# VAGAL TONE AND THE PHYSIOLOGICAL REGULATION OF EMOTION

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Because emotions are psychological processes, the experience and regulation of emotion should be functionally dependent on the state of the nervous system. If a major source of emotion variation is dependent on the nervous system, how would this be evaluated? The goal of this essay is to address this problem by introducing vagal tone as a measurable organismic variable that contributes to individual and developmental differences in the expression and regulation of emotion.

We propose that understanding the mechanisms determining individual and developmental differences in emotion expression and regulation might provide a rationale for identifying subjects who differentially express the ability to regulate emotion. Thus, there is the possibility that individual differences in the nervous system might mediate the expression and regulation of emotion. Most research on the autonomic correlates of emotion has focused on *sympathetic* activation (e.g., GSR); here, we attempt to demonstrate that individual differences in *parasympathetic* tone are related to the regulation of emotion by focusing on a construct called *vagal tone,* which reflects the vagal control of the heart.

## PHYSIOLOGY AND EMOTION: THE AUTONOMIC NERVOUS SYSTEM

The autonomic nervous system (ANS) regulates homeostatic function and is composed of two subsystems, the parasympathetic (PNS) and the sympathetic (SNS) nervous systems. The PNS and SNS represent neural systems that originate in the brain stem and contribute to the regulation of a variety of target organs, including the eyes, lacrimal, salivary, and sweat glands, blood vessels, heart, larynx, trachea, bronchi, lungs, stomach, adrenal glands, kidneys, pancreas, intestines, bladder, and external genitalia. In general, the PNS promotes functions associated with growth and restorative processes. In contrast, the SNS promotes increased metabolic output to deal with challenges from outside the body. However, there are states that require dual excitation (e.g., sexual arousal). Recent conceptualizations of the ANS by Berntson, Cacioppo, and Quigley (1991) provide insight into the complex dynamic relation between SNS and PNS processes.

In general, when a visceral organ is innervated by both the SNS and the PNS, the effects are antagonistic. For example, SNS neurons dilate the pupils, accelerate the heart, inhibit intestinal movements, and contract the vesical and rectal sphincters. The PNS neurons constrict the pupils, slow the heart, potentiate peristaltic movement, and relax vesical and rectal sphincters. The PNS deals primarily with anabolic activities concerned with the restoration and conservation of bodily energy and the resting of vital organs. In contrast, stimulation of the SNS prepares the individual for the intense muscular action required to protect and defend in response to external challenges. The SNS quickly mobilizes the existing reserves of the body.

Darwin provides insight into the potential importance of PNS processes in the regulation of emotions. Although Darwin defined emotions as facial expressions, he acknowledged the dynamic relation between parasympathetic structures and central nervous system activity that accompanied the spontaneous expression of emotions. Darwin speculated that there were specific neural pathways that provided the necessary communication between the brain states and the specific pattern of autonomic activity associated with emotions. For example, he stated, "When the mind is strongly excited, we might expect that it would instantly affect in a direct manner the heart; and this is universally acknowledged. . . . When the heart is affected it reacts on the brain; and the state of the brain again reacts through the pneumo-gastric [vagus] nerve on the heart; so that under any excitement there will be much mutual action and reaction between these, the two most important organs of the body" (1872/1965, p. 69).

Darwin attributed these ideas to Claude Bernard. Bernard developed the construct of *le milieu interieur,* which included physiological mechanisms responsible for maintaining the constancy of the internal environment. This construct evolved into our present-day concept of *homeostasis.*

In Darwin's formulation, when emotion states occur, the beating of the heart changes instantly, the change in cardiac activity influences brain activity, and the brain-stem structures stimulate the heart via the cranial nerves (i.e., vagus). Although Darwin did not elucidate the neurophysiological mechanisms that translate the initial emotion expression to the heart, this formulation provides us with three important points. First, by emphasizing the afferent feedback from the heart to the brain, Darwin anticipated the views of William James linking autonomic feedback to the experience of emotion. Second, he acknowledged the afferent capacity of the vagus to transmit sensory information from visceral organs independent of the spinal cord and the sympathetics. Third, Darwin's insight regarding the regulatory role of the pneumogastric nerve (renamed the *vagus* at the end of the nineteenth century) in the expression of emotions anticipates the major theme of this essay.

Contemporary models of emotion and emotion regulation (e.g., Ekman, Levenson, & Friesen, 1983; Kagan, in this volume; Schachter & Singer, 1962), as did their historical antecedents, have focused on the sympathetic nervous system and ignored the vagal system, the primary component of the parasympathetic nervous system. Thus, although Darwin speculated about the bidirectional communication between the brain and the heart more than 100 years ago, the importance of vagal afferents and efferents in the expression, experience, and regulation of emotion has not been addressed.

## VAGAL TONE: BACKGROUND AND DEFINITION

The vagus is the tenth cranial nerve. It originates in the brain stem and projects, independently of the spinal cord, to many organs in the body cavity, including the heart and the digestive system. The vagus is not a single neural pathway but rather a complex bidirectional system with myelinated branches linking the brain stem and various target organs. These neural pathways allow direct and rapid communication between brain structures and specific organs. Because the vagus contains both efferent (i.e., motor) and afferent (i.e., sensory) fibers, it promotes dynamic feedback between brain control centers and the target organs to regulate homeostasis.

The peripheral autonomic nervous system is asymmetrical. The peripheral target organs of the autonomic nervous system are clearly lateralized; for example, the heart is oriented to the left, the stomach is tilted, one lung is larger, and one kidney is higher. The neural wiring of the autonomic nervous system requires asymmetry, and the central regulation via the vagus is lateralized. Although asymmetry of cortical function is well known and has been theorized to contribute to emotion regulation (see Fox, in this volume), asymmetrical regulation of autonomic function has been ignored.

The vagus is bilateral, with a left and a right branch. Each branch has two source nuclei, with fibers originating either in the dorsal motor nucleus or in the nucleus ambiguus. Traditional texts in neuroanatomy and neurophysiology (e.g., Truex & Carpenter, 1969; Williams, 1989) have focused on the dorsal motor nucleus of the vagus and neglected both the asymmetry in the vagal pathways and the important functions of the pathways originating from source nuclei in the nucleus ambiguus.

The dorsal motor nucleus is lateralized. Pathways from the left and right dorsal motor nucleus to the stomach have different regulatory functions. The left dorsal motor nucleus innervates the cardiac and body portions of the stomach that promote primarily secretion of gastric fluids (Kalia, 1981; Loewy & Spyer, 1990). The right dorsal motor nucleus innervates the lower portion of the stomach that controls the pyloric sphincter regulating the emptying into the duodenum (Fox & Powley, 1985; Pagani, Norman, & Gillis, 1988).

The nucleus ambiguus is also lateralized. While the right nucleus ambiguus provides the primary vagal input to the sino-atrial (S-A) node to regulate atrial rate (Hopkins, 1987) and determine heart rate, the left nucleus ambiguus provides the primary vagal input to the atrio-ventricular (A-V) node to regulate ventricular rate (Thompson, Felsten, Yavorsky, & Natelson, 1987). Given the ipsilateral control of efferent pathways regulating the nucleus ambiguus, characteristics of right-side brain damage are associated with defective right nucleus ambiguus regulation. In this manner, the observed deficits in prosody (e.g., Ross, 1981) and in heart-rate changes during attention-demanding tasks (Yokoyama, Jennings, Ackles, Hood, & Boller, 1987) associated with right-side brain damage implicate the right nucleus ambiguus in the regulation of vocal intonation and attention. Asymmetrical nucleus ambiguus regulation is less clear in other organs, such as the soft palate, the pharynx, and the esophagus.

Functionally, the dorsal motor nucleus is involved with the vegetative functions of digestion and respiration. In contrast, the nucleus ambiguus is more involved with processes associated with motion, emotion, and communication. For example, rapid mobilization of the body may be achieved by regulating heart rate via removal of vagal input to the S-A node. Vocal intonation, mediated by vagal connections to the larynx, is intimately related to the processes of emotion and communication. Facial expressions, critical to the expression of emotion and the signaling of information, are related to vagal function. In cats, vagal afferent fibers have direct influences on facial motoneurons (Tanaka & Asahara, 1981). Thus, the vagus originating from the dorsal motor nucleus might be labeled the *vegetative vagus,* in contrast to the emotive or *smart vagus* originating from the nucleus ambiguus. Table 1 provides a list of target organs associated with each branch of the vagus.

Sympathetic innervation of the heart is also asymmetrical (Randall & Rohse, 1956). Moreover, lateralized sympathetic input to the heart has been hypothesized to relate to emotion state (Lane & Schwartz, 1987). As with vagal control of the heart and larynx, research has demonstrated that damage to the right hemisphere has greater sympathetic consequences than does

TABLE 1

TARGET ORGANS ASSOCIATED WITH THE DORSAL MOTOR NUCLEUS AND THE NUCLEUS AMBIGUUS

| Dorsal Motor Nucleus | Nucleus Ambiguus |
|---|---|
| Trachea | Heart |
| Lungs | Soft palate |
| Stomach | Pharynx |
| Intestines | Larynx |
| Pancreas | Esophagus |
| Colon | Bronchi |

left hemisphere damage (Hachinski, Oppenheimer, Wilson, Guiraudon, & Cechetto, 1992).

The central control of the vagus is ipsilateral. Thus, the right vagus originates in either the right dorsal motor nucleus or the right nucleus ambiguus. As noted above, the right nucleus ambiguus contains the primary source for the branch of the right vagus that provides input to the S-A node. Thus, output from the nucleus ambiguus can be monitored by measuring changes in vagal control of the S-A node. The S-A node is the primary pacemaker of the heart. Vagal stimulation of the S-A node delays the onset of the heart beat (i.e., slows heart rate), and vagal withdrawal (i.e., a delay or blocking of the neural transmission) shortens the time between heart beats (i.e., speeds heart rate). Most rapid heart-rate changes (i.e., chronotropic mechanisms) are mediated by the vagus. When metabolic demands increase, such as during exercise or fight-flight demands, the sympathetic nervous system influences heart rate. Thus, the study of vagal control of the heart might provide an important window on the rapid autonomic changes associated with gradations of emotion state.

### *Vagal Tone: Measurement Strategies*

An easily accessible method for evaluating the vagal control of the S-A node (i.e., cardiac vagal tone) is to quantify respiratory sinus arrhythmia (RSA). RSA is characterized by a rhythmic increase and decrease in heart rate. The heart-rate increase is associated with phases of inspiration, when respiratory mechanisms in the brain stem attenuate the vagal efferent action on the heart. The heart-rate decrease is associated with phases of expiration, when the vagal efferent influence to the heart is reinstated.

Measurement of RSA requires detection of the heart beat from the electrocardiogram (i.e., R-wave) and timing between heart beats (i.e., heart periods). To quantify the cardiac vagal tone index ($\hat{V}$) from RSA, it is necessary to detect and time with millisecond accuracy. The cardiac vagal tone index is extracted via time-series procedures. These procedures require heart-period rather than heart-rate data. On a beat-to-beat level, heart periods are the sequential time intervals between heart beats. Heart-rate data require a transformation of the heart period by determining how many of each of the heart periods scored in milliseconds could occur in a minute (i.e., 60,000 msec per minute/heart period in milliseconds). The data are processed by a method developed and patented by Porges (1985). This technique includes the application of time-domain filters designed to extract only RSA, the heart-period pattern in the spontaneous breathing frequencies. The resulting heart-period pattern is sinusoidal with an amplitude and time period. The amplitude represents the changing vagal influences to the S-A node, and the period represents the medullary inspiratory drive frequency. By calculating the amplitude or variance of the extracted pattern, RSA amplitude provides an excellent measure of cardiac vagal tone.

## VAGAL TONE: POTENTIAL LINK WITH EMOTION

Changes in RSA amplitude in response to sensory, cognitive, and visceral challenges represent a "central command" to regulate vagal efferents originating in the right nucleus ambiguus and terminating in the heart, soft palate, pharynx, larynx, bronchi, and esophagus. These changes in nucleus ambiguus regulation of peripheral autonomic activity support the expression of motion, emotion, and communication by regulating metabolic output (i.e., shifts in heart rate) and organs involved in the production of vocalizations (Porges & Maiti, 1992).

When there are no challenging environmental demands, the autonomic nervous system, through the vagus, services the needs of the internal viscera to enhance growth and restoration. However, in response to environmental demands, homeostatic processes are compromised, and the autonomic nervous system supports increased metabolic output to deal with these external challenges by vagal withdrawal and sympathetic excitation. By mediating the distribution of resources, the central nervous system regulates the strength and latency of autonomic responses to deal with internal and external demands. Perceptions and assumed threats to survival, independent of the actual physical characteristics of the stimulation, may promote a massive withdrawal of parasympathetic tone and a reciprocal excitation of sympathetic tone. These changes promote fight-flight behaviors. Less intense environmental demands, often associated with emotion expressions, might be characterized by less withdrawal of parasympathetic tone independent of, or in concert with, slight increases in sympathetic tone. This trade-off between internal and external needs is monitored and regulated by the central nervous system.

Vagal tone measured via RSA has been documented to be related to affect, attention, and metabolic demands (see below). Although the vagus is bilateral, the right branch originating in the nucleus ambiguus is the primary determinant of RSA. This laterality in the vagus is not a developmental or an individual difference. Rather, the laterality is dependent on the neurophysiology and the neuroanatomy of the mammalian nervous system. In the mammalian nervous system, the right side of the brain stem provides the primary central regulation of homeostasis and physiological reactivity. Thus, right-brain-stem structures initiate peripheral physiological states via shifts in vagal tone to facilitate the processes of attention, the expression of emotion, and the initiation of shifts in metabolic output.

## THE RIGHT HEMISPHERE: THE REGULATION OF EMOTION

Right hemisphere function, evaluated via EEG or disrupted by localized damage, is related to the same cluster of behaviors that has been linked to the vagal tone measure. Research demonstrates that the right hemisphere is implicated in both the expression and the interpretation of emotions (e.g., Bear, 1983; Heilman, Bowers, & Valenstein, 1985; Pimental & Kingsbury, 1989; Tucker, 1981) and in the regulation of attention (e.g., Heilman & Van Den Abell, 1980; Mesulam, 1981; Pimental & Kingsbury, 1989; Voeller, 1986). Research has also linked right hemisphere deficits with aprosody or lack of emotion expression in speech (e.g., Ross, 1981; Ross & Mesulam, 1979; Zurif, 1974) and attenuated autonomic reactivity (e.g., Heilman, Schwartz, & Watson, 1978). Several investigators have argued that the right hemisphere provides the primary control of emotion (for detailed reviews, see Molfese & Segalowitz, 1988; Pimental & Kingsbury, 1989; Silberman & Weingartner, 1986).

EEG research has been used to provide support for laterality theories of emotion. Fox and his colleagues (e.g., Dawson, in this volume; Fox, in this volume; Fox & Davidson, 1984) present a model of emotion expression in which positive (e.g., interest) emotions are associated with the left hemisphere and negative emotions (e.g., disgust or distress) with the right. Asymmetry of hemispheric control of negative and positive affect has also been posited by Tucker (1981). Other laterality theories focus primarily on the role of the right hemisphere in the regulation of negative emotions and fight-flight behaviors (for a review, see Silberman & Weingartner, 1986). The data strongly support the relation between right hemisphere EEG activity and the expression of negative emotions in infants, children, and adults; however, research demonstrating the relation between left hemisphere EEG activity and the expression of positive emotions is less conclusive.

In children, right hemisphere dysfunction has been associated with attentional, social, and emotional problems. Voeller (1986) reported data on 16 children with unilateral right hemisphere lesion or dysfunction as assessed by neuropsychological exam and/or CAT scan. Fifteen of these children were extremely distractible and inattentive, meeting the DSM-III criteria for attention deficit disorder; moreover, eight were also hyperactive. Eight children were shy and withdrawn, sharing some of the behavioral characteristics of the inhibited child described by Kagan (in this volume), and nine expressed atypical emotion expression (i.e., prosody, facial expression, and gesture). Most of these children made little eye contact with others, and virtually all had poor relationships with peers.

In their survey of studies with both normal and lesioned subjects, Silberman and Weingartner (1986) suggested that the right hemisphere is superior for recognizing emotional aspects of stimuli. They propose that right hemisphere dominance for emotion regulation reflects a nervous system organization that gives priority to avoidance or defensive mechanisms that have a high survival value. By inference, these avoidance and defensive mechanisms require massive and immediate shifts in autonomic function.

## THE RIGHT HEMISPHERE: AUTONOMIC REGULATION AND REACTIVITY

The right side of the brain also plays a special role in the regulation of emotion. Data supporting laterality theories of emotion have been based on studies of electrophysiological recordings from the scalp (e.g., Fox, in this volume) and neuropsychological studies of dysfunction in individuals with brain damage (e.g., Silberman & Weingartner, 1986). We propose a convergent approach by emphasizing the right brain's regulation of peripheral autonomic activity.

Asymmetry in the control of the autonomic nervous system has been documented in the previous sections. Because peripheral organs are not symmetrical in shape or placement, it is not surprising that the neural control of the autonomic nervous system is lateralized. For example, the heart is displaced to the left, with the right vagus going to the S-A node and the left vagus going to the A-V node. Other organs with dual vagal innervation are often tilted (e.g., the stomach and intestines), or are located higher on one side (e.g., the kidneys), or are larger on one side (e.g., the lungs).

Emphasis on the asymmetry of autonomic organs has implications for the evolution of central regulatory systems and cortical development. In mammals, the peripheral autonomic organs and brain-stem structures are similar across species. Asymmetrical neural control of autonomic processes is characteristic of mammals. However, the process of encephalization differs among mammalian species, with man possessing a uniquely large cerebral cortex. Because the neural control of the vagus is ipsilateral (e.g., the left vagus originates in the left side of the brain stem), the right hemisphere—including the right cortical and subcortical structures—would promote the efficient regulation of autonomic function via the source nuclei in the brain stem. For example, neuroanatomical and electrophysiological studies demonstrate the important regulatory function of the right central nucleus of the amygdala in regulating the right nucleus ambiguus.

We propose that the functional dominance of the right side of the brain in regulating autonomic function has implications for specialization of motor and language dominance on the left side of the brain. The right-sided responsibilities of regulating homeostasis and modulating physiological state in response to both internal (i.e., visceral) and external (i.e., environmental) feedback potentially enabled the control of other functions to evolve on the left side of the brain. With greater encephalization, which is characteristic of more cognitive mammalian species such as man, lateralized specialization is more observable.

A sharing of central control of voluntary and emotion-homeostatic processes would enable the individual to express complex voluntary levels of communication and movement via the left side of the brain and more intense emotion-homeostatic processes via the right side of the brain. If these processes are lateralized, they might have a degree of autonomous regulation. Of course, the central nervous system is complex and has, in many instances, both ipsilateral and contralateral communication. This provides a small percentage of individuals with central control of both language and dominant hand motor movement on the right instead of the left side of the brain. However, owing to the asymmetry of the peripheral autonomic organs and the medullary control of the autonomic nervous system, the right side of the brain is always dominant in the regulation of autonomic function and, thus, emotion.

Data from stimulation studies using left and right visual fields (e.g., Hugdahl, Franzon, Andersson, & Walldebo, 1983; Weisz, Szilagyi, Lang, & Adam, 1992) indicate that activation of the right cortex results in larger and more reliable autonomic responses. Additionally, studies of brain-damaged individuals have shown that right hemisphere damage or dysfunction is associated with a severe deficit in the facial, vocal, and autonomic components of the expression of emotions (Pimental & Kingsbury, 1989; Silberman & Weingartner, 1986). Similar asymmetry of the sympathetic nervous system has been reported, with the right stellate ganglion having greater cardiovascular control than the left stellate ganglion (Yanowitz, Preston, & Abildskov, 1966). However, no research has focused on assessment of the cardiac vagal tone measure in subjects with right hemisphere disorders. Since the cardiac vagal tone measure is physiologically linked to the right hemisphere regulation of autonomic activity, it might index the individual's functional capacity to regulate autonomic function and to express emotion.

## THE VAGAL CIRCUIT OF EMOTION REGULATION: A MODEL

The right vagus and, thus, cardiac vagal tone are associated with processes involving the expression and regulation of motion, emotion, and communication. These processes enable individuals to approach and/or withdraw from objects and events in their environment. The regulation of attention, a major substrate for appropriate social behaviors, is included among these processes. Thus, the approach/withdrawal dimension includes movement in psychological as well as physical space. Vagal regulation of the heart modulates metabolic output to physically approach or withdraw; vagal modulation of vocal intonations provides clues for an individual to approach or withdraw; feedback from our own facial muscles to the vagus and the ability to pay attention to social cues, including another person's facial muscles and verbal commands, allow us to negotiate appropriate approach or withdrawal behaviors.

Just as Schneirla (1959) proposed that all behaviors could be described in terms of approach and withdrawal actions, we too place the dimensions of approach and withdrawal in a central role in our model of the vagal regulation of emotion. Schneirla assumed that stimulus intensities modulated autonomic function to produce sympathetic dominance during high intensities and parasympathetic dominance during low intensities. However, according to our model of emotion regulation, sympathetic modulation is not always necessary, and the vagal system can promote approach or withdrawal behaviors via the right nucleus ambiguus control of heart rate and the intonation of vocalizations.

The vagal circuit of emotion regulation is schematized in Figure 1. The circuit focuses on right hemisphere regulation of emotion states via vagal projections from the nucleus ambiguus to the larynx and the S-A node of the heart. The vagal control of the right side of the larynx produces changes in vocal intonation associated with the expression of emotions. The vagal control of the S-A node produces a cardiovascular state associated with specific emotions and facilitating attention or fight-flight behaviors.

Emotion process may originate on a cortical level or may be initiated and/or regulated by afferent feedback from visceral organs. For example, if the emotion were triggered by a psychological process (e.g., perception of a specific stimulus), the following stages may occur: (1) cortical areas stimulate the amygdala; (2) the central nucleus of the amygdala stimulates the nucleus ambiguus; and (3) the right vagus regulates heart rate and vocal intonation by communicating with the S-A node and the right side of the

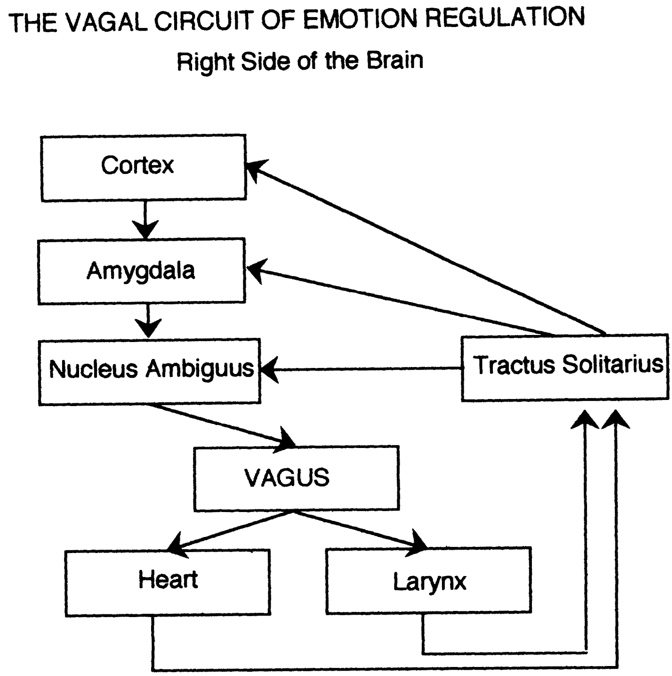


FIG. 1.—Schematization of the vagal circuit of emotion regulation

larynx. Regulation of the emotion response also may follow a specific path: (1) sensory information regarding the status of visceral organs stimulates vagal afferents, lateralized vagal afferents stimulate the nucleus tractus solitarius in the brain stem, and projections from the nucleus tractus solitarius stimulate the cortex, amygdala, and/or nucleus ambiguus to regulate the emotion expression; or (2) the emotion state could be initiated by the visceral afferent (e.g., stomach pains) and trigger the cortical, subcortical, brain-stem, and autonomic responses associated with emotion.

Interference with transmission on any level of the circuit may result in affective disorders, including emotion regulation problems or severe mood states. Dysfunction in the circuit could be caused by brain damage, neural transmission problems due to drugs, or learned dysfunction. The learning model is based on the demonstrations that classical conditioning and other associative learning paradigms that modify autonomic function are dependent on cortical-autonomic and amygdaloid-autonomic pathways. Thus, autonomic afferents to or from the nucleus ambiguus may be amplified, attenuated, or blocked via neuropathy, drugs, or associative learning to produce different affective states.

The vagal circuit of emotion regulation that we propose makes several important advances in the conceptualization of the physiology of emotion and emotion regulation. It introduces the importance of the vagal system in the physiology of emotion and emphasizes the bidirectional (i.e., afferent feedback) physiological characteristics of the vagus. Furthermore, the vagal circuit is neuroanatomically dependent on right medullary control of autonomic function via the nucleus ambiguus, has a noninvasive window of measurement via the quantification of respiratory sinus arrhythmia with the vagal tone index ($\hat{V}$), explains individual differences due both to defects in neurophysiology and to associative learning, and is consistent with brain-damage research. Finally, by emphasizing afferent feedback and communications among various levels of the nervous system, the vagal circuit of emotion regulation provides an explanation for the effectiveness of specific interventions (e.g., nonnutritive sucking, massage, eating, exercise, yoga, and cognitive strategies) in the regulation of emotions.

## VAGAL REGULATION AND EMOTION

Interest in vagal tone as a regulatory mechanism in the expression of individual differences in autonomic function is not new. Eppinger and Hess introduced the concept of vagal tone as an individual difference construct in their monograph *Die Vagotonie* (1910). They described a form of autonomic dysfunction for which there was no known anatomical basis: "It is often unsatisfactory for the physician . . . to find that he must be content to make a diagnosis of 'Neurosis'. The symptomatology and the impossibility of establishing any anatomical basis for the disease always remain the most conspicuous points in formulating the diagnosis of a neurosis of an internal organ" (p. 1). The objective of their monograph was to identify a physiological substrate that could explain this anomaly and thus provide the mechanisms for a variety of clinically observed neuroses.

Although Eppinger and Hess were interested in clinical medicine, their case studies described a problem in the regulation of autonomic function that might be intimately related to the regulation of emotion. Their observations are relevant to our interest in the regulation and expression of emotion for four important reasons: first, they alerted us to the importance of the vagal system in mediating physiological and psychological responses; second, they related individual differences in physiology (i.e., vagal tone) to individual differences in behavior (i.e., neuroses); third, they recognized the pharmacological sensitivity of the vagal system to cholinergic agents; and, fourth, they brought to the attention of the medical community the commonality of the vagal innervation of various peripheral organs.

In our model of vagal regulation, we adopt a stimulus-organism-response (SOR) approach. The expression and regulation of emotions are the responses, which are dually determined by the stimulus and the organism. It is not just the stimuli that elicit a response; rather, the response is determined by a complex system of behavioral-physiological responses that involve perception of the stimulus, afferent feedback, and the regulation of approach-withdrawal behaviors via the vagal system. Because of the link between the right vagus and the processes of motion, emotion, and communication, individuals with low vagal tone and/or poor vagal regulation would be expected to exhibit difficulties in regulating emotion state, in appropriately attending to social cues and gestures, and in expressing contingent and appropriate emotions. Thus, the possibility exists that the vagal system may provide a physiological metaphor for the regulation of emotion states. Individual differences in vagal tone may index organismic factors related to the competency of the individual to react physiologically and to self-regulate.

## VAGAL TONE RESEARCH

In testing our model of vagal regulation, we have been assessing empirically whether individuals with low vagal tone and/or difficulties in regulating vagal tone have problems with the expression and/or regulation of motion, emotion, and communication. The potential to move, express emotion, and communicate enables an individual to maneuver along a continuum of approach-withdrawal with the environment. Several behaviors are critical to this function, including behavioral reactivity, facial expressivity, and emotion regulation.

If vagal tone mediates the expression and regulation of emotion, developmental shifts in vagal tone might contribute to the observed developmental shifts in affective expression. Research has demonstrated that vagal control of the autonomic nervous system increases developmentally as the nervous system matures. We have reported a relation between gestational age and vagal tone in premature neonates (Porges, 1983) and a monotonic increase in vagal tone from birth through the first 18 days postpartum in rats (Larson & Porges, 1982). In the rat pups, these changes were paralleled by increased organization of behavior, including enhanced state regulation, exploration, and attention. Current longitudinal research with human infants has demonstrated that vagal tone increases monotonically from 3 to 13 months (Izard et al., 1991).

To evaluate whether vagal tone as a construct has properties that may be useful in explaining the expression of emotion and the regulation of affective state, the following sections review research on the relation between vagal tone and variables in the domains of reactivity, the expression of emotion, and self-regulation.

*Reactivity*

Here we provide theoretical justification and empirical support for the hypothesis that individual differences in vagal tone are related to heart rate and behavioral reactivity in young infants. The core proposition is that vagal tone indexes a dimension of central nervous system organization that disposes an individual to be hypo- or hyperreactive. Thus, subjects with higher levels of vagal tone should have more organized (i.e., consistent) autonomic responses with shorter latency and greater magnitude autonomic responses.

Before 1970, heart-rate responses were defined as rapid increases and decreases to discrete stimuli. These response patterns were interpreted as an autonomic correlate of an orienting response (see Graham & Clifton, 1966). Research was not directed at the physiological mechanisms that may mediate individual differences in autonomic reactivity. Observed variations in heart-rate response characteristics were assumed to be dependent on both the physical parameters of the stimulus and the subject's previous history with the stimulus. Individual differences that could not be attributed to these two sources were treated as experimental (i.e., measurement) error.

In the early 1970s, our research demonstrated that individual differences in spontaneous base-level heart-rate variability were related to heart-rate reactivity. These studies stimulated our interest in the vagal mechanisms mediating heart-rate variability and in the development of methods to quantify vagal influences on the heart. The first studies (Porges, 1972, 1973) demonstrated, in a sample of college students, that individual differences in heart-rate variability assessed during baseline conditions were related to heart-rate responses and reaction-time performance. These studies were followed by experiments with newborn infants that demonstrated a relation between baseline heart-rate variability and the magnitude of heart-rate responses to simple visual and auditory stimuli. Newborn infants with higher baseline heart-rate variability reacted with larger heart-rate responses to the onset and offset of auditory stimuli (Porges, Arnold, & Forbes, 1973) and with shorter latency responses to the onset of an increase in illumination (Porges, Stamps, & Walter, 1974). When the illumination was decreased, only the high heart-rate variability subjects responded. Consistent with these findings, only the neonates with higher heart-rate variability exhibited a conditioned heart-rate response (Stamps & Porges, 1975).

Recent studies using the vagal tone index have been consistent with the theme that vagal tone is an index of reactivity. Porter, Porges, and Marshall

(1988) demonstrated in a sample of normal newborns that individual differences in vagal tone were correlated with heart-rate reactivity to circumcision. Neonates with higher vagal tone exhibited not only larger heart-rate accelerations but also lower fundamental cry frequencies in response to the surgical procedures, the latter having been hypothesized to be associated with greater vagal influences (see Lester & Zeskind, 1982). Consistent with these findings, Porter and Porges (1988) have also demonstrated in premature infants that individual differences in vagal tone are related to the heart-rate response during lumbar punctures.

Behavioral reactivity and irritability in response to environmental stimuli assessed with the Neonatal Behavioral Assessment Scale (Brazelton, 1984) are also associated with vagal tone. In a sample of full-term healthy neonates, DiPietro, Larson, and Porges (1987) found that neonates who were breast-fed had higher vagal tone, were more reactive, and required more effort to test. DiPietro and Porges (1991) evaluated the relation between vagal tone and behavioral reactivity to gavage with a sample of preterm neonates. (Gavage is a commonly used method to feed premature infants by passing food through a tube inserted into the stomach via the nasal or oral passages.) Individual differences in vagal tone were significantly correlated with behavioral reactivity to the gavage method of feeding.

Similar relations between spontaneous vagal tone and reactivity have been reported for older infants. Linnemeyer and Porges (1986) found that 6-month-old infants with higher vagal tone were more likely to look longer at novel stimuli, and only those with high vagal tone exhibited significant heart-rate reactivity to the visual stimuli. Richards (1985, 1987) reported convergent findings that infants with higher levels of respiratory sinus arrhythmia (a measure of vagal tone) were less distractible and had larger decelerative heart-rate responses to visual stimuli. Huffman, Bryan, Pedersen, and Porges (1988) observed that high vagal tone infants at 3 months of age habituated to novel visual stimuli more rapidly than those with low vagal tone; the former were more likely to suppress vagal tone during attention-demanding tasks and received a better attention score than the latter.

In summary, vagal tone mediates the behavioral and emotional response of the organism, and the vagal tone index provides a measure of behavioral and emotional reactivity. Neonates, infants, children, and adults with higher vagal tone exhibit appropriate autonomic reactivity and, in turn, appropriate behavioral and emotional responses (e.g., crying, irritability) to stimulation.

### *Expression of Emotion*

Few studies have investigated individual differences in vagal tone as a mediating variable indexing individual differences in facial expressivity.

There are two important reasons for posing this research question. First, both autonomic and facial responses have been theoretically associated with the expression of emotions. Second, measurement of vagal tone may provide an index of the neural organization necessary for facial expressions—a hypothesis suggested by the nature of the neurophysiological mechanisms that mediate facial expressions and autonomic reactions. Facial expressions and autonomic reactions associated with emotion states are controlled by brain-stem structures that are in close proximity (i.e., the source nuclei of the facial nerve and the vagus). Quite often the facial nerve is included as part of the "vagus complex." Therefore, if expressivity is assumed to be an individual difference determined by the neural tone of the facial nerve, measurement of the neural tone of the vagus might be related to the expressivity of the infant. Thus, vagal tone, monitored during a nonstressed period, might index a neural propensity to produce facial expressions.

Support for this hypothesis comes from studies that have related resting levels of heart-rate variability to expressivity. Field, Woodson, Greenberg, and Cohen (1982) reported that newborn infants exhibiting greater resting heart-rate variability were more expressive, and Fox and Gelles (1984) found that 3-month-old infants with higher resting heart-rate variability displayed a longer duration of interest expressions. More recently, Stifter, Fox, and Porges (1989) evaluated the relation between the vagal tone index and expressivity in 5-month-old infants and found that infants with higher vagal tone displayed more interest, more joy, and more look-away behaviors toward the stranger.

### *Self-Regulation*

Self-regulation is a difficult process to operationalize. Behaviors as diverse as sustained attention, facial expressions, and latency to soothe can be interpreted as regulatory. Many studies have demonstrated the relation between vagal tone and attention (for a review, see Porges, 1992). In general, higher vagal tone and proper suppression of vagal tone during an attention-demanding task are related to better performance. More important for the discussion of vagal tone and emotion self-regulation, vagal tone has also been shown to be related to the ability to self-soothe.

In both full-term and premature newborns, the ability to self-soothe is inversely related to vagal tone. The higher vagal tone neonates are more irritable and exhibit greater difficulty in self-soothing. However, a subsequent increasing capacity to self-soothe is clearly seen in the high vagal tone neonates. One might speculate that the high vagal tone neonate's reactivity elicits more caregiving from the mother and that, once such an infant becomes physiologically stable, the capacity for self-soothing is consequently enhanced. Thus, the self-regulatory demands might be different for the neonate and for the older infant, and vagal tone might index this propensity to self-regulate under changing developmental demands. Support for this hypothesis comes from a study of 3-month-old infants that found significant relations between vagal tone and soothability (Huffman, Bryan, del Carmen, Pedersen, & Porges, 1992); high base-level vagal tone was correlated with a low soothing score (i.e., little soothing was required) and a high Rothbart soothability score (i.e., distress was easily reduced).

The studies summarized above support the hypothesis that base-level vagal tone is an important determinant of self-regulatory autonomic and behavioral responses. Unfortunately, the relation is more complex, and there are infants with high vagal tone who do not suppress vagal tone under regulatory demands and who show poor emotion regulation (DeGangi, DiPietro, Greenspan, & Porges, 1991; Doussard-Roosevelt, Walker, Portales, Greenspan, & Porges, 1990). According to Greenspan (1991), infants older than 6 months of age who exhibit fussiness, irritability, poor self-calming, intolerance to change, and/or a hyperalert state of arousal are best described as being regulatory disordered.

Preliminary data suggest two important points. First, these infants tend to have high vagal tone. Second, these infants tend to exhibit a deficit in the ability to suppress vagal tone during attention-demanding situations. Assessed at 9 months of age, this inability to suppress vagal tone predicts behavior problems at 3 years (Portales, Doussard-Roosevelt, Lee, & Porges, 1992). It appears that these "fussy babies" are hyperreactive not only to environmental stimuli but also to visceral feedback. The relation between higher vagal tone and greater reactivity is supported, but the relation between vagal tone and the ability to self-regulate, assessed via behavior and the suppression of vagal tone during tasks, is not consistent with that observed with normal infants.

## CONCLUSIONS

What does vagal tone convey about an individual's ability to regulate and express emotion? To answer this question, we have proposed a model that integrates information regarding lateral brain function with the regulation of the peripheral autonomic nervous system. The model is based on the following observations:

1. The peripheral autonomic nervous system is asymmetrical.
2. The medullary regulation of the autonomic nervous system is also asymmetrical, with structures on the right side exhibiting greater control of physiological responses associated with emotion.

3. The right nucleus ambiguus is a source nucleus of the right vagus, which provides control of the larynx and S-A node of the heart and controls vocal intonation and cardiac vagal tone.

4. The right central nucleus of the amygdala has direct influences on the right nucleus ambiguus to promote the laryngeal and cardiovascular responses associated with emotion (e.g., increased pitch of vocalization and increased heart rate).

5. Stimuli that are processed primarily by the right hemisphere produce greater cardiovascular responses than stimuli processed by the left hemisphere.

6. Damage to the right hemisphere blunts facial expression, vocal intonation, and autonomic reactivity.

Although each of these points has been documented, no study has as yet adequately tested the model linking vagal tone to right hemispheric regulation of emotion. Since the cardiac vagal tone index is an accurate measure of the input to the S-A node from the right nucleus ambiguus, it provides a noninvasive measure of right hemisphere capacity to process emotion stimuli and to regulate emotional responses. To test this model adequately, it will be necessary to conduct experiments to evaluate vagal tone and vagal reactivity of individuals with known right hemisphere disorders and evaluate covariations between individual differences in vagal tone and vagal reactivity and the expression and interpretation of emotions in non-brain-damaged subjects.

Providing evidence in support of this model, previous studies have addressed the relation between vagal tone and three dimensions related to the expression and regulation of emotion: reactivity; expressivity; and self-regulation. The literature and our ongoing research permit the following generalizations.

First, independent of developmental stage, vagal tone is highly correlated with autonomic reactivity; individuals with higher vagal tone consistently exhibit larger and more reliable autonomic responses. Second, the relation between vagal tone and emotion expressivity appears to be dependent on development. A preliminary study has demonstrated that higher vagal tone was associated with greater facial expressivity in 5-month-old infants but failed to establish any such relation in 10-month-old infants. These data suggest that there is a developmental shift in the neurophysiological control of facial expressivity: as infants become older, facial expressivity may become more dependent on higher brain control and less related to individual differences in brain-stem function, manifest in the tonic outflow of the cranial nerves.

Third, independent of developmental stage, vagal tone is correlated with self-regulation. Individuals with high vagal tone consistently suppress vagal tone or heart-rate variability to enhance the intake of information from the environment. Fourth, there is a subset of individuals who have high vagal tone and who do not suppress vagal tone or heart-rate variability during information processing. These individuals appear to have a *regulatory* disorder that is displayed on both behavioral and physiological levels; regulatory disordered infants are often labeled as *fussy* because of their continuous crying and disorganized behaviors, and they have difficulty self-soothing and maintaining a calm state.

Finally, as the infant matures, the range of expressivity increases, the self-regulation of emotion is enhanced, and vagal tone increases; in the course of normal development, the increased myelination and regulation of autonomic function associated with enhanced vagal tone parallels the range and control of emotion states. Thus, on both developmental and individual difference levels, vagal tone is clearly related to the processes of reactivity, expressivity, and self-regulation.

We introduce vagal tone as a physiological construct that is useful in explaining individual and developmental differences in the expression and regulation of emotion. As an organizing construct, vagal tone is useful in integrating central, autonomic, and psychological components of emotion. Vagal tone may index individual differences in the homeostatic capacity of the autonomic nervous system to foster rapid expression and attenuation of sympathetic reactions. This function is dependent on neural regulation of the reciprocal relation between the antagonistic branches of the autonomic nervous system.

During emotion states, normal homeostatic function is perturbed to express emotions. Initially, sympathetic activity is expressed owing primarily to the withdrawal of the antagonistic vagal tone. Even without discrete sympathetic excitation, the vagal withdrawal will enhance the expression of sympathetic activity when the two systems have antagonistic influences on specific organs. The vagal withdrawal triggers the autonomic correlates of emotions.

If the emotion state is prolonged, the physiological state will be maintained by activation of sympathetic and endocrine systems. Excessive sympathetic activity reflects a deviation from normal homeostatic autonomic function, which then elicits vagal activity to self-regulate and return the autonomic state to homeostasis. In individuals with high vagal tone and appropriate vagal regulation capacities, the autonomic nervous system has the capacity to react (i.e., appropriate reactivity and expressivity) and to return rapidly to homeostasis (i.e., self-regulation and self-soothing).

The relation among the right hemisphere, the right vagus, and the processes involved in the expression and regulation of motion, emotion, and communication makes apparent the relevance of examining individual differences in vagal tone in studies of emotion regulation. Vagal tone and vagal regulation in the context of the vagal circuit of emotion regulation that we proposed may provide the physiological measures of the individual's ability to regulate motion, emotion, and communication.

## SUMMARY

On the basis of current knowledge of neuroanatomy and our previous research with cardiac vagal tone, we have proposed the vagal circuit of emotion regulation. The vagal circuit of emotion regulation incorporates lateral brain function with the regulation of the peripheral autonomic nervous system in the expression of emotion. The vagus and the vagal circuit do not function independently of other neurophysiological and neuroendocrine systems. Research on brain activity (see Dawson, in this volume; Fox, in this volume) and research on adrenocortical activity (see Stansbury & Gunnar, in this volume) demonstrate that EEG and cortisol are related to emotion states and to individual differences similar to those that we have investigated.

The vagal circuit emphasizes not only the vagus but also the lateralization of specific brain structures in emotion regulation. The emphasis of the vagal circuit on right-brain-stem structures stimulates several testable hypotheses regarding the function of specific structures in the right brain in emotion regulation. These speculations are consistent with other reports (see Dawson, in this volume; Fox, in this volume) describing asymmetrical EEG activity during expressed emotions. Moreover, the vagal circuit does not exist independently of the brain structures and peptide systems regulating cortisol (see Stansbury & Gunnar, in this volume). Areas in the brain stem regulating vagal activity are also sensitive to the peptides that regulate cortisol (e.g., vasopressin and corticotropin-releasing hormone).

In this essay, we have provided information regarding the relation between vagal tone and emotion regulation. A review of research indicates that baseline levels of cardiac vagal tone and vagal tone reactivity abilities are associated with behavioral measures of reactivity, the expression of emotion, and self-regulation skills. Thus, we propose that cardiac vagal tone can serve as an index of emotion regulation.

Historically, the vagus and other components of the parasympathetic nervous system have not been incorporated in theories of emotion. Recent developments in methodology have enabled us to define and accurately quantify cardiac vagal tone. Theories relating the parasympathetic nervous system to the expression and regulation of emotion are now being tested in several laboratories.