throughout, we aim to provide greater insight into a few of the many interesting issues and exciting avenues of work in the study of emotion, biology, and development.

### DEFINING EMOTION

Functional and evolutionary theories of emotion posit that emotions are biologically based processes that facilitate adaptation to changing conditions (Campos, Mumme, Kermoian, & Campos, 1994; Cole, Martin, & Dennis, 2004). In response to an evocative situation, emotions ready the body to respond in order to either maintain circumstances that are positive or change those that are negative. Thus, emotions regulate thoughts, physiology, and behavior. Yet, emotions themselves can also be targets of regulation. Emotion regulation typically involves efforts to change the onset, duration, offset, or intensity of the physical, cognitive, and behavioral components of an emotion. How, and even whether, emotions are dissociable from emotion regulation is an area of ongoing discussion (Cole *et al.*, 2004; Thompson, 2011). In most of the work we describe here, the observed physiological and neural responses to emotion likely partially reflect children's attempts at regulating emotion in addition to their experience and expression of emotions themselves.

Another important distinction is that of trait versus state measures of emotion. Persistent moods or tendencies to feel certain emotions are distinct from emotion experiences that are temporary or in-the-moment. Similarly, baseline measures of physiology more likely reflect trait-like levels of activity in the brain and body, while measures of reactivity to an event or stimulus reflect a more specific, contextually-bound response. For example, we would expect a tendency to feel fear and anxiety to be reflected in a baseline measure of physiology, such as high resting heart rate. A transient fear experience would more likely relate to reactive physiology, such as an increase in heart rate. We discuss research addressing both of these issues.

An exciting problem for developmentalists is that all of these components undergo change during childhood. Physiological systems change with experience and maturity, meaning that even trait-like baseline measures can look different over time. Children increasingly experience more varied and nuanced emotions and become able to implement more sophisticated forms of emotion regulation. We next summarize classic and cutting-edge research that addresses these complicated developmental issues.

## FOUNDATIONAL RESEARCH

### AUTONOMIC NERVOUS SYSTEM

As the longest studied and arguably most well-understood aspect of emotion physiology, there is a rich history of work on the ANS. It is also a critical system for the functional aspects of emotion in that it prepares the organs and muscles of the body to act in accord with an emotion (e.g., releasing glucose in order to run in response to fear). The ANS is the bidirectional connection between brain and body, and while we argue later that studying both systems is important to capture this communication, examining the ANS provides an indirect way of studying central processing. We first summarize some foundational research using heart rate as an index of autonomic activity before discussing more recent attempts to parse the activity of the two autonomic branches from other cardiac measures.

Early work by Joseph Campos tended to conclude that in infants, heart rate deceleration was indicative of interest or attention, while heart rate acceleration was associated with fear or wariness, or negative affect more generally (e.g., Campos, Emde, Gaensbauer, & Henderson, 1975). In a handful of studies, sadness has been fairly consistently linked with slower heart rate in children, while anger and fear have been related to faster heart rate (e.g., Eisenberg *et al.*, 1988; Lewis, Ramsay, & Sullivan, 2006). Other researchers have interpreted heart rate acceleration as general arousal, which could be negatively or positively valenced (Field, 1982). The interpretation of changes in heart rate continues to be debated (Obradović & Boyce, 2012). Developmental changes in emotion processes may be one reason for the lack of clear associations between physiology and distinct emotions. Work by Campos and colleagues showed that autonomic responses to the same stimulus can change over time. As infants gained experience with crawling and heights, they began to show heart rate acceleration to a visual cliff, suggesting a fear response, while younger infants tended to show heart rate deceleration, indicative of interest (Schwartz, Campos, & Baisel, 1973).

Multiple factors determine heart rate, which may be another reason for inconsistencies. The parasympathetic nervous system (PNS) is generally

associated with restorative actions (e.g., digestion, sleep) while the sympathetic nervous system (SNS) generally prepares the body for activity (e.g., fight or flight behaviors), and both are associated with emotion. These opposing effects initially led researchers to consider the activity of the two branches as antagonistic; however, further work showed that the SNS and PNS interact in complex ways, including being coactivated or coinhibited (Berntson, Cacioppo, Quigley, & Fabro, 1994). Heart rate reflects the activity of both branches, but certain aspects of the cardiac cycle have been specifically attributed to PNS or SNS influence. Respiratory sinus arrhythmia (RSA) is a measure of heart rate variability that is controlled by the vagus nerve, which reflects PNS influence. Higher RSA means greater PNS influence. Preejection period (PEP) indexes heart contractility, the elapsed time between depolarization of the left ventricle and the opening of the aortic valve, which is under SNS control. Shorter (i.e., faster) PEP means more SNS influence.

Developmental work examining the specific role of the PNS in responding to social and emotional stimuli has been based considerably on Porges' polyvagal theory (1995, 2007). Because the vagus nerve, the primary efferent of the PNS, tonically downregulates cardiac activity, decreases in vagal influence can increase heart rate without mounting a sympathetic response, which has high metabolic costs. Research has generally shown that high baseline parasympathetic influence is related to more adaptive patterns of emotion expression and regulation (Beauchaine, 2001). However, what constitutes "adaptive" may change over development. An influential study by Porges and colleagues (1994) showed that at 9 months, greater parasympathetic influence was positively correlated with concurrent maternal ratings of difficult temperament, but predicted lower ratings of difficult temperament at 3 years. Early difficult behaviors might elicit parent responses that effectively support the child's attaining better regulation of emotion. Alternatively, the links between the PNS and emotion might undergo fundamental changes in early childhood.

A large body of work has also examined reactive change in parasympathetic activity during emotion. Emotion inductions tend to produce a decrease in PNS influence, or increases in arousal, but comparisons across different emotions in children are rare. In adults, anger and fear are associated with decreases in PNS influence, while sadness tends to be associated with parasympathetic activation. Positive emotions are often also linked with parasympathetic activation, although findings are more mixed (Kreibig, 2010). In general, a modest withdrawal of parasympathetic influence in response to social, emotional, or cognitive challenges tends to reflect self-regulation and positive functioning in children (Beauchaine, 2001; Blair & Peters, 2003; Marcovitch *et al.*, 2010). However, in line with

the polyvagal theory, maintaining high parasympathetic influence has been shown to support positive social engagement (Hastings & Miller, 2014; Hastings *et al.*, 2008).

The SNS is also sensitive to emotion. While RSA is the only noninvasive index of PNS activity, SNS activity can be measured several ways in addition to PEP. The SNS controls sweat gland activity, so skin conductance levels (baseline) or responses (reactivity) proxy SNS activity. Levels of the enzyme alpha amylase in saliva have also been linked to SNS activity. In children, having higher resting levels of sympathetic influence has been related to showing fearful behaviors, even in very mildly threatening circumstances (Buss, Davidson, Kalin, & Goldsmith, 2004). Fear and anger have been associated with increases in sympathetic activity reflected in shortening PEP or increases in skin conductance in children and adults (Baker, Baibazarova, Ktistaki, Shelton, & Van Goozen, 2012; Kreibig, 2010). Interestingly, research with adults also has distinguished between different aspects of positive emotional states. For example, happiness has been associated with increased SNS activity, but contentment with decreased (Kreibig, 2010). A parallel distinction has not been made in studies of children to our knowledge.

Recently, researchers have begun to look at the joint contributions of both autonomic branches by examining children's profiles of autonomic activity. Maturation changes lead to higher RSA and longer PEP at baseline, reflecting a resting state that becomes more parasympathetically dominated (Alkon, Boyce, Davis, & Eskenazi, 2011; Hinnant, Elmore-Staton, & El-Sheikh, 2011). There is some evidence for an analogous shift in reactive ANS activity as well (Alkon *et al.*, 2003), but more work is needed to confirm this finding. Profiles of autonomic activity also vary depending on the emotional context. In one study, a reaction time task produced profiles that involved sympathetic activation (and either parasympathetic activation or withdrawal), while a social interview produced patterns of parasympathetic withdrawal (and either sympathetic activation or withdrawal; Salomon, Matthews, & Allen, 2000). Some progress has thus been made in integrating the activity of the two branches of the ANS. However, the rest of the body's systems are similarly interconnected (Berntson & Cacioppo, 2007). Next, we discuss work that is beginning to examine these connections across multiple systems.

## CUTTING-EDGE RESEARCH

### MULTIPLE LEVELS OF ANALYSIS

Research on the physiology of stress overlaps with emotion research, and one reason why these constructs are connected is because the systems that

respond to stress and emotion intersect. One key stress-response system in the body is the HPA axis, which has as one of its primary outputs, cortisol, a neuroendocrine hormone that is easily measured via salivary secretions. Cross-talk among the brain and the autonomic and endocrine systems is critical to coherent and appropriate responses to emotions. Some brain structures appear to be especially involved in this integration of emotion information across systems, such as the anterior cingulate cortex and the hypothalamus (Berntson & Cacioppo, 2007; Dennis, 2010).

Some research has examined emotion processes across systems. In two studies, ANS activity was associated with young children's approach behaviors and emotions—both happiness and anger—while cortisol was associated with withdrawal emotions—fear and sadness (Fortunato, Dribin, Granger, & Buss, 2008; Lewis *et al.*, 2006). These systems show selective responses to stimuli, with the ANS priming the body to engage and act and the HPA axis promoting withdrawal. This also suggests that emotions associated with withdrawal behaviors (e.g., sadness) may produce more of a stress response than other emotions. This kind of specificity in emotion may facilitate targeted actions, thoughts, and behaviors to the situation at hand.

One reason why this line of research has not advanced further may be the dearth of theoretical models for how and when multiple systems coordinate. Miskovic and Schmidt (2012) have recently drawn on classic principles of approach/avoidance behavior to put forth a theoretical framework for brain–body interactions. They argue that the brain hemispheres, as well as autonomic inputs and outputs, are lateralized, such that the right side is associated with energy-consuming activities (SNS-driven cardiac acceleration, cortisol secretion), while the left side is associated with energy-replenishing activities (PNS-driven cardiac deceleration, inhibition of the amygdala). In support, they showed that fearful children had greater right frontal brain activity (as measured by electroencephalography; EEG), higher heart rate, and increased SNS and amygdala activity.

The notion that the brain and body encompass multiple, dynamically interacting systems may seem obvious, but the measurement, analysis, and interpretation of integrative physiology is extremely complex. Given that the connections between these systems—and the systems themselves—develop and change across childhood, much more theoretical and empirical work is needed to establish normative and aberrant patterns of physiological responses that correspond with emotion processes across development.

## FUTURE DIRECTIONS

Next, we highlight two directions for future work that would contribute to our understanding of the physiology of children's emotions. First, we suggest



a greater focus on the biology of social emotions, which have been underinvestigated in both children and in adults. Second, we recommend a closer look at the temporal dynamics of emotion physiology, particularly the termination of emotion responses and the return or recovery to baseline.

#### SOCIAL EMOTIONS

With the exception of empathy (Hastings, Miller, Kahle, & Zahn-Waxler, 2014), the biological correlates of social emotions have received less attention than those of basic emotions, particularly in the developmental literature. Emotions such as guilt, shame, pride, embarrassment, and empathy are termed “social” because some understanding of others’ minds is required. For example, in order to feel guilt, one needs to understand that they have caused some harm or disappointment to someone else. These emotions are also social in that they serve to promote social norms and rules.

Brain areas that are associated with social emotions are also implicated in other processes related to understanding the self and others, such as theory of mind, and broadly include the amygdala and areas of the frontal and temporal lobes (for a review, see Beer, 2007). One study has compared brain activity to embarrassment and guilt (vs basic emotions) in adolescents and adults (Burnett, Bird, Moll, Frith, & Blakemore, 2009). Both groups showed activity in the anterior rostral area of the medial prefrontal cortex (mPFC); but adolescents showed more lateral anterior rostral mPFC activation, whereas adults showed more left temporal activation. The suggestion that regions associated with these emotions change with development mirrors aspects of B.J. Casey’s work (Casey, Jones, & Hare, 2008) showing that differential trajectories of brain maturation influence adolescents’ impulsive decision making. It will be important for developmental affective neuroscientists to identify the functional or behavioral effects of these differences.

Embarrassment and shame have been associated with cortisol and protracted arousal in preschoolers (Lewis & Ramsay, 2002; Mills, Imm, Walling, & Weiler, 2008). Interestingly, Lewis and Ramsay (2002) found that this was only true for embarrassment that was in response to failure. Decreases in cortisol were associated with preschoolers showing embarrassment due to their success. This shows distinct associations between emotions and physiology that are context dependent, and is another instance of specificity in physiological responses.

Baker and colleagues (2012) found an interesting developmental association between fearlessness and guilt: behavioral and physiological indicators of fearlessness (low heart rate and SCL) in infancy predicted low physiological arousal during a guilt paradigm in toddlerhood. In order to feel guilt, one needs to understand that one’s actions caused someone else to feel bad, an

insight that infants may not be yet capable of. Yet, physiological signals to fear, which are present early in development and alert the infant to potential threats in the environment, may support the future interpretation of physiological responses to their own wrongdoing as threats to their social self. How earlier physiological responses to basic emotions may lay the foundation for later, more complex emotion experiences is an interesting question for future work.

Just as positive emotions, such as joy and contentment, have received less empirical attention than negative emotions, there have been fewer studies of the physiology of pride than of embarrassment, guilt, or shame. In a few adult studies, pride has been associated with increases in skin conductance, but little or no change in many other measures (Kreibig, 2010). Lewis and Ramsay (2002) found cortisol to be unrelated to pride in children, but further examinations of systems that are more likely to be active in response to positive emotions are needed in children.

#### TEMPORAL DYNAMICS

The experience and expression of emotion are processes that unfold over time. Thus, the physiological and neurological activity that accompanies emotion experience and regulation is dynamic; the systems that become active and the intensity of their activity varies over time (Fox, Kirwan, & Reeb-Sutherland, 2012). However, the use of repeated physiological measurements to capture these patterns (vs levels) of change are rare, perhaps due to the challenges involved in the measurement and analysis of dynamic change. Statistical methods that estimate latent variables—such as latent growth curve (LGC) models—are preferred for examining dynamic change because they account for measurement error and handle missing data (Bollen & Curran, 2006; Burt & Obradovic, 2013; Ram & Grimm, 2009). A few studies have moved beyond the use of simple change scores to examine patterns of change. Brooker and Buss (2010) provide one notable example. They found that highly temperamentally fearful 2-year-olds showed a pattern of increases followed by decreases in parasympathetic activity (as measured by RSA) when they were approached by a stranger (a somewhat frightening event for a toddler), whereas children low in temperamental fear showed stable levels of parasympathetic activity. However, fearful children who showed the dynamic pattern more strongly also showed greater positive affect, suggesting that this was a supportive physiological response for these fearful children. Examining the chronology of parasympathetic influence revealed that children with different temperaments might also utilize different regulatory mechanisms to achieve behaviorally similar responses to emotional challenges.



Recent work in our laboratory used LGC modeling to track RSA changes in 4- to 6-year-olds during a video clip of an angry vignette (Miller *et al.*, 2013). RSA decreased (i.e., parasympathetic withdrawal) when the anger theme was introduced, suggesting an orienting response, and then RSA increased as anger intensified in the video, suggesting a regulatory or calming response to the escalating emotion. Greater change in both directions was associated with better regulation of aggression, showing that more dynamic RSA change over the course of an anger episode is indicative of better parasympathetic regulation of anger.

Examinations of the dynamics of brain activity are gaining prominence, but thus far have been pursued primarily with adults. For example, Immordino-Yang and colleagues (2009) showed that feeling compassion for physical pain was associated with an earlier peak and faster extinction of activity in the anterior insula than for other social emotions. Thus, specificity in the physiological concomitants of emotions can be seen both in terms of which systems become active as well as the timing of this activity.

#### THE TERMINATION OF EMOTION: PHYSIOLOGICAL AND NEUROLOGICAL RECOVERY

Researchers are beginning to touch on one aspect of the time course of emotion that we think is particularly important but relatively understudied—the termination of the emotion and return to baseline. While physiological reactivity prepares the body to act in accord with an emotion, prolonged activation may inhibit adaptive behavior and flexible responding to ongoing events. Adult studies have begun to show that autonomic recovery from negative emotion is indeed distinct from reactivity, and is independently associated with variables such as social isolation, poor mental health, hostility, and high negative affect (Llabre, Spitzer, Siegel, Saab, & Schneiderman, 2004; Steptoe & Marmot, 2006; Zellars, Meurs, Perrewe, Kacmar, & Rossi, 2009). Similarly, delayed recovery in amygdala responses to negative images relates to higher levels of neuroticism (Schuyler *et al.*, 2012).

Only a handful of studies have examined recovery processes in children, and some links have been found with emotion regulation (Santucci *et al.*, 2008; Willeman, Schuengel, & Koot, 2009). We recently examined patterns of sympathetic and parasympathetic activity in 3 1/2-year-olds during a frustration induction and a post-task recovery period (Kahle, Lopez, Miller, & Hastings, 2013). During the task, sympathetic activity increased (shorter PEP) while parasympathetic activity decreased (lower RSA), meaning that both branches were working reciprocally to upregulate activity. After the task, sympathetic activity began to decrease but parasympathetic withdrawal continued, a pattern called coinhibition, indicating that the

branches were working in opposition. Only children's sympathetic recovery from frustration was associated with their mother's reports of adjustment. Children who showed greater sympathetic recovery (longer PEP in the post-task period) had higher levels of emotion regulation and effortful control. These relations suggest that while it is perhaps appropriate to show physiological activation to frustration, the ability to quickly shut off the sympathetic response once the situation improves is an adaptive response. This is also another example of a system-specific response. Only sympathetic activity during anger was related to regulation. While Miller and colleagues (2013) found meaningful relations between PNS activity and regulation in response to *observing* an angry interaction, this study found that SNS activity in response to the *experience* of anger and frustration was related to regulation. More work is needed to further investigate such possible contextual effects on the physiology of emotion.

## CONCLUSION

To describe one's racing heart or cold sweat in response to emotion is simple, but the scientific examination of these physiological phenomena is less so. Our synthesis of the careful work done thus far shows that we have learned quite a bit about emotions in the developing brain and body, but it has also been revealed how much we still need to learn. For example, one theme that emerged across studies is that some systems respond in specific ways to some emotions some of the time. Difficult questions about these aspects of context, timing, and multisystem involvement remain to be answered. Happily, in addition to gaining knowledge about these processes, we have seen important developments in the tools that might answer some of these tricky questions, such as multimethod, longitudinal designs, and dynamic analysis approaches. Further elucidation of the developmental aspects of the neurobiology and physiology of emotion will have important implications for our understanding of emotion. To answer questions about why people act and feel the way they do, we must look to the roots of emotional experience and responding in childhood.

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