



Review article

The hierarchical basis of neurovisceral integration

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ABSTRACT

The neurovisceral integration (NVI) model was originally proposed to account for observed relationships between peripheral physiology, cognitive performance, and emotional/physical health. This model has also garnered a considerable amount of empirical support, largely from studies examining cardiac vagal control. However, recent advances in functional neuroanatomy, and in computational neuroscience, have yet to be incorporated into the NVI model. Here we present an updated/expanded version of the NVI model that incorporates these advances. Based on a review of studies of structural/functional anatomy, we first describe an eight-level hierarchy of nervous system structures, and the contribution that each level plausibly makes to vagal control. Second, we review recent work on a class of computational models of brain function known as “predictive coding” models. We illustrate how the computational dynamics of these models, when implemented within our proposed vagal control hierarchy, can increase understanding of the relationship between vagal control and both cognitive performance and emotional/physical health. We conclude by discussing novel implications of this updated NVI model for future research.

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1. Introduction

There is now very compelling evidence that parasympathetic or vagal tone – often measured using the high frequency component of heart rate variability (HRV) – is associated with a variety of psychological and behavioral variables on the one hand, and a variety of health outcomes on the other. With regard to psychological/behavioral variables, there now exist several replicated findings suggesting that higher HRV is associated with greater capacity for emotion regulation (Appelhans and Luecken, 2006; Butler et al., 2006; Ingjaldsson et al., 2003; Lane, 2008; Melzig et al., 2009; Ruiz-Padial et al., 2003; Thayer and Brosschot, 2005) and with greater performance on several cognitive tasks involving attention, working memory, and inhibitory control (Hansen et al., 2009, 2004, 2003; Johnsen et al., 2003; Saus et al., 2006; Thayer et al., 2005). With regard to health outcomes, higher HRV has also been associated with better glucose regulation, better hypothalamic-adrenal-pituitary (HPA) axis function, reduced inflammation, and reduced risk for stroke, cardiovascular disease, and all-cause mortality (Brosschot et al., 2007; Liao et al., 2002; Thayer and Fischer, 2009; Thayer and Lane, 2007; Thayer and Sternberg, 2006); lower HRV has also been associated with affective disorders such as depression and anxiety (Gorman and Sloan, 2000; Kemp and Quintana, 2013; Kemp et al., 2012, 2010). As is true of most correlational findings in mind-body medicine, the demonstration of mechanisms mediating these observed relationships can potentially extend both understanding and practical utility. One such attempt at mechanistically explaining the HRV-related findings highlighted above is the “neurovisceral integration” (NVI) model (Thayer and Lane, 2000), which represents an integrative effort to combine current knowledge about the relationship between mental states, autonomic function, and health outcomes into a single framework centered on a network of reciprocally connected brain regions called the “central autonomic network” (CAN; Benarroch, 1993). This model was first presented in 2000; it was then updated in 2009 by reviewing new evidence supporting the original proposal and providing an updated characterization of the multiple circuits linking the heart and brain (Thayer and Lane, 2009).

A primary goal of the current paper is to extend the original model further by providing additional specificity and detail. This appears important because previous presentations of the NVI model have been somewhat vague about the specific neuroanatomical loci involved in vagal tone regulation. For example, many separable network regions have previously been grouped together, and the functions of each of these different regions have not been thoroughly specified. Moreover, the way these different regions interact has not been fully addressed. This paper therefore aims to fill that gap and present an updated model of how the different brain regions implicated in vagal regulation work together. This update is informed by more recent studies on brain-HRV interactions, as well as by more general developments in computational neuroscience. In particular, we will suggest below that recent developments in neuroscience may allow for a more detailed characterization of the multi-level control architecture that allows for adaptively coordinated cognitive, affective, autonomic, and behavioral responses. Before doing so, however, it is important to review current knowledge of the general structural anatomy relevant to

vagal control, and to review where gaining increased understanding of function may be important.

2. A gap between understanding of structure and function

In earlier presentations of the NVI model, the CAN (Benarroch, 1993) was described as being made up of several regions. These included the anterior cingulate cortex (ACC), the anterior (AI) and posterior (PI) insula, the ventromedial prefrontal cortex (VMPFC) and orbitofrontal cortex (OFC), the amygdala, the bed nucleus of the stria terminalis (BNST), the hypothalamus, the periaqueductal gray (PAG), the parabrachial nucleus (PBN), the nucleus of the solitary tract (NTS), the nucleus ambiguus (NA), the dorsal motor nucleus of the vagus (DMNV), the noradrenergic locus coeruleus (LC), and the rostral (RVLM) and caudal (CVLM) ventrolateral medulla (among others). The primary output of the CAN was described as occurring via preganglionic sympathetic and parasympathetic neurons, which innervate the heart through both stellate ganglia and the vagus nerve. The integrated effects of these different signal pathways, when they reach the sino-atrial (SA) node of the heart, were also described as the proximal factor determining HRV. Given that the CAN also receives a large amount of afferent information from both the body and the external world – allowing for context-specific cardiac regulation – it was argued that HRV can be understood as an important index of the level of integration between the peripheral autonomic and central nervous systems. Further, because the timescale for changes in sympathetic tone is relatively slow compared to that of parasympathetic tone (on the order of seconds vs. milliseconds; Saul, 1990), it was argued that faster, moment-to-moment adjustments in autonomic function (e.g., as in cognitive/affective contexts) primarily reflect the addition or withdrawal of vagal influence.

The overarching structure of the CAN described above has been supported by retrograde viral staining studies of parasympathetic cardiac regulation in both rodents and primates (Chuang et al., 2004; Ter Horst and Postema, 1997); these studies provide evidence of (1) structural connections between the ventricular myocardium and vagal motor neurons, and (2) connections between those vagal motor neurons and a series of hierarchically organized higher-order control neurons in a number of brain regions. These include brainstem regions (i.e., the DMNV, NA, NTS, area postrema, LC, and PBN), higher subcortical regions (i.e., PAG, hypothalamus, amygdala, and BNST), and cortical regions (i.e., ACC, insula, and frontal cortex). More recently, retrograde viral staining studies have also provided evidence of structural connections between sympathetic effector organs and (1) visceromotor, (2) skeletomotor, and (3) higher prefrontal cortical regions involved in cognition and affect (Dum et al., 2016). As stated above, however, although the NVI model proposed that the regions listed above form a distributed control network, allowing for the integration of cognitive, affective, attentional, and autonomic information to guide adaptive goal-directed behavior, a detailed account of this network architecture (and the different functions of the regions involved) was not provided.

Instead, the original NVI model appealed to the dynamical systems (DS) perspective to provide an abstract mathematical language for understanding the complex functional dynamics of the CAN (Thayer and Lane, 2000). The DS perspective abstractly con-

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