



Toward a biologically grounded understanding of autonomic function in developmental science

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ABSTRACT

For over half a century, developmental scientists have used autonomic measures to draw inferences about the physiological mechanisms underlying infant attention, self-regulation, and social behavior. These interpretations rest on a binary model of the autonomic nervous system that divides it into opposing sympathetic and parasympathetic branches, a model established more than a century ago. This review traces the historical description of the autonomic nervous system and summarizes three challenges to the traditional model with evidence from contemporary biology and neuroscience suggesting that the classical model is incomplete. Spanning anatomy, molecular profiling, neurotransmitter phenotypes, and modes of autonomic control, we argue that the autonomic nervous system is more integrated than typically thought. These findings have practical consequences for how developmental scientists interpret physiological signals, including the commonly used measure of respiratory sinus arrhythmia (RSA). We conducted a survey of 316 peer-reviewed publications published in the past six and a half years that use RSA in developmental populations, showing that interpretations linking RSA to psychological outcomes relies heavily on the traditional autonomic model. We therefore ask what it would look like to reassess the autonomic nervous system free of the assumptions of the traditional model, providing considerations, guidelines, and recommendations for measurement, analysis, interpretation, and transparency. We support a modern, integrated, and multidimensional account of autonomic function grounded in contemporary biology and neuroscience, with data-driven models and interpretations of physiological signals in developmental science.

1. Introduction

For nearly 70 years, developmental scientists have measured the activity of the autonomic nervous system (ANS) in the pursuit of understanding the biological mechanisms underlying infant behavior and cognition (Bartoshuk, 1962a; 1962b; Bradshaw and Abney, 2021; Bridger and Reiser, 1959; Forte et al., 2019; Richmond and Lustman, 1955), from self-regulation (Fox et al., 2023; Pinto and Figuerido, 2023; Zeytinoglu et al., 2022) and attention (de Barbaro et al., 2017;

Lansink et al. Richards, 1985; 2010; 2011; Richards and Cameron, 1989; Richards and Casey, 1991; Tonnsen et al., 2018; Wass et al., 2016; 2019; Zhang et al., 2025), to attachment (Burgess et al., 2003; Roder et al., 2020; Madden-Rusnak et al., 2025), emotion (Abney et al., 2021a; Gatzke-Kopp and Ram, 2018; Lewis et al., 2006; Weiss et al., 2024; Zeskind, 2013), and emerging social interaction (Curtindale et al., 2019; Feldman, 2007; Feldman et al., 2011; Grochowska et al., 2024; Leclère et al., 2014; Stallworthy et al., 2024). Physiological measures derived from heart rate variability (Boris, 2022; Fox, 1989; Porges et al., 1973;

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Richards and Casey, 1991), such as respiratory sinus arrhythmia (RSA) (Abney et al., 2021b; Bradshaw et al., 2025; Richards, 1985; 1987; Steffen et al., 2026; Yurkovic-Harding et al., 2026), are widely used to infer the behavioral state and cognition of infants in screen-based tasks (Richards and Casey, 1991), naturalistic play settings (Borjon et al., 2024; Maitha et al., 2020), and at home (Geangu et al., 2023). Interpretations of how ANS activity influences behavior and cognition are typically guided, implicitly or explicitly, by a conceptual model of the ANS that is divided into sympathetic and parasympathetic branches defined by anatomical origin and presumed functional opposition (Box 1; Fig. 1). This binary push-pull framework dates back more than a century (Barboi and Macefield, 2025; Langley, 1903; Langley, 1921) and remains deeply embedded across the field of developmental science, shaping experiments, inspiring theories, and influencing interventions.

In this review, we trace the historical origins of the traditional ANS model (Section 2), and evaluate anatomical, molecular, and physiological evidence that reveals exceptions to the traditional dichotomy and instead favors an integrated model of ANS function (Section 3). Critiques of the traditional binary model are not new; evidence challenging the strict separation and functional opposition of sympathetic and parasympathetic activity have accumulated for decades (Barboi and Macefield, 2025; Ernsberger and Rohrer, 2018). This review strives to bring that evidence to the attention of developmental scientists and to ask what the consequences are for how developmental science should approach autonomic function. We examine how longstanding assumptions about the binary nature of the ANS have shaped key measures and developmental theories in a corpus of 316 peer-reviewed papers published in the past six and a half years (Section 4). We reflect more specifically on the need to revisit developmental theories and constructs including polyvagal theory (Section 5), RSA (Section 6), and arousal (Section 7). Across these examples, our aim is to bring attention to the inferential claims linking physiological and psychological functioning that arise from these embedded assumptions. We further outline recommended future directions for experimental approaches and for measurement and analysis practices that are grounded in multidimensional, data-driven dynamics, in order to provide developmental science with a more comprehensive, and reproducible account of how internal physiological states shape early behavior (Section 8).

2. Historical origins

The traditional model of the autonomic nervous system was built from anatomical and pharmacological observations in non-human

species more than a century ago, but its roots extend much further back. The Greek physician Galen (129–c. 216 CE) described nerves of involuntary motion that controlled the viscera, including the heart, stomach, and intestines. He distinguished these from nerves to muscles under voluntary control but did not define them as a separate system (May, 1968). Galen's descriptions were expanded upon during the Islamic Golden Age by physicians such as Al-Razi (854–925 CE) (Rhazes, 1486) and Ibn Sina (980–1037 CE) (Avicenna, 1593). Both emphasized that functions such as heartbeat and digestion occurred without conscious control, though neither proposed a distinct autonomic division; visceral innervation was still viewed as continuous with the rest of the nervous system.

The first major step toward isolating the ANS from the rest of the nervous system came in the late nineteenth century. Working with many non-human, non-primate, species, including rabbits, dogs, and dogfish, William Gaskell (Gaskell (1886); (1889)) mapped cranial (head), thoracolumbar (torso), and sacral (pelvis) outflows. He grouped the cranial and sacral outflows into a single “craniosacral division,” later formalized as the parasympathetic branch, based on an apparent shared feature of the efferent pathways: their projection to distal ganglia within or near the target tissue, bypassing the paravertebral chain, a distinction later summarized in terms of long preganglionic fibers synapsing on postganglionic neurons within the target tissue. In contrast, the thoracolumbar efferent pathways projected to paravertebral and prevertebral ganglia, where they synapsed onto postganglionic fibers that extend to effector tissues and were later characterized as short preganglionic fibers. These anatomical features seeded the conceptual opposition between “parasympathetic” and “sympathetic” branches and established the view that the two were anatomically distinct, occupying non-overlapping regions along the neuraxis (Barboi and Macefield, 2025).

In the early 1900s, John Newport Langley (Langley (1903); (1905); (1921)) extended Gaskell's structural framework with pharmacological experiments, linking sympathetic stimulation to mobilization-related functions and parasympathetic stimulation to restorative processes. Langley compared direct electrical stimulation of autonomic nerves with the systemic administration of pharmacological agents. Many responses to sympathetic nerve stimulation, such as increased heart rate, vasoconstriction in the skin and viscera, pupillary dilation, and reduced gut motility, were reproduced by adrenaline, consistent with a sympathetic role in mobilization and energy expenditure. On the other hand, pilocarpine and other muscarinic cholinergic agonists produced effects consistent with stimulation of the parasympathetic nerves, reproducing

Box 1

The classical view of autonomic function.

The autonomic nervous system (ANS) is classically defined as a set of involuntary circuits regulating internal organ function (Jänig, 2022; Langley, 1903; 1921). It comprises afferent sensory and efferent motor pathways linking the central and peripheral nervous systems (Loewy and Spyer, 1990) and influences diverse processes including heart rate, blood pressure, respiration, digestion, thermoregulation, and pupillary responses (Gibbons, 2019).

The ANS is classically divided into subdivisions based on anatomical classification and on assumed functional opposition between branches. Anatomically, thoracolumbar (torso) pathways are traditionally designated “sympathetic” and are bracketed by cranial (head) and sacral (pelvis) pathways which are designated “parasympathetic”. In addition, the “enteric” division, governing gastrointestinal function, is described as semi-independent but extensively interconnected with the other two (Furness, 2006; Langley, 1921). Functionally, sympathetic pathways are linked to mobilization, vigilance, and energy expenditure, while parasympathetic pathways are associated with rest, restoration, and reproduction (Cannon, 1928; 1929a; 1929b; Hess, 1948). In many accounts, these divisions act in a reciprocal “push–pull” fashion: sympathetic output accelerates heart rate and inhibits digestion, parasympathetic output slows the heart and stimulates digestive activity. Similar reciprocal logic has been applied to urinary, sexual, and pupillary reflexes (Gibbons, 2019; Jänig, 2022).

Although this binary model has been foundational for over a century, it represents a simplification that is increasingly challenged by modern anatomical, physiological, and genetic evidence, as discussed in the main text.

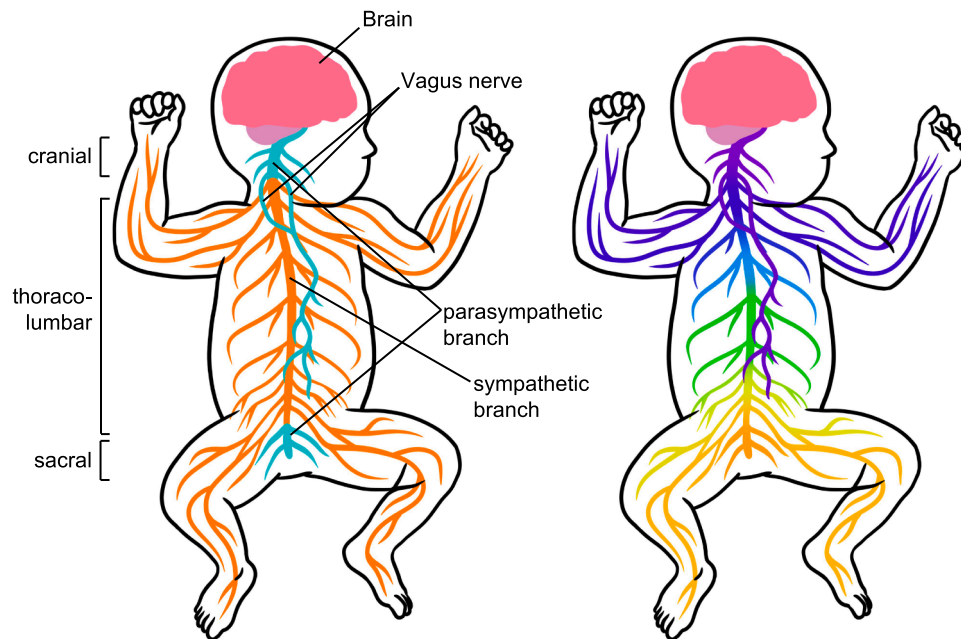


Fig. 1. Models of the Autonomic Nervous System. (Left) Traditional model of the ANS, with parasympathetic nerves in blue, and sympathetic nerves in orange. (Right) Integrated model of the ANS based on contemporary evidence, in which functional roles are not assigned to distinct anatomical regions but are instead distributed and mixed along the neuraxis.

their functional role in rest, digestion, and reproduction. Given the dual innervation of most visceral organs by both sympathetic and parasympathetic nerves, the relationship between the two came to be interpreted as one of functional opposition. In the 1920s and 1930s, Otto Loewi (1921) and Henry Dale (1934) built on this research to propose that most parasympathetic postganglionic neurons release the neurotransmitter acetylcholine. Ulf von Euler (1946) then identified norepinephrine as the neurotransmitter associated with the sympathetic nervous system, thus outlining a functional delineation between the two branches.

Langley's work and the synthesis that followed established the ANS as a distinct division of the nervous system, defined by the binary opposition of sympathetic and parasympathetic branches (Cannon, 1929b; 1939; Hess, 1948). This model has become deeply embedded in modern psychology and developmental science, where it continues to guide how autonomic measures are interpreted in relation to a range of constructs, including attention, regulation, and social behavior. However, at the time the model was developed, available physiological measurement tools were limited in their ability to capture simultaneous, system-wide activity. As the next section will show, modern molecular biology and neuroscience techniques reveal that key elements of the traditional model are no longer aligned with current evidence and the organization of the ANS is more integrated than previously thought.

3. Pitfalls of the traditional autonomic nervous system model

The traditional organization of the ANS into anatomically and functionally distinct sympathetic and parasympathetic divisions rests on three interrelated assumptions: (1) cranial and sacral outflows form a coherent parasympathetic system distinct from the thoracolumbar sympathetic division; (2) each division is characterized by a uniform and exclusive neurotransmitter type; and (3) the two divisions exert reciprocal control over shared targets. Most modern discussions related to ANS physiology rarely address exceptions to these assumptions, while others have noted that the underlying biology is considerably more complex and integrated (Barboi and Macefield, 2025; Verlinden et al., 2024; Jänig, 2022; Hayano and Yuda, 2019; Ernsberger and Rohrer, 2018). Here we describe three challenges to the traditional assumptions,

derived from contemporary biology, showing that the anatomical grouping of a craniosacral division should be re-evaluated, the binary divisions are not exclusively comprised of distinct molecular markers, and reciprocity is only one of several operational modes in autonomic control.

3.1. Challenge 1: Anatomical distinctions between parasympathetic and sympathetic divisions

The anatomical features of the cranial and sacral outflows, upon which Gaskell proposed a unified parasympathetic division, do not appear to be well supported by contemporary neuroanatomy. Gaskell assumed that the anatomical organization of the brainstem mirrored that of the spinal cord, but there are differences. Autonomic neurons of the spinal cord exit through ventral roots alongside somatic motor axons, whereas cranial autonomic neurons have a dedicated dorsolateral exit point, so preganglionic sacral neurons appear to share more gross anatomical organization with the rest of the spinal outflow than with cranial neurons (Espinosa-Medina et al., 2018). The brachial and lumbar "gaps" in autonomic outflow that Gaskell used to bracket the thoracolumbar region, framing the cranial and sacral outflows as a matched pair, do not hold up as true discontinuities: the lower-lumbar gap coincides with the lumbar plexus, while the rostral gap extends beyond the brachial plexus across the entire cervical cord (Espinosa-Medina et al., 2018). The sacral paravertebral chain, moreover, receives its preganglionic input not from the adjacent sacral cord but from the lumbar cord by way of the sympathetic chain, and the pelvic ganglion receives dual lumbar and sacral input, an arrangement more consistent with spinal than with craniosacral organization (Espinosa-Medina et al., 2018). On these grounds, an organization of the peripheral autonomic outflow into a cranial division and a spinal division encompassing the entire spine has been argued to describe the anatomy more accurately than the craniosacral grouping (Brunet, 2025; Espinosa-Medina et al., 2016; originally proposed by Nilsson, 1983). If the cranial and sacral ANS cannot be grouped together on anatomical grounds, then the parasympathetic may not be organized the way the classical model assumes.

3.2. Challenge 2: Molecular identity and neurotransmitter phenotypes across divisions

Molecular profiling also does not support a unified cranio-sacral division and instead reveals greater heterogeneity of ANS neurons than expected by the traditional model. Gene expression data shows that developing sacral preganglionic neurons in the mouse embryo express transcription factors associated with sympathetic neurons such as *Foxp1*, but lack markers associated with parasympathetic neurons such as *Phox2b*, *Phox2a*, *Tbx2/3*, and *Tbx20* (Espinosa-Medina et al., 2016, 2018; Brunet, 2025). Postganglionic neurons in the pelvic ganglion and associated intramural ganglia likewise exhibit a transcriptional identity consistent with sympathetic neurons, expressing *Islet1*, *Gata3*, and *Hand1* but lacking markers found in cranial ganglia such as *Hmx2* and *Hmx3* (Espinosa-Medina et al., 2016, 2018). The sacral autonomic outflow, thus, shares a developmental origin and molecular features with thoracolumbar, spinal, neurons, but not with cranial neurons.

In addition, recent transcriptomics show that the ANS contains multiple, molecularly distinct neuron types with specialized, tissue-specific functions rather than two opposing sets found in non-overlapping regions of the spinal cord. For example, single-cell RNA sequencing reveals four molecularly distinct neuronal classes in the postnatal mouse pelvic ganglion, which are more similar to thoracic sympathetic than to cranial parasympathetic neurons (Sivori et al., 2024). The thoracolumbar division also harbors molecularly distinct cell types. For instance, two mutually exclusive neuron classes exist in the coeliac–superior mesenteric ganglion, a cluster of nerve cells in the upper abdomen, one of which projects to the pancreas and bile tract to regulate bile and glucagon secretion, while the other projects to the stomach and lower intestines to control gut motility (Wang et al., 2025). Many further examples demonstrate that the ANS is comprised of a multitude of neuron types with modular and tissue-specific functions (Ernsberger and Rohrer, 2018; Furlan et al., 2016; Wang et al., 2025). Thus, the ANS may have clearer molecular subdivisions organized by target tissue than by position along the neuraxis.

Neurochemically, even Langley's early functional division of the ANS did not hold up to detailed examination. As early as 1921, it was known that the effects of sympathetic stimulation and adrenaline diverged during bladder contraction, certain bucco-facial vascular responses, and activation of skin muscles (Langley, 1921). Differing effects were also found between parasympathetic stimulation compared to pilocarpine during secretion from the sweat glands, contraction of the uterus, contraction of the spleen, effects on the small intestines, and on the retractor muscle of the penis (Langley, 1921). Although most sympathetic neurons release norepinephrine, some, such as those innervating sweat glands or the adrenal medulla, release acetylcholine or dopamine (Dale, 1934; Douglas and Rubin, 1961). Parasympathetic transmission is likewise non-uniform, with some neurons releasing nitric oxide or expressing catecholamine-synthesizing enzymes (Keast, 2006). Indeed, catecholamine markers are found throughout the nervous system, including nerves classically considered parasympathetic, such as the greater petrosal nerve, which is involved in tear and nasal gland secretion, and the pelvic splanchnic nerves, which target the bowel and reproductive organs (Verlinden et al., 2024). These markers do not by themselves establish noradrenergic transmission, since many such cells are sensory, transiently catecholaminergic during development, or dopaminergic (Verlinden et al., 2024), but their broad distribution is difficult to reconcile with an outflow partitioned cleanly by neurotransmitter phenotype. Together, these findings converge on the conclusion that mixed neurotransmitter phenotypes occur in both the parasympathetic and sympathetic divisions (Gibbins, 1995; 2004), contradicting the expectations of the traditional ANS model. Langley himself also cautioned that pharmacological sensitivity varied markedly across species and individuals within species (Langley, 1921). The molecular evidence redraws the boundary between sympathetic and parasympathetic and points to organization by target tissue, and the

neurochemical evidence shows that neurotransmitter phenotype does not track that boundary cleanly. The traditional division of the ANS, therefore, does not consistently rest on either molecular or neurochemical grounds.

3.3. Challenge 3: Reciprocity is one of several modes of autonomic control

The assumption that sympathetic and parasympathetic divisions exert reciprocal control over shared targets also faces many exceptions. Autonomic reciprocity has been based on the observation that most organs are dually innervated, and on the assumption that each division acts antagonistically to the other. However, a century of physiology and modern systems work shows that this is not a universal rule. Some targets are singly innervated, for example the sweat glands receive only sympathetic input, and the light and accommodation reflexes in the eye are controlled only by parasympathetic input (Richter, 1927). Even where dual innervation exists, effects can be cooperative rather than antagonistic, as in the synergistic control of erection and ejaculation (McKenna, 2013; Giuliano and Clément, 2005; Sjöstrand and Klinge, 1979), and control of the bladder and micturition (de Groat, 2013; de Groat et al., 2015; Espinosa-Medina et al., 2018).

Efforts to formalize autonomic control have gone further to apply flexible modes of control to the ANS as a whole. Berntson et al. (1991), (1993) proposed a two-dimensional autonomic space in which sympathetic and parasympathetic control constitute orthogonal axes rather than poles of a single continuum. Within this space the branches may change reciprocally, nonreciprocally (coactivation or coinhibition), or independently, with reciprocity representing only one diagonal of the proposed plane. A direct consequence is that a given end-organ state is ambiguous with respect to its autonomic origin. For example, multiple combinations of sympathetic and parasympathetic activity yield identical heart period values, so an observed cardiac response cannot by itself identify the pattern of control that produced it. This constrains what can be inferred from any index of "sympathetic-parasympathetic balance," which presupposes that the branches operate in obligatory opposition such that high parasympathetic tone implies low sympathetic activity and vice versa (Berntson et al., 2008).

While a two-dimensional view more comprehensively captures autonomic dynamics, it still presupposes that ANS activity is the product of two distinct systems. Recent multi-measure work suggests that high-density autonomic data does not inherently fall into the two-branch structure. Pasquini et al. (2023) recorded eight cardiac, vascular, respiratory, and dermal channels continuously during an emotional reactivity task and submitted the time series to principal components analysis. The recovered components did not map onto individual signal classes, and channels recombined across components in ways that the binary ANS model does not predict. Unsupervised clustering of the component time series yielded five recurring physiological states, each predominant during a different emotion-eliciting video. While this study was not designed to test branch structure directly, these results give no indication that a two-branch decomposition emerges from the data when it is not imposed. The biological validity and explanatory utility of the two-branch models warrants direct testing.

3.4. Summary of challenges to the traditional autonomic nervous system model

Combined, these findings invite us to reassess the assumptions of a traditional ANS model that is divided into sympathetic and parasympathetic branches with opposing functions. The parasympathetic grouping of cranial and sacral pathways was based on anatomical descriptions made a century ago, however the sacral outflows share neither anatomical nor molecular identity with cranial neurons but instead align more closely with the thoracolumbar division. Functional opposition was based on patterns observed in pharmacological experiments, however these experiments revealed exceptions early on, and

neurotransmitter phenotypes are not exclusive to either branch, with mixed and overlapping neurochemical profiles present across both divisions. Sympathetic-parasympathetic reciprocity is only one of several possible interaction modes, with context-dependent coactivation, synergy, and uncoupling, resulting in a potentially multidimensional autonomic state space. The traditional ANS model, along with the logic of dually opposing systems that promote either “rest and digest” or “fight or flight” functions, is appealing as a simple heuristic for thinking about autonomic physiology. However, the accumulating biological evidence suggests that the organization of the ANS is more complicated, with intermingled neuronal subtypes, organ-specific functionalization, and multivariate modes of autonomic control, not to mention variability between individuals, species, organs, and methods. This does not make autonomic measures uninformative. However, it means that mechanistic explanations involving the ANS need to move beyond the simple heuristics of the traditional model and towards biologically grounded and data-driven hypotheses, experiments, and interpretations.

4. Implications for developmental and psychological research

The biological validity of our model for the ANS has direct and important implications for developmental scientists. Interest has increased in recent years in understanding how the ANS influences developmental outcomes, often using autonomic measures to make inferences about regulatory capacity (Gower et al., 2011; Taylor et al., 2015), vulnerability to stress (Pereira et al., 2017), and social functioning (Patriquin et al., 2014). Autonomic measures and interventions are routinely interpreted in branch-specific terms, for instance, describing a reduction in heart rate variability following stress as reflecting sympathetic dominance, or attributing increased RSA during calm caregiving interactions to parasympathetic upregulation. RSA is a particularly poignant lens through which to examine these interpretive practices because it is regarded as one of the most highly validated measures of autonomic activity originating from the traditionally differentiated parasympathetic branch (Berntson et al., 1993; Porges, 2007) and is often used to draw conclusions about psychological and behavioral processes.

We conducted a survey using PubMed to produce a corpus of 316 papers published between January 1, 2020 and July 1, 2026 that measured RSA in participants under the age of 18 (see [Supplemental Appendix A1](#) and [B](#) for a detailed description of the search conducted and coding performed). Several clear and recurring themes are evident. First, nearly all papers (315, 99.7%) characterized RSA as an index of parasympathetic activity. It therefore appears likely that the traditional two-branch model of the ANS is still widely accepted within developmental science, despite evidence that the two branches may be less cohesive and less functionally distinct than the model assumes. The framing of these developmental papers therefore rests on a chain of inferential steps: first, that the ANS can be meaningfully partitioned into clear parasympathetic and sympathetic branches and second, that RSA is a sufficiently specific indicator of parasympathetic activity. Next, most (271, 85.8%) used RSA as a proxy for a psychological or behavioral construct such as self-regulation, stress response, or emotional reactivity. Thus, the inferential chain is extended further, with 257 (81.3%) of the papers reinforcing their interpretations through highly cited theories of autonomic control, particularly polyvagal theory, which proposes that a vagal “brake” regulates the heart to support flexible engagement with changing social and environmental demands (Beauchaine, 2001; Porges, 2007). Invocation of such theoretical frameworks can lend an appearance of biological validation to the inferential chain, even when the biological assumptions underlying the theory itself remain contested and justify re-examination (see [Section 5](#) below).

Furthermore, if repeated use is treated as evidence that the inferential chain is sound, then the same assumptions can become self-reinforcing. The limited use of complementary autonomic measures is

one indication of the extent to which confidence in the ubiquity of RSA is reflected in research practice. As it stands, within our corpus, only 95 papers (30.1%) included a second measure of autonomic activity, such as heart rate, cardiac preejection period (PEP), electrodermal activity (EDA), or cortisol, etc., meaning that in more than two-thirds of studies (221, 69.9%), conclusions about autonomic functioning were based exclusively on RSA or other measures of heart rate variability. This limitation has consequences in developmental science because it means researchers entrust their psychological and behavioral conclusions to a single reciprocal dimension that risks discarding information that may be essential for understanding individual differences and their developmental consequences. Alternatively, multivariate models of autonomic control built on multiple measures have been discussed for decades (Berntson et al., 1991; 1993; 1994a; 1994b; 1994c; 2008; Pasquini et al., 2023). For example, efforts to measure activity across the presumed branches of the ANS have produced composite indices of autonomic influence on the heart. Thus, combining RSA with pre-ejection period, a sympathetic index, yields cardiac autonomic balance (CAB) and cardiac autonomic regulation (CAR) (Quigley and Moore, 2018; Berntson et al., 2008). Pairing RSA instead with electrodermal activity extends the approach across organ systems (Stone et al., 2020). These measures reflect a growing recognition that autonomic activity is distributed. Nonetheless, these measures retain the sympathetic and parasympathetic branches as their organizing axes. We advocate for relaxing the assumption that those two axes are the natural decomposition of autonomic activity.

Nonetheless, most of the work that approaches autonomic activity from a multivariate perspective has been done with adults, who are usually still, in a seated or lying position, and often within clinical settings or pharmacological blockades (Cacioppo et al., 1994). Whether the assumptions underlying models derived from such paradigms generalize to the developing nervous system remains unclear. Developmental research often examines autonomic functioning in infants and children as they move, interact with caregivers, and encounter changing social and environmental demands, conditions in which autonomic control may be particularly dynamic (Stallworthy et al., 2024). Pharmacological blockade, which can provide an important means of experimentally isolating autonomic contributions in adults, is not feasible in developmental research.

Whether or not the growing biological evidence will ultimately fully refute the division of the ANS into sympathetic and parasympathetic branches, we propose that it is worth entertaining the counterfactual. What would it look like to assess the ANS and its influence on cognition and behavior without relying on the assumptions of the traditional model? If the two-branch model is correct, it should be evident from the data collected. But continuing to rely on the same assumptions limits the scope of experimental approaches and runs the risk of producing incomplete conclusions. For the remainder of the review, we delve into more detail for the most commonly applied autonomic theory (polyvagal theory), measure (RSA), and composite concept (arousal). We discuss prevailing shortcomings in their usage and interpretation, followed by recent advances and recommendations for building a data-driven model of the ANS throughout development.

5. Reassessing polyvagal theory

Polyvagal theory has played a prominent role in shaping how psychologists interpret ANS activity, especially in relation to emotion (Austin et al., 2007), self-regulation (Della Longa and Farroni, 2025), and social behavior (Welch, 2016). Introduced in the 1990s, the theory proposes a hierarchical organization within the parasympathetic branch of the ANS, reflecting evolutionary stages of defensive responses. It has been widely adopted in developmental and clinical research, influencing how measures such as RSA (respiratory sinus arrhythmia) are used and interpreted (Porges, 1995a, 1995b). Respiratory sinus arrhythmia refers to the biological phenomenon whereby the inter-beat interval of heart

beats expand and contract as a function of breathing: inhalation induces contracted inter-beat intervals (faster heart rate) while exhalation induces protracted inter-beat intervals (slower heart rate). In developmental science, the same term is also used for derived statistical approximations of this pattern from interbeat intervals (e.g., RSA computed with the Porges-Bohrer algorithm in software such as *CardioBatch*; [Brain-Body, 2016](#)). This dual usage means that RSA can refer either to a physiological coupling mechanism or to the numerical outcome of a particular analytic method. The appeal of measuring RSA amplitude is that it could serve as an index of heart rate fluctuations mediated by the activity of the vagus nerve, a cranial nerve which is traditionally classified as parasympathetic ([Grossman and Taylor, 2007](#); [Grossman, 2024](#); [McAllen and Spyer, 1978a; 1978b](#); [Porges, 1995a; 1995b](#)). The use of RSA as an index for parasympathetic state is discussed further in the next section (see [Section 6](#) below).

The central premise of polyvagal theory is that the ANS comprises three functionally distinct branches arranged hierarchically by presumed phylogenetic age. The most ancient system, the dorsal vagal complex, is thought to arise from the dorsal motor nucleus to mediate metabolic conservation or shutdown in life-threatening contexts. Above this, the sympathetic nervous system mediates fight-or-flight responses. The most recent system, the ventral vagal complex, is thought to originate in the nucleus ambiguus, to regulate heart rate in the service of social communication, and to coordinate motor outputs from cranial nerves controlling facial expression, vocalization, and auditory engagement, and is collectively described as the “social engagement system” ([Porges, 2001](#); [Porges and Carter, 2017](#)). Part of the reasoning for separating the ventral and dorsal vagal systems is that the vagal nerves supplying the larynx, pharynx, and heart are mostly myelinated, while the nerves leading to the abdominal organs are mostly unmyelinated, which polyvagal theory presumed to be a consequence of each system’s evolutionary age. RSA amplitude, as an indirect measure of myelinated vagus nerve activity, is therefore posited to index ventral vagal tone and, by extension, the overall capacity for calm, socially engaged states regulated by the parasympathetic nervous system.

Some anatomical and developmental findings are consistent with aspects of this theory. In mammals, brainstem vagal circuits contribute to rapid, coordinated motor behaviors such as swallowing and vocal output, showing that signals from the nucleus ambiguus via the vagus nerve are involved in communicative behaviors ([Taylor et al., 2022](#)). Developmental studies in humans have linked higher RSA to greater emotional expressivity ([Taylor et al., 2015](#)), longer attention spans ([Richards, 1987](#); [Woody et al., 2019](#)), and more effective co-regulation in early caregiver–infant interactions ([Armstrong-Carter et al., 2021](#); [Porter et al., 2022](#)). These associations have made the theory attractive to developmental scientists seeking to connect autonomic physiology with socioemotional development.

However, when evaluated through what we know about the ANS, many of the core claims of polyvagal theory become difficult to sustain. First, the mapping of ventral and dorsal vagal branches to discrete brainstem nuclei is imprecise: the nucleus ambiguus lacks clear boundaries, and its projections overlap with those of the dorsal motor nucleus ([Altschuler et al., 1989](#); [Cheng and Powley, 2000](#); [Izzo and Spyer, 1997](#); [Kalia and Mesulam, 1980](#)). This structure undermines the assumption that functional subdivisions within the parasympathetic system map cleanly onto separate nuclei of the brain. Furthermore, the phylogenetic progression claimed by the theory is problematic. Myelinated vagal fibers are present in non-mammalian species ([Nilsson, 2012](#); [Taylor et al., 2012](#); [Taylor et al., 2022](#)), and myelin content within mammals varies across target tissues ([Berthoud and Neuhuber, 2000](#); [Williamson and Lyons, 2018](#)). In the context of specific organs, fiber properties are interpreted in relation to developmental lineage and target specialization, not as universal markers of evolutionary stage, undercutting the premise that myelination neatly reflects behavioral complexity or evolutionary novelty ([Berthoud and Neuhuber, 2000](#); [Grossman and Taylor, 2007](#); [Grossman, 2024](#); [Monteiro et al., 2018](#)).

Polyvagal theory assigns a swath of physiological outcomes to the function of a single cranial nerve, the vagus, while ignoring the contribution of other pathways. The functional assignment of the dorsal vagal complex and dorsal motor nucleus as the driver of emotional “shutdown” is also challenged by modern physiology. This nucleus appears to play a primary role in digestive regulation, while defensive immobilization is more strongly linked to other brainstem and hypothalamic circuits ([Ulrich-Lai and Herman, 2009](#)). In a more contemporary account, such behaviors emerge from context-specific recruitment of multiple distributed circuits rather than activation of a single phylogenetically ranked pathway ([Ulrich-Lai and Herman, 2009](#)). Similarly, the claim that a single vagal system coordinates facial expression, vocal tone, auditory processing, and cardiac regulation is anatomically implausible; these functions involve multiple cranial nerves and distinct brainstem-cortical pathways ([Standring, 2021](#)). Coordination across them is better explained as an emergent property of network integration, not as evidence of a dedicated “social engagement” circuit.

Polyvagal theory has offered developmental science an accessible framework linking autonomic regulation to social and emotional behavior and has inspired decades of empirical work. Yet when tested against anatomical, developmental, and molecular evidence, its core premises are not consistent. Indeed, a recent consensus paper written by 39 experts in physiology and vertebrate social behavior has concluded the theory to be inaccurate and untenable ([Grossman et al., 2026](#)). The ability to index the overall activity of the parasympathetic nervous system and its sweeping consequences with a single numerical value continues to hold appeal, even for researchers who do not necessarily espouse all aspects of polyvagal theory. Within the last six and a half years, 81.3% of papers (257) measuring RSA during development mention polyvagal theory or reference Porges to contextualize their conclusions. How then do we interpret RSA as a measure of autonomic activity without relying on polyvagal theory?

6. Reassessing respiratory sinus arrhythmia

Respiratory sinus arrhythmia (RSA) refers to the coupling of heart rate and respiration characterized by an acceleration of heart rate during inhalation and a deceleration of heart rate during exhalation. RSA has often been attributed to signals from the nucleus ambiguus through the vagus nerve that induce slowing of the heart during exhalation ([Porges 1995](#); [McAllen and Spyer, 1978a; 1978b](#)). However, RSA itself is the result of multiple physiological processes. Respiratory heart-rate variability arises from both central and reflex mechanisms, the latter driven by lung-inflation sensory afferents ([Anrep et al., 1936a, 1936b](#)) and mechanical factors including intrathoracic-pressure changes and their effect on venous return contribute to the coupling between respiration and the heartbeat ([Hayano et al., 1996](#)). Therefore, measures of RSA incorporate multiple neural, reflex, and mechanical contributions. An evolutionary perspective reinforces this point: RSA is a conserved cardiorespiratory coupling mechanism in air-breathing vertebrates, hypothesized to optimize gas exchange, conserve cardiac energy, and support rapid shifts between behavioral states ([Ben-Tal et al., 2012](#); [Hayano et al., 1996](#)). Although RSA is only one measure of cardiac variability, we focus on it here because of its prominence in developmental science and its role in theories and measures of regulatory capacity. RSA is appealing to developmental scientists because it provides an accessible non-invasive measure that poses low participant burden and can be implemented in children with an ECG monitor and pediatric-grade adhesive electrodes. In much of the developmental science literature, RSA has been linked to attention, emotion regulation and self-regulation, social engagement, caregiver–infant coregulation, stress reactivity, temperament, and a range of clinical outcomes including autism, ADHD, and externalizing and internalizing problems (see [Supplemental Appendix B](#)). It is often treated as an index of “regulatory capacity”, with resting levels understood as physiological readiness to regulate, and task-related responses as active regulatory effort.

However, a recent international expert recommendation (Menuet et al., 2025) argues that traditional interpretations of RSA should be re-evaluated. Menuet et al. (2025) states that respiratory variation in heart rate is shaped by both sympathetic and parasympathetic brainstem pathways, as well as sensory feedback and mechanical contributions, so it is neither a selective nor an absolute marker of "vagal tone" or parasympathetic regulation. The authors note that there is no evidence that RSA amplitude reflects parasympathetic outflow to any organ other than the heart and hold that reading it as a measure of overall vagal tone or autonomic balance is at odds with an autonomic nervous system that operates in an organ-specific, tissue-specific, and context-dependent manner. Further, the anatomy of cardiac innervation differs from one person to the next (Box 2) and the functional impact of differing cardiac innervation patterns on measured cardiac indices, including RSA, is unknown.

RSA is estimated by recording the timing of successive cardiac R waves, converting these measurements into a series of interbeat intervals, and then quantifying the rhythmic variation in those intervals that occur at the frequency of respiration. Note that RSA is differentiated from more general heart-rate variability (HRV) in that HRV is an umbrella term for variability in cardiac interbeat intervals, which can be quantified through time-domain, frequency-domain, and nonlinear methods, while RSA is a specific form of HRV defined by its relationship to respiration (Berntson et al., 1997; Quigley et al., 2024). Within frequency-domain approaches, RSA is commonly approximated by quantifying power within a prespecified high-frequency band intended to encompass an individual's respiratory frequency. Time-domain approaches also use predefined bands to calculate respiratory-related variation in the interbeat-interval series over time, while peak-valley approaches determine the change in heart period between respiratory-linked cardiac maxima and minima. Other HRV measures such as RMSSD (root mean square of successive differences), which quantifies short-term interbeat-interval variability and is often interpreted as reflective of cardiac vagal activity, do not specifically isolate variability at the frequency of respiration, although they may be strongly influenced by RSA (Quigley et al., 2024). Measures of RSA are by necessity indirect. Nonetheless, researchers using RSA have made strides in standardizing the way they measure it. The statistical approximation of RSA has relied largely on proprietary software, with MindWare (MindWare Technologies, 2018) and CardioBatch (Brain-Body Center, 2016) the most prevalent within our corpus, each of which derives RSA from variability in a prespecified high-frequency band but by different routes. MindWare, by default, computes spectral power in the frequency domain, using an FFT or autoregressive method to integrate power within the specified high-frequency band (Task Force of the

European Society of Cardiology, 1996; Berntson et al., 1997). CardioBatch and its related software MxEdit (Porges, 1989) instead implement the Porges-Bohrer method, a time-domain procedure that detrends the inter-beat-interval series with a proprietary moving polynomial filter, applies a bandpass filter to isolate the respiratory band, and takes the natural logarithm of the variance of the filtered series (Lewis et al., 2012). The two therefore target respiratory-band variability in cardiac activity through distinct methods, and their estimates are not guaranteed to be equivalent (Lewis et al., 2012). However, band specification is fundamental to both frequency and time domain RSA measurement, as the bands must correspond to individuals' actual respiration.

Within our corpus, 161 papers (50.9%) used MindWare and a further 69 (21.8%) used CardioBatch or MxEdit, meaning nearly three quarters of the developmental literature we reviewed relied on one of these two pre-processing infrastructures. Other represented proprietary software included the James Long Company (16 papers; 5.1%), VU-AMS (14 papers; 4.4%), AcqKnowledge (8 papers; 2.5%), Kubios (8 papers; 2.5%), CardioPro (2 papers; 0.6%), VivoSense (2 papers; 0.6%), and Vsrrp98 (1 paper; 0.3%) (see Supplemental Appendices for counts and citations). Across proprietary software, those implementing peak-valley approaches comprised 32 papers (10.1%) and time-domain RMSSD approaches were used as RSA approximations in 8 papers (2.5%). The proprietary packages identified within our corpus (see Supplemental Appendix A2 for a detailed description of each) feature graphical interfaces that lower the technical barrier to signal processing and make RSA measurement feasible for researchers without extensive programming experience, but they come at a cost to researchers. Open-source methods for calculating RSA also exist. However, they often require programming environments such as MATLAB, Python, or specialized signal-processing expertise, which may explain their low prevalence in our corpus (for example, only 12 papers (3.8%) used the RSAToolbox (Schulz et al., 2009)) or RSAseconds (Gates et al., 2015)) packages in MATLAB, 1 paper used the open-source command-line program CMetX (Allen et al., 2007), and an additional 20 (6.3%) implemented a custom-built pipeline). Two papers (0.6% of the total corpus) did not provide sufficient documentation of their RSA calculation method to be counted. Altogether, our corpus demonstrated at least 12 different categories of approaches to RSA approximation, most of which contain settings a user can adjust.

A particular benefit of proprietary software for developmental scientists is that these tools make it straightforward to match the analysis band to the participant's age. Both allow users to apply fixed frequency bands that correspond to expected age-related differences in respiratory rate, such as the 0.30–1.30 Hz band (approximately 18–78 breaths per

Box 2

Variability in cardiac innervation.

Comparative and clinical anatomy both show that the autonomic innervation of the heart is highly variable between species and individuals. Across primate clades, from New World and Old World monkeys to apes and humans, differences are observed in the organization of cervical and thoracic ganglia and in the presence or absence of major cardiac nerves, such as the superior cardiac nerve (Kawashima et al., 2005; 2008). Once thought to be uniquely human (van den Broek, 1908; Perman, 1924; Schumacher, 1902), this pathway is also present in gibbons but absent in macaques, indicating evolutionary heterogeneity in sympathetic inputs to the heart. Within humans, there is wide disagreement on the number and origin of cardiac sympathetic nerves, with contributions reported from cervical ganglia, the stellate ganglion, and from thoracic ganglia ranging from T1 to T4 in most accounts and extending to T5 through T7 in others (Wink et al., 2020). Left-right asymmetries and inter-individual differences in nerve composition further complicate the picture.

These findings imply that when we measure indices of cardiac activity, we may be recording from hearts whose wiring diagrams differ not only across species but also across individuals within a species. The functional impact of such anatomical variability remains largely unknown, but it cautions against assuming that heart rate or RSA reflect uniform physiological substrates across contexts, populations, or developmental stages

minute) recommended for infants and toddlers, and the 0.24–1.04 Hz band (approximately 14–62 breaths per minute) recommended for children from roughly 2.5–7 years (Lewis et al., 2012; Shader et al., 2018). This is because fixed high-frequency bands developed for adults misalign with developmental physiology: respiration is faster and more variable early in life and slows substantially across childhood (Fleming et al., 2011; Wallis et al., 2005). Applying an adult band below a young child's respiratory range incorporates non-respiratory spectral power, inflating resting RSA and deflating RSA reactivity, with both distortions largest in the youngest participants (Shader et al., 2018). In neonates and young infants the problem compounds, because respiratory frequency can overlap with the conventional low-frequency band entirely (Harper et al., 2000; Patural et al., 2004). That 213 papers (67.4%) in our corpus used age-appropriate bands shows that this practice is moving towards becoming the field standard.

However, some researchers argue that respiration is too variable between individuals and across development, and that even age-adjusted frequency bands are too broad to derive accurate measures of RSA. Alternative approaches incorporate measured or empirically derived respiration frequencies. Bradshaw et al. (2025), for example, used a continuous wavelet approach with age-specific respiration ranges that shifted from 0.33 to 1.33 Hz at birth to 0.25–0.80 Hz by 36 months, allowing the frequency range used to extract RSA to change continuously with development. This distinction may be especially consequential when RSA is used to identify developmental risk or characterize psychopathology, where relatively small differences in autonomic measures may be read as markers of vulnerability, resilience, or atypical development.

Another methodological consideration that has become fairly standardized is the temporal resolution of RSA measurement. Thirty-second epochs have become a common convention in RSA research (Berntson et al., 1997), and in our corpus 125 papers (39.6%) quantified RSA using 30-s windows. Although such windows may be appropriate for some research questions, any fixed temporal window by its nature determines which aspects of autonomic variation can be observed and which cannot. Larger temporal windows allow more low frequency oscillations to be captured, while shorter windows do not. This is particularly relevant for developmental research, where autonomic responses may unfold at multiple timescales, frequency bands, and in contexts characterized by movement, interaction, and rapidly changing environmental demands. A software default or field convention can therefore function as an analytic assumption about the temporal structure of the phenomenon itself.

Movement further impacts RSA in two distinct ways. First, motion corrupts the ECG signal itself, introducing artifacts into the R-wave series; excluding these segments is a reasonable and long-standing practice. Second, movement itself is a driver of cardiorespiratory activity. RSA amplitude varies not only with vagal efferent activity but also with respiratory rate and depth, body position, and metabolic demand (Grossman and Taylor, 2007; Grossman, 2024; Hirsch and Bishop, 1981), all of which are impacted by movement. Therefore, movement could be a relevant signal that may account for or contribute to observed changes in RSA, especially in infants and young children for whom movement and postural change are intrinsic to naturalistic behavior. Yet in our corpus movement was almost never treated as a physiological variable: 289 papers (91.5%) handled it primarily as an artifact to be excluded, while only two included movement as a covariate in their analyses (Foss et al., 2023; Heilman et al., 2022). The remainder did not explicitly address how they accounted for movement.

While proprietary software provides accessibility and standardization for portions of the analytic workflow, it also comes with the potential danger of hidden assumptions and separation between the numerical output and the physical phenomenon it represents. In our corpus, 222 papers (70.3%) did not specify the units in which RSA was reported, with many giving only general descriptions such as "high-frequency heart rate variability" without enough information to

determine the precise unit of the calculated quantity. Established conventions for reporting HRV units do exist. Spectral power is conventionally reported in absolute units (ms^2), often after natural-log transformation to reduce skew ($\ln(\text{ms}^2)$), or in normalized units representing a band's power relative to total power (Task Force of the European Society of Cardiology, 1996; Berntson et al., 1997). The Porges-Bohrer metric, in turn, is reported in its own log-transformed units. The lack of units despite available conventions is worrying and suggests an over-reliance on automated algorithms. Furthermore, the paucity of methodological details leaves ambiguous whether values are absolute, log-transformed, or normalized, which hinders replication, interpretation, and comparison across studies. The convenience and usability of automated software should be accompanied with enough transparency for researchers to evaluate and adapt their measurement choices.

Better measurement, however, can only take RSA so far. Even a perfectly estimated respiratory-band signal remains a single index, and a growing body of work suggests its limits are intrinsic to what the measure represents. Recent work relating cardiac rhythms directly to the brain suggests that even a well-estimated RSA signal captures only part of the coordination it is assumed to reflect. Steffen et al. (2026) recorded prefrontal activity with fNIRS alongside cardiac signals in children aged five to seven years and used wavelet coherence to test brain-heart coupling across a graded set of timescales. Coupling was present overall, but not at the short respiratory-band timescale (3–5 s) where RSA's presumed vagal mechanism operates. For both RSA and untransformed heart rate, reliable coupling emerged only at longer timescales, the strongest in the baroreflex and neurovascular range of roughly fifteen to sixty-five seconds. RSA, confined to the respiratory band, therefore misses the occurrence of low frequency coupling. This is consistent with evidence in infants and adults that demonstrate no coupling between prefrontal cortex activity and RSA (Nguyen et al., 2022) and separate findings in adults, where the respiratory cycle itself, inhalation and exhalation, modulates cortical oscillations (Kosik-Rose et al., 2026; Kluger and Gross, 2021). Thus, from the perspective of the brain, RSA may be a less relevant signal than breathing itself, an avenue of research to be studied.

What, then, does it look like to use RSA as a measure without assuming the underlying mechanism is related to the parasympathetic nervous system or the tenets of polyvagal theory? From our perspective, there is considerable room for discovery, innovation, and advancement in this regard, especially by taking a multimodal approach that integrates multiple physiological measures in addition to RSA, without presupposing a two-branch system as the organizing principle. Promisingly, 21 papers (representing 22.1% of the 95 papers that used more than one autonomic measure), explicitly recognized the need to move beyond a global binary conceptualization of the ANS (e.g., Rudd et al., 2021; Cohen et al., 2020; see Supplemental Appendix B for a complete list), at times motivated by accounts such as the two-dimensional autonomic space model (Berntson et al., 1991; 1993; 2008). However, nearly all (89; 93.7%) of these 95 papers approached multidimensionality by pairing RSA, as a proxy of parasympathetic activity, with an additional measure (typically PEP, EDA, or cortisol levels) as a proxy for sympathetic nervous system activity, which in practice doesn't move far from the traditional binary. We argue that instead of prespecifying that certain measures represent general readouts of a particular ANS branch, the value of multimodal measurement is its ability to determine how organ-specific signals converge, dissociate, and reorganize in response to changing demands through time. Without the assumptions of the traditional ANS model, our typical autonomic measures limit potential findings to correlations between individual organs (i.e. the heart) with psychological and developmental outcomes. Collecting multiple parallel streams of physiological data would instead enable the search for systemic internal processes and states (akin to arousal, discussed in Section 7 below), which may shape behavior and cognition. Data-driven approaches to characterizing these processes may better identify

individual differences in development or risk of atypical development, and are promising avenues for future research.

7. Reassessing arousal

Arousal has long been treated in neuroscience as a fundamental brain-body state influencing sensory processing, motor readiness, and emotional reactivity; more aroused organisms tend to be more responsive to stimuli, more active, and more reactive (Pfaff, 2006). In much of the developmental and behavioral literature, arousal has been conceptualized as a single dial controlling the organism's state, causing it to be more or less responsive to stimuli. Like RSA, arousal has been used as a stand-in for the complexity of the ANS, but unlike RSA, arousal does not aim to isolate an individual ANS branch. Nevertheless, many approaches to arousal are based on simplifications that obscure the fact that "arousal" is not a single quantity but a multidimensional process emerging from coordinated neural, physiological, and behavioral changes (Sander, 2025; Smith et al., 2025).

Within psychology and neuroscience, there is no uniformly agreed upon definition of what exactly constitutes arousal (Sander, 2025; Smith et al., 2025). Across studies, "arousal" has been used to mean subjective alertness, cortical activation, or changes in autonomic function, the dynamics of which often diverge. Various studies have selected unitary or combinatorial measures of physiological, motor, or neural signals in the service of collapsing the multiple components of arousal into a single value (Pfaff et al., 2006; Avery and Krichmar, 2017). Some studies treat pupil dilation alone as a direct index of arousal state (Niikuni et al., 2022; Raiturkar et al., 2016; Urai et al., 2017), while others rely exclusively on cardiac measures (Marín-Morales et al., 2021; Wass et al., 2019) or electrodermal activity (Bach et al., 2010; Picard et al., 2016). In addition to such peripheral measures, arousal studies can also include measures of brain activity. For example, the late positive potential, a centroparietal event-related potential measured with EEG, increases with both pleasant and unpleasant content, making it an index for emotional arousal largely independent of valence (Cuthbert et al., 2000; Hajcak et al., 2010). Its amplitude also varies with attention allocation, the motivational relevance of the stimulus, and deliberate emotion

regulation (Hajcak et al., 2010). However, given the considerable differences in timescales and physiological underpinnings of these unitary measures, it is unlikely that each is measuring the same underlying process. The same experimental conditions could produce increased electrodermal response, decreased heart rate, and enlarged pupils (as in "freeze" or high-alert orienting states, Berntson et al., 1991), each of which may reflect a separate component of the broader state. These measurement constraints parallel those present when trying to infer branch-level activity from single autonomic measures such as RSA, EDA, and PEP.

There are further challenges for developmental science; the physiological signals commonly used to index arousal are not developmentally stable, and the relationship between these signals and behavior may shift across development (Quigley and Moore, 2018). Resting RSA increases across infancy and childhood (Alkon et al., 2011), while pre-ejection period decreases (Bar-Haim et al., 2000). Heart and respiratory rate ranges also shift across the lifespan (Fig. 2, Fleming et al., 2011). The same signal may therefore reflect different underlying processes at different ages. Hypothetically, cardiac measures in early infancy may more strongly reflect metabolic demands or immature regulatory systems, while later in infancy they may more closely track attentional engagement or emotional activation. In parallel, these physiological processes are impacted by the infant's developing motor capacity, with increasing muscle tone, locomotion, and fine motor skills placing new demands on cardiorespiratory coordination. Accurate interpretation therefore benefits from age-appropriate physiological norms and sensitivity to how these measures change across development.

Quantitative approaches to brain-body dynamics emphasize that no single channel, whether pupil size, heart period, electrodermal activity, or neural activity, provides a privileged index of arousal or autonomic state (Berntson et al., 1991; 1993; 1994a; 1994b; 1994c; 2008; Pasquini et al., 2023; Pfaff, 2006; Pfaff, 2019; Stone et al., 2020; Quigley and Moore, 2018). In this vein, additional measures change what can be inferred: they distinguish processes that produce the same change in any one channel, reveal structure along dimensions that a single measure cannot define, and allows physiological activity to be described as

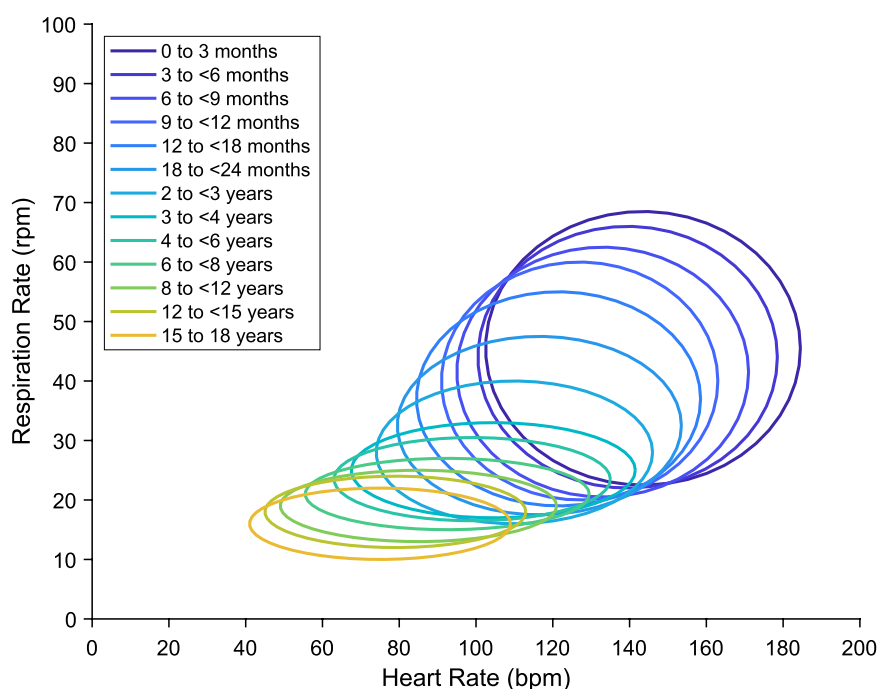


Fig. 2. The autonomic nervous system changes over development. Normal ranges of heart rate and respiratory rate in children from birth to 18 years of age. Multivariate gaussian distributions fit to data from Fleming et al. (2011) *Lancet*. Compiled over 69 studies with heart rate data for 143,346 children and respiratory rate data for 3881 children.

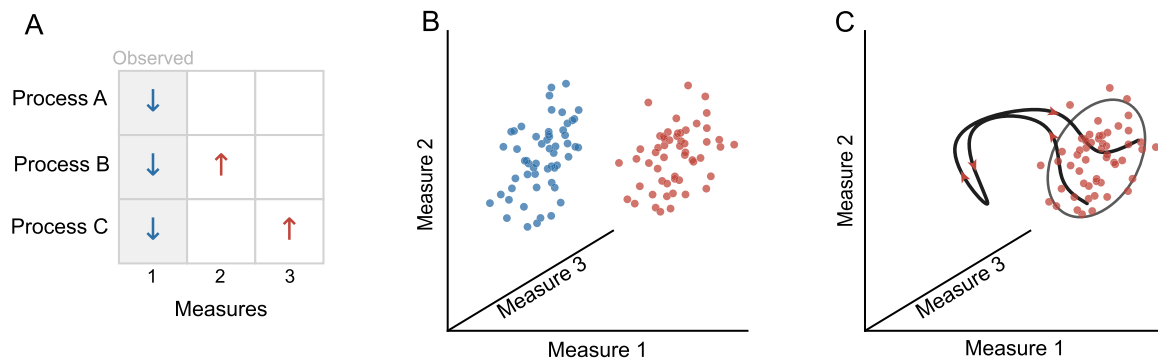


Fig. 3. Three inferential problems that a single measure cannot resolve. (A) Distinct processes can produce the same change in one measure while differing in their effects on others, so the observed change alone does not identify the process that generated it. (B) With additional dimensions, clusters can emerge that are not recoverable from any constituent measure on its own. (C) A multivariate Gaussian fit to the joint distribution of the collected measures (outline) provides a reference against which dynamic activity can be described with red arrows showing the direction of change. Such excursions may not be apparent in any single measure. All panels are schematics.

movement through a state space (Fig. 3). Indeed, some analytic approaches treat autonomic and motor function as a multidimensional state and reveal characteristic, recurring dynamics. Fitting multivariate Gaussian distributions to heart rate, respiration rate, and movement has demonstrated attractor-like states, preferred regions of the state space that the system returns to after perturbation, in nonhuman primates (Borjon et al., 2016). In this case, spontaneous vocal production appeared to serve as an arousal regulating mechanism, whereby heart rate, respiration rate, and movement exited a preferred state space, then a vocalization occurred causing a switch in the dynamics resulting in the return back to the preferred, attractor-like region (approximated in Fig. 3C). Comparable dynamics have been found in movement data captured over infant development (Borjon et al., 2018; Jahn et al., 2026).

Other approaches sidestep the label of arousal altogether and map reproducible patterns of physiological state instead. The recurring states identified by Pasquini et al. (2023), described above, were defined by higher-order patterns across signals rather than by any individual measure, and their structure was recovered only when multiple measures were considered jointly. This approach is a first step to addressing our persistent chain of inferential constraints. Absent direct validation, no single physiological signal can be assumed to index global arousal, just as RSA amplitude cannot be assumed to index global parasympathetic tone. A change in one measure tells us only that something changed in the control of the relevant organ. It does not necessarily tell us that there was a change in the global state of the organism. While what constitutes arousal remains an unresolved and empirical question, it is clear that drawing conclusions about global state requires knowledge about how multiple physiological systems change together.

Encouragingly, the field is already moving toward multimodal approaches that capture the joint organization and dynamics of multiple signals. Nonetheless, multimodality itself can be defined in different ways. Many existing approaches combine multiple physiological and computational methods to allow structure to emerge from the data. Characterizing the joint organization of multiple channels rather than collapsing them may offer a more faithful representation of the multidimensional organization of the ANS, and provide a stronger foundation for identifying developmental processes than any single-channel proxy can provide. This promising avenue awaits validation in future studies.

8. Implications for study design and measurement in developmental science

The evidence reviewed here has practical implications for how we as developmental scientists design studies and interpret autonomic data. We outline six areas where updated biological assumptions can inform

measurement and analytic practice. (1) Multimodal measurements better capture the distributed nature of autonomic function than single-index approaches. Supplementing RSA with continuous measures of movement, respiration, heart rate, electrodermal activity, etc., when possible, provides a fuller picture of the specific biological processes associated with behaviors of interest, rather than collapsing that complexity into a single channel. (2) Organ- and context-specific language more accurately describes autonomic responses than branch-level terminology. Characterizing a cardiac response in terms of the mechanisms acting on the heart, rather than invoking "parasympathetic withdrawal" or "sympathetic activation," keeps the mechanistic interpretation closer to the physiology and avoids relying on assumptions of the classical model. (3) Autonomic development is likely asynchronous across the body and through time, and modeling approaches that accommodate this, such as multilevel modeling, time series analysis, and latent variable modeling, will provide more accurate characterizations of their maturation than those assuming uniform developmental trajectories. (4) Transparency in measurement and analytic decisions enables readers to evaluate findings in context. Reporting should include, at minimum, sampling rate, preprocessing and cleaning procedures, analytic pipelines, and the specific algorithms used to derive RSA or arousal estimates, given that these choices meaningfully shape the resulting measures. (5) Beyond collecting multiple measures, an important next step is developing analytic approaches and tools that capture how physiological systems are coordinated over time (Maita et al., 2020; Abney et al., 2025; Gerosa et al., 2025). This includes modeling temporal coupling, coactivation, and dynamic transitions across systems, rather than treating each measure independently. (6) Standardized reference measures of autonomic activity will only represent the variability inherent to the population the data was collected from. To better capture the true range of variability in human development, the field must continue striving to collect data from individuals and families representative of the massive variability found across the globe (Borjon et al., 2026; Bentil et al., 2024; Ugarte et al., 2026).

9. Conclusion: Toward a biologically grounded understanding of autonomic function in developmental science

For over a century, the ANS has been studied through a binary model that continues to shape developmental science and psychology. While this classification provided a scaffold for early discovery, contemporary neurobiology favors an integrated system organized around organ-specific, context-dependent modules rather than two rigidly opposed branches. This reframing carries significant implications for interpreting psychophysiological indices such as RSA and composite arousal

measures, and for evaluating developmental theories that rest on assumptions of the classical model.

Central to the scientific process is the revising and updating of knowledge in light of new evidence, making even long-held ideas subject to revision. The principle that a neuron releases the same, single neurotransmitter at all its synapses and throughout its life, gave way to evidence of neurotransmitter co-release (Burnstock, 2009) and of neurotransmitter switching across both development and experience (Spitzer, 2012; Dulcis et al., 2013). The assumption that synaptic transmission flows only from the pre- to postsynaptic neuron gave way to retrograde messengers such as nitric oxide and endocannabinoids (Kano et al., 2009; Garthwaite, 2008). Glia, once regarded as passive support in neural transmission, are now known to actively regulate it (Araque et al., 1999; Perea et al., 2009). Every rule in biology ends up having an exception. Whether the scientific consensus will uphold the sympathetic-parasympathetic division of the ANS remains to be seen, but the existence of exceptions and doubt regarding its division and functional opposition should caution us from basing psychological and developmental theories on these assumptions. Biology continues to move forward to expand our foundational understanding of the ANS, for example with the recent release of the first comprehensive anatomical map of the human vagus nerve (Zanos et al., 2026). As biology advances, so should developmental science, especially when its measures and theories reference biological processes as mechanistic and explanatory links.

An index that treats autonomic output as a single quantity, whether vagal tone, RSA, or a composite arousal score, compresses many biological processes into one number, so that similar values can arise from different underlying configurations and accompany different behavioral states. We therefore see two needed shifts: toward multimodal, data-driven measurement that reflects the distributed, dynamic nature of autonomic activity, and toward theoretical precision matched to what those measures can actually resolve. Grounding interpretation in processes from contemporary biology and neuroscience strengthens the bridge between physiology and behavior and will yield developmental theories that are more biologically plausible, more reproducible, and better matched to the complexity of early development.

Although we have focused on developmental science, reinterpreting the ANS bears on any discipline that studies human behavior, from cognitive and affective science to clinical psychology and psychiatry. A more modern account of autonomic organization could improve how these fields interpret widely used physiological measures.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.neubiorev.2026.106984](https://doi.org/10.1016/j.neubiorev.2026.106984).

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