Central and autonomic nervous system integration in emotion

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Abstract

Emotions involve physiological responses that are regulated by the brain. The present paper reviews the empirical literature on central nervous system (CNS) and autonomic nervous system (ANS) concomitants of emotional states, with a focus on studies that simultaneously assessed CNS and ANS activity. The reviewed data support two primary conclusions: (1) numerous cortical and subcortical regions show co-occurring activity with ANS responses in emotion, and (2) there may be reversed asymmetries on cortical and subcortical levels with respect to CNS/ANS interrelations. These observations are interpreted in terms of a model of neurovisceral integration in emotion, and directions for future research are presented.

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1. Introduction

Emotions involve a complex mix of cognitive, affective, behavioral, and physiological responses (e.g., Birbaumer & Ohman, 1993; Oatley & Jenkins, 1996). At a physiological level of analysis, much current research in affective neuroscience seeks to elucidate the neural networks that underlie emotion. In this regard, results of numerous investigations of the central nervous system (CNS) concomitants of emotion suggest the involvement of multiple cortical (e.g., frontal, temporal, and parietal) and subcortical (e.g., basal ganglia, thalamus, amygdala, and hippocampus) regions across a variety of positive and negative emotions such as happiness, anxiety, anger, sadness, disgust (for reviews, see Borod, 2000; Lane & Nadel, 2000).

A separate body of psychophysiological research has sought to identify patterns of autonomic nervous system (ANS) correlates of emotion. Although several investigations have noted emotion-specific autonomic response patterns (e.g., Ekman, Levenson, & Friesen, 1983; Sinha, Lovallo, & Parsons, 1992), the majority of studies suggest greater similarities than differences among physiological activation patterns during various emotional states (for reviews see Cacioppo, Berntson, Larsen, Poehlmann, & Ito, 2000; Neumann & Waldstein, 2001; Stemmler, 1996).

Study of the linkage between central and autonomic correlates of emotion is relevant to numerous fields of investigation including affective neuroscience, neuropsychology, psychophysiology, and behavioral medicine. Yet, relatively few studies have simultaneously examined CNS and ANS responses during emotion. In this paper, we provide an overview of such investigations. Previously, it has been suggested that the right hemisphere may be dominant in eliciting autonomic responses during emotion (e.g., Borod & Madigan, 2000; Gainotti, 1989; Wittling & Roschmann, 1993). However, others have proposed more complex models of association between emotion-related central and autonomic response patterns (Lane & Jennings, 1995; Lane & Schwartz, 1987; Thayer
& Lane, 2000); many of these models focus on both cortical and subcortical interconnections (such as frontal–subcortical systems). We present results from the literature on concomitant CNS and ANS response to emotional stimuli to suggest the viability of the latter position. We discuss findings from lesion studies, visual half field studies, and investigations that have directly measured CNS activity with the spontaneous electroencephalogram (EEG), evoked potentials (EPs), or neuroimaging techniques, along with measures of ANS activation. We also highlight a recent model of neurovisceral integration (Thayer & Lane, 2000) to enhance the findings of the present review. This model relies on principles of dynamical systems to suggest that different neural networks are flexibly recruited according to situational demands to integrate the central and autonomic response to emotional stimuli. We use findings from our overview of the CNS/ANS literature and the theoretical position of the model of neurovisceral integration to provide suggestions for future research directions.

Prior to the review of relevant studies, some remarks on the definition of “emotion” and additional technical issues may be helpful. First, defining “emotion” has been a controversial issue, both historically (e.g., Epstein, 1984), and currently (e.g., Scherer, 2000). For the purpose of the present review, we use a working definition that focuses on the functional aspects of emotions (e.g., Frijda, 1986, 1988; Levenson, 1988; see Thayer & Lane, 2000): Emotions may be characterized as an organismic response to an environmental event that facilitates the rapid mobilization for action. This response involves multiple systems of the organism, such as cognitive, behavioral, and autonomic sub-systems. When these response systems are efficiently coordinated, they allow for goal-directed behavior in the service of flexible adaptation of the organism to changing environmental demands.

Second, several researchers have classified emotional responses in terms of a number of discrete “basic emotions” such as surprise, interest, happiness, rage, fear, sadness, and disgust (e.g., Ekman, 1984; Izard, 1977; Tomkins, 1962). In contrast, other investigators have argued that emotions—at least on the level of subjective experience—may be more parsimoniously described by only two dimensions, which are “valence” (pleasant–unpleasant) and “arousal” (low–high intensity) (e.g., Larsen & Diener, 1992; Russell, 1980). Several researchers have suggested that these two dimensions are hierarchically related to discrete emotions (e.g., Diener, Smith, & Fujita, 1995; Russell & Barrett, 1999). Nonetheless, these different theoretical orientations have given rise to different emotion induction procedures for experimental research (for general overviews, see Gerrards-Hesse, Spies, & Hesse, 1994; Oatley & Jenkins, 1996), and concomitant physiology has been contrasted in various experiments between basic emotions, or between pleasant and unpleasant states. For example, a variety of discrete emotions such as happiness, sadness, anger, fear, and disgust have been elicited with procedures such as presentation of film clips (Lane, Reiman, Ahern, & Thayer, 2000), presentation of pictures of respective facial expressions (Schneider et al., 1995), recall and re-experience of personal life episodes (Waldstein et al., 2000), anticipation of electric shock (Slomine, Bowers, & Heilman, 1999), or hypnotic induction (de Pascalis, Ray, Tranquillo, & D’Amico, 1998). In contrast, pleasant and unpleasant emotions have typically been induced by the presentation of affective slides (e.g., Cuthbert, Schupp, Bradley, Birbaumer, & Lang, 2000; Lane et al., 1997; Palomba, Angrilli, & Mini, 1997).

Third, the studies described in this review have used a variety of variables to measure ANS activity. The ANS has two main branches—the sympathetic and parasympathetic (vagal) nervous systems—that innervate visceral organs, blood vessels, and glands, and which exert opposite effects on the innervated organs (for an overview, see Lovallo & Sollers, 2000). The most frequently used measure of ANS activity is heart rate (HR), which is antagonistically affected by sympathetic and parasympathetic activity. This dual influence renders considerable ambiguity to the interpretation of HR responses, but inclusion of other cardiovascular measures can help to avoid this problem: HR variability and particularly its high frequency component primarily reflect cardiac parasympathetic activity whereas measures of myocardial performance indicate primarily β-adrenergic sympathetic activity. Another widely used ANS measure is blood pressure, which is also influenced by sympathetic and parasympathetic activity, and skin conductance response (SCR), which primarily reflects sympathetic activity.

2. Studies of CNS and ANS correlates of emotion

2.1. Lesion studies

Most lesion studies have contrasted autonomic responses in individuals with right versus left hemispheric brain lesions. Results suggest a critical role of the right hemisphere in mediating the ANS response to emotional stimuli. In this regard, many, though not all (e.g., Slomine et al., 1999), studies demonstrated a diminished SCR or HR response to pleasant or unpleasant stimuli in right brain-damaged patients compared with left brain-damaged patients or control subjects (Andersson & Finset, 1998; Caltagirone, Zoccolotti, Originale, Daniele, & Mammucari, 1989; Heilman, Schwartz, & Watson, 1978; Meadows & Kaplan, 1994; Morrow, Vrtunski, Kim, & Boller, 1981; Zoccolotti, Caltagirone, Benedetti, & Gainotti, 1986; Zoccolotti, Scabini, & Violani, 1982).
In contrast, several recent investigations that examined patients with more distinct cerebral lesions suggest that a right/left distinction in hemispheric dominance for central and autonomic linkages during emotion is too simplistic. Tranel and Damasio (1994) found that bilateral lesion of the ventromedial prefrontal region, unilateral lesion of the right inferior parietal region, and unilateral left or right lesion of the anterior cingulate gyrus were associated with a diminished SCR to emotional stimuli. This observation suggests that structures of both hemispheres are important sites for the neural networks that link emotional stimuli to ANS responses. Bechara et al. (1995) found that bilateral lesion of the amygdala prevented the acquisition of a conditioned aversive SCR. However, other studies have suggested a lack of involvement of the amygdala, or hippocampal regions, in the SCR to emotional stimuli (Tranel & Damasio, 1989; Tranel & Hyman, 1990).

However, there are problems with lesion studies. For example, lesion studies are often limited by small sample sizes. In addition, because naturally occurring lesions typically do not respect neuroanatomical boundaries (see Kolb & Taylor, 2000), these types of investigations yield interpretive difficulties with respect to definitive localization of function. As well, the considerable plasticity of the brain allows post-lesion relocation of functions, which also hampers the interpretation of findings.

2.2. Visual half field studies

Central and autonomic responses have also been examined in visual half field studies in normal subjects (for a review, see Wittling, 1995). In these studies, a visual stimulus is presented selectively to the right or left hemisphere and the ANS response is measured. Similar to the lesion studies, several investigations in this area also suggested a right-hemispheric dominance for HR responses to (or in anticipation of) unpleasant stimuli (Dimond & Farrington, 1977; Hugdahl, Franzon, Andersson, & Waldebo, 1983; Spence, Shapiro, & Zaidel, 1996), although findings related to cardiovascular response to pleasant stimuli were inconsistent (Dimond & Farrington, 1977; Wittling, 1990).

In contrast, several recent visual half field studies challenge the hypothesis of right-hemispheric dominance for ANS responses. Some preliminary evidence has suggested a right hemispheric dominance for emotion-induced sympathetic nervous system response (as measured by various indices of myocardial function), and a left hemisphere dominance for the parasympathetic response (as assessed by HR variability) (Wittling, Block, Genzel, & Schweiger, 1998a; Wittling, Block, Schweiger, & Genzel, 1998b). Unfortunately, visual half field studies are limited in number. As well, this research approach does not allow for a localization of function within the cerebral hemispheres.

2.3. Spontaneous electroencephalography (EEG) studies

A promising approach for the study of central and autonomic integration in emotion utilizes the spontaneous EEG to localize cortical activation while assessing an index (or indices) of autonomic function. In a recent investigation of self-generated happy and sad emotions and a relaxation condition, de Pascalis et al. (1998) found that bilateral arousal at the midfrontal cortex, arousal asymmetry at the precentral cortex (i.e., right-sided asymmetry during sadness and left-sided asymmetry during relaxation), and HR responses all followed the same response pattern across all conditions. Both midfrontal and relative right-sided precentral cortical activation and HR were largest in the sad and smallest in the relaxation condition. However, there was no co-occurrence of cortical arousal and HR across the three conditions for parietal sites.

Further studies extended these findings. Schmidt, Fox, Schulk, and Gold (1999) found that shy, as compared to non-shy, children showed a greater increase in right midfrontal cortical activation and a greater increase in HR during a task designed to induce self-presentation anxiety. However, no group differences were noted in the left midfrontal, parietal, and occipital scalp regions, or in a measure of cardiac vagal tone. Demaree, Harrison, and Rhodes (2000) found increases in bilateral frontal cortical activity and HR immediately before and after a cold pressor test in high hostile, but not low hostile, men. In a recent study of young adults, Waldstein et al. (2000) noted positive correlations between left and right midfrontal cortical activation and HR during an anger recall condition. Subjects who displayed a lateralized right midfrontal cortical activation response during anger-inducing tasks also showed enhanced blood pressure responses. In addition, exploratory analyses indicated that men who showed a lateralized left midfrontal cortical activation response during happiness-inducing tasks also displayed the greatest concomitant increase of systolic blood pressure and HR. Davidson, Marshall, Tomarken, and Henriques (2000) examined social phobics and normal controls during anticipation of public speaking. The social phobics showed increased state anxiety and increased relative right-sided hemispheric activity during anticipation of the speech, whereas controls showed no substantive changes. However, the corresponding increase in HR and blood pressure during anticipation was similar in both groups, which suggests a lack of correspondence between CNS and ANS measures in this study. Using a very different experimental paradigm, Gilbert et al. (1999) noted that one month of smoking abstinence was associated with decreased cortical activation, particularly at bilateral parietal sites, and a decreased HR. However, there were no significant changes in positive or negative mood.
In sum, the spontaneous EEG studies have employed very different types of samples and have utilized disparate experimental paradigms. It therefore is not surprising that the findings are somewhat heterogeneous. Nonetheless, preliminary evidence suggests a positive association between an increased bilateral or right-sided activation of the anterior cortex and increased HR or systolic blood pressure in unpleasant emotional states. Interestingly, none of these studies observed similar associations for posterior sites. However, the evidence for pleasant emotional states is not consistent, and preliminary evidence suggests the possibility of sex differences. These findings require replication before definitive interpretations are tenable. In addition, major limitations of the spontaneous EEG include the inability to record subcortical activity, low spatial resolution, and mediocre temporal resolution (in the second range).

2.4. Evoked potential studies

Two recent studies evaluated evoked potential (EP) and autonomic response to emotional stimuli. EP allows a registration of brain activity with a temporal resolution in the millisecond range. Palomba et al. (1997) noted a large positive correlation between the amplitude of the electrocortical response at vertex (averaged across a time range between 600 and 900 ms after picture onset) and HR deceleration during presentation of pleasant, unpleasant, and neutral pictures. In another study, Cuthbert et al. (2000) noted that the amplitude of the electrocortical response (averaged across anterior and posterior sites and across a time range between 400 and 1000 ms after picture onset) to pleasant, unpleasant, and neutral pictures was associated with an increased SCR, but not with the HR response. The contradictory findings of these two studies do not permit conclusions at present. Although EP methods have superior temporal resolution compared with other measures of CNS activity, EPs are also not well suited for the registration of subcortical activity, and have a low spatial resolution.

2.5. Neuroimaging studies

Major advantages of neuroimaging methodology include the co-registration of cortical and subcortical activity and good spatial resolution. Several recent investigations simultaneously collected measures of regional cerebral blood flow with \(^{15}\)O-water positron emission tomography (PET), and measures of ANS activation during the induction of emotions. Schneider et al. (1995) found that sad and happy moods, induced by a combined imagination and picture presentation task, were associated with different patterns of regional brain activation, but similar HR accelerations. There were, in addition, no significant correlations between cerebral blood flow and HR. Soufer et al. (1998) recorded HR and blood pressure during a neutral control task and an unpleasant emotional state that was induced with a mental stress task. Subjects who showed an increased rate pressure product (which is predominantly due to sympathetic activity) during the emotional state also showed increased brain activation in the cerebellum, the periaqueductal gray, right inferior frontal gyrus, and middle frontal gyrus/orbitofrontal cortex. Lane et al. (1997) noted that both pleasant and unpleasant picture presentation were associated with greater activation of left prefrontal cortex, left thalamus, left hypothalamus, and left midbrain structures compared with neutral picture presentation. These valence-independent effects were accompanied by greater SCR to pleasant and unpleasant pictures than to neutral stimuli. In a further investigation, Lane, Chua, and Dolan (1999) examined separately the effects of valence and arousal on regional blood flow and autonomic activity. Irrespective of valence, highly arousing stimuli (relative to low arousing stimuli) elicited both greater SCR, in addition to activation in the medial prefrontal cortex, right anterior temporal cortex, right extrastriate cortex, as well as in the left amygdala and left thalamus. More recently, Damasio et al. (2000) induced sadness, happiness, anger, and fear with recall of personal life experience, and compared simultaneously registered PET, HR, and SCR with a neutral control condition. In addition to a multitude of emotion-specific effects on regional blood flow, there was common activation during all four emotions (compared with the neutral state) in the right insula, the left midbrain, and the left mesial cerebellum, in addition to a common deactivation in the right lateral frontal lobe. Increases in HR and SCR were also noted during sadness, happiness, anger, and fear as compared to the neutral control condition. Lane et al. (2000) induced happiness, sadness, and disgust using film clips and personal recall tasks. HR variability was correlated with regional brain activation during the emotion conditions, a neutral condition, and the subtraction of neutral from emotion conditions. Of particular note, a positive correlation between HR variability and regional brain activation in the medial prefrontal cortex and the left posterior orbitofrontal/ anterior insular cortex was found for the subtraction comparison. More specifically, emotional arousal was associated with a decrease in HR variability and concomitant decreases in brain activation in these regions.

To date, relatively few studies have simultaneously measured CNS activation using neuroimaging procedures and ANS activity during emotional states. Nonetheless, the preliminary evidence suggests a co-occurrence of left subcortical activation and increased SCR during both pleasant and unpleasant emotional states. These subcortical structures comprise the amygdala, thalamus, and hypothalamus, in addition to midbrain regions of the left hemisphere. For cortical structures, however, such lateralization is less clear. Some findings point to a
co-occurrence of greater relative left-sided activation of the frontal lobe and increased SCR during pleasant and unpleasant emotion. However, other findings suggest a co-occurrence of right frontal lobe, insular, anterior temporal lobe, and extrastrate cortical activation and increased SCR or rate pressure product during pleasant and unpleasant states. Considered together, these findings again indicate that a left/right dichotomy is too simplistic to describe CNS/ANS relations in emotion, and suggest that localization on the anterior–posterior and the cortical–subcortical dimensions is also important. Interestingly, the preliminary evidence also suggests that the co-occurrence of CNS and ANS activity may be mediated by the arousal component of emotional stimuli, rather than by valence. These observations require replication, particularly because many of these studies are limited by relatively small sample sizes (particularly in relation to the number of relevant variables), which hampers statistical conclusions. Although the spatial resolution of neuroimaging methods is good compared with EEG and EP methods, PET has a low temporal resolution (in the minute range).

3. Conclusion

The data reviewed above support two primary conclusions. First, there is ample support for the notion that numerous cortical and subcortical regions show co-occurring activity with ANS responses in emotion. Such a coupling between CNS and ANS activity may be inferred for frontal, temporal, parietal, and anterior cingulate cortices together with subcortical structures including the amygdala, thalamus, hypothalamus, and the midbrain. In this regard, lesion studies indicate that the ventromedial prefrontal region, the right inferior parietal region, and the anterior cingulate gyrus are important sites for the neural networks that link pleasant and unpleasant stimuli to the SCR (Tranel & Damasio, 1994), and that selective bilateral lesions of the amygdala prevent the acquisition of conditioned aversive SCR (Bechara et al., 1995). In addition, spontaneous EEG studies suggest a positive association between an increased bilateral or right-sided activation of the anterior cortex and increased HR or systolic blood pressure in unpleasant emotional states (de Pascalis et al., 1998; Schmidt et al., 1999; Waldstein et al., 2000). Finally, neuroimaging evidence reveals a co-occurrence of activation in cortical (frontal, insular, and anterior temporal), subcortical (amygdala, thalamus, and hypothalamus), and midbrain structures and increased SCR and HR during pleasant and unpleasant emotional states (Damasio et al., 2000; Lane et al., 1999; Lane et al., 2000; Lane et al., 1997). Importantly, although the observed covariation of CNS and ANS activity across different emotion induction tasks is suggestive, it must be noted that definitive conclusions are hampered by the limited number of emotional states assessed, and the absence of appropriate statistics to quantify and directly test for correspondence in CNS and ANS responses (for exceptions, see Cuthbert et al., 2000; Lane et al., 2000; Palomba et al., 1997; Schneider et al., 1995; Soufer et al., 1998; Waldstein et al., 2000). In addition, it is important to note that there is variability in findings across studies.

Second, results of the studies reviewed herein suggest that a simple left/right dichotomy with respect to hemispheric specialization for the autonomic component of the emotional response is probably untenable. The empirical data suggest that cortical and subcortical asymmetries in the CNS/ANS processing of emotional information may be reversed. The lesion and spontaneous EEG studies reviewed above provide some evidence for right-sided cortical involvement in ANS responses to unpleasant stimulation (de Pascalis et al., 1998; Schmidt et al., 1999; Tranel & Damasio, 1994; Waldstein et al., 2000). In contrast, results of neuroimaging studies suggest a greater involvement of left-hemispheric subcortical structures (e.g., amygdala, hypothalamus, and thalamus) in ANS responses to emotional stimuli irrespective of valence (Damasio et al., 2000; Lane et al., 1999; Lane et al., 1997). It thus appears that neuroimaging studies generally point to left subcortical activation during emotional arousal, whereas electrophysiological evidence suggests right cortical activation at least for unpleasant emotion.

Such a reversal of cortical/subcortical activation asymmetry may be explained by the joint function of two inhibitory mechanisms. Specifically, the mechanism of ipsilateral inhibition (e.g., Tucker, 1981; Tucker, 1984) suggests that activation of a cortical region results in inhibition of efferent subcortical structures. This is related to Hughlings Jackson's classic principle of "hierarchical integration through inhibition" (Jackson, 1879; Tucker, Derryberry, & Luu, 2000). In addition, the mechanism of contralateral inhibition (e.g., Sackheim et al., 1982) suggests that activation of a cortical area leads to an inhibition of homologous contralateral cortex. The parallel functioning of both mechanisms readily implies a reversal of cortical and subcortical activation asymmetries as is suggested in this review (see Liotti & Tucker, 1995; for a combination of these mechanisms). However, the present evidence for the proposed reversal of cortical/subcortical activation asymmetry in emotion should be explicitly tested in future studies.

We suggest that the present conclusions, derived from the extant empirical literature, can be enriched by consideration of a recent theoretical model of neurovisceral integration in emotion. This model was elaborated by Thayer and Lane (2000), who proposed a network of neural structures that generate, receive, and integrate internal and external information in the service of goal-directed behavior and organism adaptability. One such
functional unit is the central autonomic network (CAN; Benarroch, 1993, 1997). Functionally, this network is an integrated component of an internal regulation system through which the brain controls visceromotor, neuro-endocrine, and behavioral responses that are critical for goal-directed behavior and adaptability (Benarroch, 1993). Structurally, the CAN involves a number of structures throughout the neuraxis including the anterior cingulate, insular, and ventromedial prefrontal cortices, the central nucleus of the amygdala, the paraventricular and related nuclei of the hypothalamus, the periaqueductal gray matter, the parabrachial nucleus, the medulla, and the medullary tegmental field. These structures are reciprocally interconnected, this allows for continuous positive and negative feedback interactions and integration of autonomic responses. Next, the CAN comprises a number of parallel, distributed pathways, which allows for multiple avenues to a given autonomic response (e.g., increased sympathetic or decreased parasympathetic activity or any combination of the two). Moreover, within the CAN, both direct and indirect pathways can modulate the output to the preganglionic sympathetic and parasympathetic neurons. Furthermore, the activity of the CAN is state dependent and thus sensitive to initial conditions (see Glass & Mackey, 1988).

The model of neurovisceral integration proposes that the CAN (or related systems that have been identified by other researchers such as the anterior executive region of Devinsky, Morrell, & Vogt, 1995; or the “emotion circuit” of Damasio, 1998) constitutes a network of CNS structures that is associated with the processes of response organization and selection, and serves to modulate psychophysiological resources in both emotion and attention (Friedman & Thayer, 1998; Thayer & Friedman, 1997). Thus, according to the model, the core neural ‘wetware’ underpinning cognitive, affective, and physiological regulation may be one and the same. Additional structures are flexibly recruited in the service of specific behavioral adaptations. This sparsely interconnected neural network allows for maximal organism flexibility in adapting to rapidly changing environmental demands. When this network is either completely uncoupled or rigidly coupled the organism is less able to dynamically assemble the appropriate neural support structures to meet a particular demand and is thus less adaptive.

The main conclusions and caveats of this review, in conjunction with the model of neurovisceral integration in emotion, suggest a number of future directions for research in this new area of affective neuroscience. First, given the suggestion of widespread cortical and subcortical involvement, and the possibility of reversed asymmetries on cortical and subcortical levels, research on central and autonomic integration in emotion should utilize neuroimaging as the preferred method for assessing CNS activity. Second, there is ample evidence that the emotional ANS response includes a complex pattern of sympathetic and parasympathetic activation (for a review, see Cacioppo et al., 2000), and preliminary evidence suggests that different ANS components may have different CNS concomitants (Witting et al., 1998a, 1998b). Given that frequently used ANS measures like HR or blood pressure are antagonistically influenced by the sympathetic and parasympathetic nervous systems (Berne & Levy, 2001), future research will greatly benefit from examination of both sympathetic and parasympathetic activity. Furthermore, evaluation of distinct sympathetic response patterns (i.e., cardiac versus vascular) would be useful.

Third, there is some evidence that men and women differ in the experience and expression of emotions (see Hagemann et al., 1999; and the literature cited there),
and preliminary evidence also suggests that the association between CNS and ANS activity during emotional states might be moderated by sex (Waldstein et al., 2000). Thus, future studies might further examine this individual difference variable. Additional dimensions of individual differences (e.g., personality) might also influence CNS/ANS integration in emotion.

Fourth, although numerous brain regions display activation during emotion, this does not necessarily imply that each of these regions has direct involvement in autonomic responding. In this regard, associations between individual differences in CNS and ANS responses during emotional states should be directly quantified and tested, preferably with multivariate methods (for an example of a cross-condition correlation approach, see Cuthbert et al., 2000; and for examples of cross-subjects correlations, see Palomba et al., 1997; Schneider et al., 1995; Waldstein et al., 2000). It must be noted, however, that multivariate statistics require larger sample sizes than those employed in most of the studies reviewed above.

Fifth, a main conclusion of the present paper is that different basic emotions might share common CNS and ANS concomitants, which are linked to the arousal dimension of emotion. A rigorous test of this notion will include not only induction variations with respect to arousal and valence, but will also test the alternative hypothesis that different basic emotions share only a few neural (CNS and ANS) concomitants. The envisioned study on CNS/ANS integration in emotion will therefore sample activity in multiple cortical and subcortical regions and from several sympathetic and parasympathetic response systems during the induction of several basic emotions and control conditions. Interrelations between CNS and ANS activity will then be examined with multivariate statistics. This integrated approach will help to consolidate and extend our knowledge on the physiological concomitants of the emotional response.

Finally, the model of neurovisceral integration in emotion may have important implications for the study of central and autonomic integration in emotion. First, attempts to localize the cortical concomitants of emotion in any simple way may be untenable. The literature suggests that a number of neural structures and autonomic changes are associated with emotional states. Indeed, across investigations, sometimes the same central and autonomic activation patterns are associated with different emotions and sometimes different central structures and autonomic changes are associated with the same emotion. These findings can be reconciled in the context of dynamical systems models where structures dynamically organize to meet the demands of specific situations. Healthy systems are characterized by this emotional complexity and diversity whereas unhealthy systems show perseverative activity and a lack of complexity (Friedman & Thayer, 1998; Thayer & Friedman, 2002). This perseverative activity reflects the inability of the system to flexibly assemble the necessary structures into appropriate functional units in response to changing environmental demands.

Next, different methods are needed to examine the dynamics of the physiological activity that support emotional states. The common procedure of averaging over large periods of time may obscure important cortical and autonomic dynamics that in themselves may be the distinguishing features of different emotional and behavioral states (cf. Vaadia et al., 1995). An additional corollary is that the typical strategy of averaging data over individuals also obscures the dynamics and specificity associated with individual differences in the physiological correlates of emotion (Friedman, Santucci, Curtis, & Pumphrey, 1999).

Last, the neural structures that support emotional behavior need not differ from those that support other types of behavior. Indeed, behavior of all types is most certainly built upon the same physiological wetware. This presents a challenge for researchers to identify experimental paradigms that will allow us to examine the system in a more fully integrated fashion.

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