The strong relationship between emotion and the autonomic nervous system has been appreciated throughout the contemporary study of animal behavior. With his publication of *The Expression of the Emotions in Man and Animals*, Charles Darwin (1872) provided a foundation for over 140 years of debate on the nature of emotions and their physiological and behavioral manifestations. In this work, Darwin suggested the existence of distinct kinds of emotional expressions, both somatic and visceral, across phylogeny that gradually evolved as a result of their adaptive function. Twelve years later, William James (1884) first articulated his theory of emotion where he suggested the subjective experience of certain emotions were the result of their adaptive function. Twelve years later, William James (1884) first articulated his theory of emotion where he suggested the subjective experience of certain emotions were the result of particular changes in somatovisceral and behavioral responses. Darwin’s and James’s views on emotion and their physiological manifestations and antecedents served to set the stage for what is still one of the most intensely debated topics in psychology and neuroscience, namely, the nature of emotions and their relationship with specific patterns of somatovisceral activity. In the nearly century and a half of research that has followed, psychology has benefited from numerous technological and theoretical innovations that Darwin and James could have hardly imagined. We can now peer into the inner workings of the brain with in vivo neuroimaging techniques and are beginning to gain an understanding of the molecular and anatomical underpinnings of various psychological processes. Despite these advances, considerable debate exists as to the proper definition of an emotion, the extent to which emotions can be thought of as discrete, and whether different emotions are associated with distinct patterns of somatovisceral activity—topics that would seem quite familiar to both Darwin and James.

Some of the most contentious topics in the field revolve around the appropriate way to describe emotion constructs (from neuropsychological constructions to “natural kinds”), the appropriate levels of analysis (self-report to neurobehavioral) and their structure in affective space (from discrete to dimensional; Coan, 2010; Lang, 2010; Lang & Bradley, 2010; LeDoux, 2012; Levenson, 2011; Lindquist, Siegel, Quigley, & Barrett, 2013; Norris, Gollan, Berntson, & Cacioppo, 2010; Russell, 2003; Scherer, 2009). Clearly all approaches have their own strengths and weaknesses, in that each focuses on one aspect of emotional processes often by ignoring or disregarding...
others. For example, the discrete emotions perspective emphasizes the situational specificity and generalizability of emotional experience and expression to better understand the evolutionary history and, ultimately, the functional roles that emotions serve. The discrete emotions approach, however, tends to overlook the global underlying mechanisms of emotional processes in favor of a focus on specific antecedents, consequents, and correlates of a small set of emotions, such as happiness, sadness, anger, disgust, fear, and surprise. Similarly, dimensional approaches emphasize the fundamental underlying components of emotional processes, whether valence and arousal (e.g., Russell & Carroll, 1999), positivity and negativity (Watson, Wiese, Vaidya, & Tellegen, 1999), appetition and aversion (Lang, 1995), behavioral activation and behavioral inhibition (Gray, 1982), or similar conceptualization, without regards to discrete states. The discrete emotion and dimensional approaches clearly have merit. More importantly, both approaches provide complementary information and limiting conditions for the understanding of emotion and affect. Although some view these two approaches as mutually exclusive, the evaluative space model (Cacioppo & Berntson, 1994) provides a framework that is capable of integrating both discrete and dimensional approaches to affect while simultaneously remaining neutral with regards to the ontological status of emotions as psychological constructions or “natural kinds.” Accordingly, the framework provided by the evaluative space model, discussed next, has the potential to promote theory and research on the affect system both at the level of the individual components and at the level of the integrated network.

In the current article, we provide an overview of the current state of the literature regarding the relationship between emotions and patterns of autonomic nervous system activity. We begin with a brief overview of the historical and contemporary perspectives on autonomic specificity and emotions. We then discuss the somatovisceral afference model of emotion (SAME) and how it relates to the discussion regarding emotion specific patterns of ANS activity. We conclude with a brief discussion of the underlying neuroarchitecture of evaluative processes and how it may relate to the SAME and emotion specific patterns of ANS activity.

### Emotion and Patterns of ANS Control: Brief Historical Perspective

William James’s (1884) proposal that specific somatovisceral patterns generate the experience of emotion set the stage for the ongoing debate into the nature of emotion and their neurophysiological correlates and mechanisms. Walter Cannon (1927) provided an early criticism on James’s interpretation of emotions as a manifestation of specific patterns of somatovisceral activity. Cannon argued that ANS responses were the accompaniments, not the cause, of emotional processes, and that physiological responses were too undifferentiated to account for the variety of distinct emotional feeling states. Cannon’s views were bolstered when early research failed to demonstrate replicable and generalizable emotion-specific autonomic patterns (Harlow & Stagner, 1932). Subsequent work by Schachter and Singer (1962) was suggested to provide evidence that the same pattern of autonomic activity (arising from epinephrine administration) could result in the experience of different emotions depending on situational cues, which lent further evidence to the view that emotions were not exclusively the result of specific patterns in ANS responses. While this view remains highly influential, it is worth noting that this view has been roundly criticized on a number of grounds, but perhaps its greatest limitation is the naive assumption that the drug manipulation resulted in an equivalent autonomic state independent of the psychological context. It is now well understood that drug effects (autonomic as well as cognitive) are context dependent. Consequently, the drug manipulation was inconsistent across groups and any inference about the potential influence of ANS state on emotion resulting from the epinephrine administrations must be qualified by this limitation.

In their seminal article in 1983, Ekman, Levenson, and Friesen reignited the debate over autonomic specificity and emotions. Eckman et al. attributed much of the previous inconsistency between emotions and ANS function to a variety of methodological limitations such as failure to equate the intensity of different emotions and lack of appropriate synchronization between physiological recordings with the likely onset and offset of the elicited emotion. In their study, Ekman et al. measured heart rate, finger temperature, skin resistance, and forearm flexor muscle tension as participants completed two sets of tasks designed to elicit anger, fear, sadness, happiness, surprise, and disgust. In one task, participants were asked to remember and relive past emotional episodes. Participants also completed a directed facial action task in which they were asked to contract sets of muscles to produce facial expressions associated with each emotion. The authors’ found that in addition to differentiating positive from negative emotions, combinations of autonomic measures could differentiate some negative emotions (e.g., fear) from others (e.g., anger). For example, anger was characterized by increased heart rate and increased skin temperature, and fear by increased heart rate and decreased skin temperature. Based upon these data and subsequent studies, Levenson, Ekman, and Friesen (1990) proposed that each discrete emotion is associated with an innate affect program that coordinates changes in the organism’s biological states. They further argued that such changes support prototypical behavioral reactions most often associated with particular emotions.

Levenson and colleagues’ (1990) work sparked a considerable increase in research on emotion-specific autonomic patterning. Subsequent work suggested that the degree of emotion-specific ANS activity was context dependent such that the specificity was greatest in real-word emotion induction procedures (Stemmner, 1989). Furthermore, criticisms emerged based upon the observation that different emotion induction procedures appear to elicit different patterns of ANS activity (Zajone & McIntosh, 1992). For example, although skin resistance level declines more during sadness than during other
negative emotions when emotions are induced with imagery tasks, the relationship was not apparent when emotions were induced with facial action tasks. Such findings led to a series of meta-analyses conducted by Cacioppo and colleagues (Cacioppo, Berntson, Larsen, Poehlmann, & Ito, 2000; Cacioppo, Gardner, & Berntson, 1997) on all published studies comparing the effects of at least two discrete emotions on at least two autonomic measures. Although the results were mixed, these analyses found some evidence of emotion-specific ANS responses. For example, the meta-analyses found that fear, sadness, and anger were associated with larger heart rate responses as compared to disgust. Additionally, anger was associated with elevated diastolic blood pressure as compared to fear, and disgust was associated with larger skin conductance response as compared to happiness. However, the meta-analysis failed to find discrete patterns of emotion specific ANS responses. For instance, fear was not associated with larger decreases in finger temperature than control conditions, nor was fear associated with larger increases in skin conductance level. Furthermore, the meta-analyses revealed a number of emotion related patterns of autonomic functioning that are apparent at a systems level. For instance, anger, as compared to fear, was found to be associated with diminished heart rate acceleration, dampened stroke volume, and cardiac output responses coupled with increased total peripheral resistance and finger pulse volume. In this case, it appears that anger is more strongly associated with vascular response whereas fear is more closely tied to cardiac responses.

In a recent systematic review on the topic of emotion specific patterns of autonomic functioning found, Kreibig (2010) reviewed 134 prior studies on the relationship between emotion and peripheral physiological responses and found some evidence that different emotions were associated with various patterns of ANS response. While the review found that there were some differences in ANS correlates across emotions, it also found that no basic emotion was entirely unique across the ANS measurements, a result consistent with the findings of the Cacioppo et al., (2000) meta-analysis. Subsequent studies have employed multivariate approaches and reported some success in finding emotion-specific patterns of ANS function. For example, Stephens, Christie, and Friedman (2010) had 49 participants view emotion-inducing music and affective films while recording various ANS measures. Pattern classification analysis found that ANS variables were able to correctly classify predicted emotions at a rate of 44.6%. Using a comparable approach, Kragel and LaBar (2013) found that autonomic measures predicted distinct affective states at a rate of 58.0%. While such findings are a clear improvement over previous univariate approaches, such findings are far from demonstrating discrete emotion-specific patterns of ANS responses. Aside from the fact that the studies are comprised of relatively small sample sizes, the prediction rates of 44–58% are consistent with aspects of the aforementioned meta-analyses (Cacioppo et al., 2000) and do not provide strong evidence for emotion specific patterns of ANS responses. That is, these studies found that while emotions are clearly related to ANS functioning, the patterns of ANS functioning do not appear to follow a highly specific pattern that reliably distinguishes them from other related emotions. To be fair, there are numerous explanations for such findings. There are likely to be individual differences in emotional intensity in reaction to the emotion induction techniques or may be mislabeling the emotion (i.e., feeling anxious but labeling it as fearful). Regardless, these studies and others like them have yet to provide sufficiently convincing evidence for emotion specific patterns of ANS activity to rule out competing hypotheses that are equally capable of explaining the results of the study.

The Somatovisceral Afference Model of Emotion (SAME)

The somatovisceral afference model of emotion (SAME; Cacioppo, Berntson, & Klein, 1992) provides a general framework for conceptualizing the various routes through which ascending information from the periphery can mold emotional processes while simultaneously integrating both basic and dimensional perspectives of emotion. At one extreme of the continuum, discrete emotional experiences can result from the apperception of distinct somatovisceral patterns (e.g., Ekman et al., 1983; James, 1884; Levenson et al., 1990). There is overwhelming evidence that ascending visceral information has dramatic influences on cognitive and affective processes including emotions (Berntson, Sarter, & Cacioppo, 2003). For instance, work by Harrison, Gray, Gianaros, and Critchley (2010) found that aspects of disgust were related to distinct patterns of autonomic responses with “nauseating” disgust being associated with tachygastria responses and right insula activity and “bloody disgust” being associated with parasympathetic regulation of the heart and activity in the left insula. Consistent with James’s (1884) views on emotion, the dissociation of these peripheral autonomic changes in response to different types of disgust predicted activity within the insula. Furthermore, it has also been shown that emotional judgments are influenced by transient variations in cardiovascular afferent signaling through modulation of midbrain structures such as the periaqueductal gray (Gray et al., 2012). Specifically, cardiac cycle and baroreceptor activation at systole are associated with increased intensity ratings of expressions of disgust in conjunction with an attenuation of evoked cardiac responses to both happy and disgusted faces (Gray et al., 2012). Alterations in visceral signaling in pathologies associated with aberrant visceral signaling such as irritable bowel syndrome and Crohn’s disease have been shown to influence a broad range of affective and cognitive processes (Kennedy et al., 2012; Mayer, 2011). A recent study found that intragastric infusion of fatty acid reduced subsequent subjective and neurobiological responses to experimentally induced sad emotion through a mechanism likely dependent on vagal afferent signaling (van Oudenhove et al., 2011). Furthermore, these findings are consistent with a growing literature on somatovisceral influences on cognitive processes including decision making, memory, and attention (Bechara, Damasio, Tranel, & Damasio, 2005; Garfinkel et al., 2013; Ohira et al., 2013) and a
the literature on the influence of the immune system on affect and behavior through, in part, modulation of vagal afference (Dantzer et al., 2008).

On the other extreme of the SAME continuum, attributional processes instigated by an active perceptual processing of undifferentiated physiological arousal generate discrete emotional experiences. As noted before, the work by Schachter and Singer (1962), while influential, contains within it a series of assumptions regarding the influence of epinephrine injection on ANS activity that dramatically limit one’s ability to draw conclusions from their results. However, there is evidence that individual differences in interoceptive awareness can modulate emotional intensity without strongly influencing valence ratings of the emotional stimuli. For example, Herbert, Pollatos, and Schandry (2007) found that individuals who scored high on measures of interoceptive sensitivity showed greater P300 and slow wave amplitudes in response to both positive and negative emotional pictures in addition to reporting higher levels of emotional arousal as compared to individuals low in interoceptive sensitivity. Barrett, Quigley, Bliss-Moreau, and Aronson (2004), found that greater interoceptive accuracy was related to more apparent contrast in self-reported emotion activation and deactivation during an experience sampling procedure. These findings and others suggest that individual differences in the ability to accurately represent activity in visceral states alter the way individuals subjectively perceive emotions.

Occupying the middle ground between the extremes proposed by William James (1884) on one hand and Schachter and Singer (1962) on the other, are situations where the ascending somatovisceral information is somewhat vague, necessitating an active perceptive processes whereby these patterns are disambiguated to produce distinct emotional experiences (Cacioppo et al., 1992). It is within this middle ground that the ability to discern signal from noise becomes most difficult, necessitating immediate and spontaneous disambiguation. This process has been likened to the perceptual processes associated with viewing ambiguous visual scenes (see Figure 1). Even though the figure itself is unchanging, top-down processes allow viewers to perceive two very different images: a young woman facing left or an elderly woman facing right (Leeper, 1935). Clearly, in this example the image remains constant and what is changing is the processing of the afferent sensory information leading to the perception of one or the other image but not both simultaneously. Therefore, the same visual afference can lead to two different, discrete, and indubitable perceptual experiences, even in a sensory system known for its contrast sensitivity, just as Schachter and Singer (1962) argued that the same physiological afference may lead to more than one discrete emotion. Thus, if individuals are susceptible to visual illusions such as that displayed in Figure 1, where it is clear the object being viewed remains stable and unchanging, it is reasonable to propose that the perception of somatovisceral states, which are in continuous flux as the result of neural and endocrinological signals, could be subject to comparable perceptive illusions whereby a priori assumptions regarding the nature of the particular context (i.e., threatening, exciting) are able to alter the real-time interpretation of autonomic states leading to the experience of different emotions with the same pattern of ANS input. This view is consistent with the model recently put forth by Seth and Critchley (2013) incorporating expectations of somatovisceral responses to situational contexts, and the potential mismatch with ascending visceral information into models of emotions (also see Seth, Suzuki, & Critchley, 2011). By this account, “somatovisceral illusions” represent the result of an active perceptual process by which ambiguous patterns of somatovisceral afference are immediately and spontaneously disambiguated to produce distinct emotional experiences (see Figure 2). This view is in accord with robust findings in the literature that discrete emotional percepts can occur even when the measured autonomic changes do not fully discriminate the emotions that are experienced (Cacioppo, Berntson, Klein, & Poehlmann, 1997; Cacioppo et al., 2000), and that autonomic activation can alter the intensity, if not the nature, of emotional experience (Critchley & Harrison, 2013). From this perspective, the question is not whether emotion-specific autonomic patterns occur, but under what conditions and contexts such patterns occur. Whether or not the conditions for and elements of emotion-specific peripheral patterns of activity can be identified, what does seem clear from the extant research is that discrete emotions can be experienced even in the absence of completely differentiated autonomic patterns. While this has been viewed by some to be grounds for minimizing the role of somatovisceral afference on emotion, the SAME model outlined before.
provides three routes by which somatovisceral afferents may influence emotional experience: emotion-specific autonomic patterns, somatovisceral illusions, or cognitive labeling of unexplained physiological arousal. From this perspective, the traditional tendency to view the mechanisms underlying emotion in terms of a simple central–peripheral dichotomy is untenable.

In the next section, we highlight general neuroarchitectural features underlying evaluative processes as they relate to motivation and emotion and discuss some potential implications that the broad distribution and rerepresentation of information across the neuraxis have on our understanding of the relationship between affective processes and activity within the autonomic nervous system.

Rerepresentation of Function, Emotion, and ANS Function

Around the same time Darwin (1872) and James (1884) were laying the foundation for various aspects of the contemporary study of the relationship between emotion, somatovisceral activity, and evolutionary function, John Hughlings Jackson (1884) provided an early description of the hierarchical structure and the rerepresentation of function across levels of neural hierarchy. Jackson’s view has particular relevance for understanding affective processes, the autonomic nervous system, and their interactions as it suggests that the underlying neural systems responsible for processing efferent and afferent neural information, and behavioral responses, are distributed across spatial and temporal time scales. Jackson’s conceptualization of the nervous system was based on the observation that information was processed at multiple levels within the neuraxis and that the evolutionary appearance of “higher level” neural structures (i.e., cortex) did not necessitate the replacement of more primitive neural organizations (i.e., brainstem). Rather, Jackson noted that the brain was organized in a rerepresented manner whereby information was processed at various levels of the neuraxis, each mining the information with different analytical capacities and temporal constraints. For instance, primitive protective responses to potentially noxious stimuli apparent in the pain withdrawal reflexes at the level of the spinal cord can effectively operate even in the absence of communication with the brain. These primitive protective responses are embellished at higher levels of the nervous system providing organisms a further expanded behavioral and motivational repertoire that can capitalize on experience-dependent associative knowledge, distributed information-processing networks, and cognitive strategies that anticipate and prepare for or avoid aversive encounters altogether (see Berntson, Boysen, & Cacioppo, 1993). This suggests that the evaluation of stimuli is not the result of a unitary or discrete process, rather, evaluative processes occur in temporal layers that are the result of the rerepresentation of information at various levels of the neuraxis. The evolutionary

Figure 2. The somatovisceral afference model of emotion (SAME). The same pattern of somatovisceral activity has been associated with surprisingly different emotions, and the same emotion has been associated with different patterns of somatovisceral activity. These results have been viewed as evidence against the importance of somatovisceral afference in emotion. The SAME, depicted before, encompasses both of these findings while emphasizing the instrumental role of somatovisceral afference and cognitive/perceptual processes in producing each. Adapted from Cacioppo et al. (1992).
layering of higher processing levels onto lower substrates has adaptive advantage in that lower and more efficient processing levels may continue to be utilized, and may be sufficient in some circumstances. Reflex responses to noxious or threatening stimuli, for example, provide a rapid, somewhat rigid, response aimed at immediately removing the organism from the source of aversion. The rapid and reflexive actions are typically followed by more complex motivational and affective processes that subsequently guide behavior based upon prior experiences and contextual cues. Moreover, learned anticipatory processes may promote more strategic avoidance of adaptive challenges prior to their occurrence and are capable of modulating the initial reflexive responses to stimuli. The increasing amount of information that must be processed and integrated by progressively higher level systems may lead to neurocomputational bottlenecks which require a slower and more serial mode of processing. Based on hierarchical interconnections, higher level systems may depend heavily on lower level systems for the transmission and preliminary processing and filtering of afferent sensory and perceptual data and for implementing sensory motor subroutines that support executive outputs. The advantages and disadvantages associated with higher level (integrative, flexible, but capacity limited) and lower level (rapid, efficient, but rigid) processing were a likely source of evolutionary pressure for the preservation of lower level substrates, despite higher level elaborations and rerepresentations.

The rerepresentation of information across the nervous system suggests that sensory (both interoceptive and exteroceptive) information relevant to the experience of emotion, and subsequent physiological responses, are processed across a distributed set of neuroaxial networks leading to different temporal responses. Such conceptions of the nervous system have important theoretical and methodological implications for the study of emotion and patterns of ANS activity. For example, although fear may appear to be a discrete phenomenal experience, it is now clear that fear can come in many flavors (i.e., fear of predation, fear of starvation, fear of pain) each associated with the integration of information at different levels of the neuraxis which are subsequently associated with distinct neurobehavioral and physiological responses that extend across different temporal scales (Gross & Canteras, 2012). The intentionalness and multirealizability of fear, and other emotions, may help explain why emotion-specific patterns of neurobehavioral an autonomic control can be quite variable across individuals. Of course, this does not mean that basic emotions do not exist nor does it suggest the impossibility of ever finding highly reliable emotion specific patterns of ANS responses, rather, it implies that even with the most basic emotions there exists a broad distribution of physiological, motivational, and behavioral responses that can be expressed in a context dependent fashion. In the following sections, we will discuss in more detail the relationship between the rerepresentation of function across the neuraxis and its potential influence on understanding emotion specific patterns of ANS response.

### Rerepresentation of Function: Evaluative Processes

The rerepresentation of information across the nervous system implies that the functional architecture of affective and motivational responses is the result of processes occurring at various levels of the neuraxis with differing functional and temporal signatures (Berntson, Boysen, & Cacioppo, 1993). In accord with this perspective, the evaluative space model (ESM) posits that affective states and responses are mediated by a network of distributed interacting neural circuits ranging from the spinal cord to the limbic system and neocortex (Cacioppo & Berntson, 1994; Norris et al., 2010). Moreover, the ESM recognizes that behavioral outputs, including somatovisceral indices used to infer emotion states, are multiply determined. Although the activities of the components of the affect system generally appear to be integrated into a coherent cognitive-behavioral stream, the existence of multiple processing levels affords considerable flexibility in behavioral action as well as the potential for interference and conflict. In cases where relatively low-level processing is sufficient, or higher level processing is precluded due to temporal or contextual constraints, lower substrates may predominate in behavioral expression. However, given sufficient information and processing time, higher level cognitive processes are able to modulate these lower level responses in order to achieve a goal. In fact, although integrated to some extent, the multiple levels of processing allow for response conflicts, with different levels of processing each disposing the individual toward different behavioral responses. These conflicts may facilitate an outcome, or may interfere with it (allowing a broken arm to be reset by an orthopedist). In part, the latter arises from the fact that physical constraints preclude an individual from simultaneously pulling way and remaining still, as the arm cannot extend or reach out and flex or pull back at the same time. This physical constraint, however, belies the complexity of the underlying dispositions. Although the limb may not be able to extend and flex at the same time, the underlying flexor and extensor muscles can, in fact, be coactivated. This may lead to inaction, but that inaction is not sufficient evidence for a lack of underlying response dispositions. The limb response may be skeletal constrained along a single bipolar continuum of flexion or extension, but the underlying neurobehavioral and neuromuscular processes giving rise to such behavior are not so constrained and may reveal a broader fundamental bivariate structure. This fundamental logic holds with more complex neurobehavioral processes, including emotions, as well. Indeed, although behavior may be constrained to a single bipolar dimension defined by the opposing movements of approach and avoidance, the neurobehavioral mechanisms of the affect system are capable of a significantly larger dynamic range. Moreover, the physical constraints on the behavioral manifestation of the affect system do not necessarily require that the underlying neurophysiological constituents of the system conform to the same structure. That is, the physically constrained end-organ responses of the affect system, whether
somatic or visceral, are likely to have an underlying structure that allows for greater flexibility of responses at a systems level. The ESM (Cacioppo et al., 1997) proposes that behavioral predispositions are the ultimate output of the affect system, which is defined by separable systems for processing positivity and negativity, each characterized by unique operating characteristics. The ESM is not a theory of what elicits affective states or emotions. Rather, it is a theory of the mechanisms that underlie affect, how these mechanisms are engaged in theoretically predicted circumstances, and how temporal constraints and levels of rerepresentation influence possible affective responses within this space.

The neurobehavioral processes underlying positivity and negativity represent two systems that underlie emotion and affect. Although moods, self-reported feeling states, and emotions can vary across individuals, contexts, cultures, and their interactions, when considered in terms of their behavioral profiles two clusters of emotional experiences emerge: positive (pleasant, appetitive) and negative (unpleasant, aversive) states (Berntson, Boysen, & Cacioppo, 1993; Cacioppo & Berntson, 1994; Norris et al., 2010). Furthermore, the ESM posits that although there are distinctions among both positive and negative emotions, positive emotions are more similar to each other than they are to negative emotions, and vice versa. This organization is suggestive of two partially separable underlying dimensions of the affect system: one focused on processing appetitive stimuli, such as food and sex, and a second on aversive stimuli, such as toxins and predators. Thus, the ESM argues that the dimensions of positivity and negativity are at least partially separable, in that they are not equivalent in their neurobehavioral constitution, processes, or consequences. In this respect, the ESM is consistent with models that incorporate appetite and aversion as two distinct dimensions (e.g., Lang, 1995).

What separates the ESM from other models is the postulation that these dimensions are not necessarily reciprocal and, much like the relationship between sympathetic and parasympathetic output discussed before, can operate in a bivariate manner resulting in coactivation and coinnihilation of positivity and negativity (i.e., ambivalence, see Larsen & McGraw, 2011). Moreover, the ESM differs from other models in that it argues that positivity and negativity have differential influence on neurobehavioral processes as a function of the perceived spatiotemporal proximity of the target stimuli being evaluated. Neal Miller (1959, 1961) provided much of the foundation for this postulate. Miller recognized that approach and withdrawal are behavioral manifestations that can come from distinguishable motivational substrates. His conflict theory was enriched by conceptualizing approach and withdrawal separately, investigating their unique antecedents and consequences, and examining the psychological constraints that led to the activation of approach and withdrawal tendencies. Moreover, Miller’s conception of motivation provided a better understanding for conditions through which the underlying motivational processes (approach vs. avoid) interact to create conditions of ambivalence where organisms vacillate between approaching and avoiding a particular target.

The ESM extends the work of Miller through the recognition that evaluative processes are characterized by distinct activation functions, are related differentially to ambivalence, have distinguishable antecedents, and tend to gravitate from a bivariate toward a bipolar structure when the underlying beliefs are the target of deliberation or a guide for behavior (Cacioppo et al., 1997). Although some of these calculations may be straightforward, such as avoiding a potentially harmful stimulus out of fear (e.g., snake, angry person), others require more complicated algorithms. For example, animals must approach a water source in order to drink even though doing so means increasing one’s exposure to potential predation. The ability to simultaneously hold two opposing motivations, to approach the water and avoid being eaten, is clearly adaptive and requires nuanced and flexible evaluative processes. The affect system performs such calculations to ultimately determine behavior toward or away from a stimulus. As alluded to before, the ability of the affect system to be modified by contextual factors highlights the dynamical nature of affective processes in general and highlights the difficulty of isolating one emotion with sufficient resolution to reliably examine emotion-specific patterns of autonomic activity.

In the next section, we briefly discuss the general neuroarchitecture of autonomic regulation and how it relates to our understanding of affective processes in general, and emotion-specific patterns of ANS responses in particular.

Rerepresentation of Function: The Autonomic Nervous System

Walter Cannon (1929) proposed that a primary role of the ANS was in maintaining the constancy of the internal milieu, a regulatory process he termed “homeostasis.” Cannon viewed the sympathetic branch as the primary homeostatic regulator, with the parasympathetic branch serving to fine-tune reactions across organs. Historically, the two autonomic branches have been considered to be reciprocally regulated by central systems (Fulton, 1949), a view that continues to be promoted in the contemporary literature (Malliani, 1999). There is ample evidence for a reciprocal mode of autonomic control in simple reflex responses such as the baroreceptor–heart rate reflex. Reciprocal control of this type would have considerable regulatory advantage as reciprocal changes would synergistically amplify actions at the end organ and expand the dynamic range of control of the heart (Berntson, Cacioppo, & Quigley, 1993). The homeostatic model of autonomic function dominated early conceptions of the relationship between psychological stress and autonomic functioning, and behavioral–autonomic relations were often viewed as hierarchical extensions of homeostatic processes. In a hierarchical system, rostral levels could access a wider range of response mechanisms, but the actions of these systems would be constrained by the more primitive organizations at lower levels. Hence, this model of neurobehavioral–autonomic relations predicts that the basic reciprocal
mode of control apparent in brainstem reflexes might be expected to manifest in behavioral contexts as well. However, it is now clear that the nervous system is not organized in a strict hierarchical fashion. Indeed, descending pathways originating in cortical structures are capable of bypassing intermediate levels and directly influence brainstem structures directly regulating motor output (Porter, 1987; Wakana, Jiang, Nagae-Poetscher, van Zijl, & Mori, 2004). Conversely, ample evidence exists that ascending visceral information is equally capable of bypassing intermediate levels and directly influencing cortical processes (Berntson et al., 2003). This organizational pattern, previously described as a neural heterarchy (Berntson & Cacioppo, 2000), contains the components of hierarchical systems, as higher levels are in continuous communication with lower level systems via intermediate levels, but have the additional capacity to interact over widely separated levels via direct connections (see Figure 3). In addition to the well-known anatomy of somatomotor systems (Porter, 1987; Wakana et al., 2004), this pattern of organization is also apparent in both the ANS (Berntson & Cacioppo, 2000; Critchley, 2005) and hypothalamic-pituitary-adrenal (HPA) axis (Radley, Williams, & Sawchenko, 2008; Sullivan & Gratton, 2002). Of particular importance to emotion specific patterns of ANS activity, this provides a means through which psychological stressors may change reciprocally, independently or coactively in behavioral contexts (Berntson, Cacioppo, & Quigley, 1993; Berntson et al., 1994). This has necessitated an expansion in the simple reciprocal bipolar model of autonomic control, in which autonomic states are considered to lie along a single continuum with maximal sympathetic (and minimal parasympathetic) activity at one end and maximal parasympathetic (and minimal sympathetic) activity at the other. Although this model may apply to reflexive brainstem circuits, the greater output flexibility of higher neural systems necessitates a bivariate model of autonomic space with sympathetic activity along one axis and parasympathetic activity along the other (Berntson, Norman, Hawley, & Cacioppo, 2008).

In addition, there may be far greater individual differences in autonomic responses arising from the operations of rostral neural systems in psychological contexts. For example, the heart rate responses of human subjects to orthostatic stress and to standard psychological stressors (mental arithmetic, speech stress, reaction time task) are similar when analyzed at a group level (Berntson et al., 1994; Cacioppo, Uchino, & Berntson, 1994). Analysis of the separate contributions of the two autonomic branches by the use of single and dual pharmacological blockades revealed that the orthostatic stress (transition from sitting to standing) yielded a rather consistent response across subjects, characterized by a highly correlated sympathetic activation and parasympathetic withdrawal. However, psychological stressors yield a more varied pattern of response across subjects, with no overall correlation between the responses of the autonomic

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**Figure 3.** Heterarchical information processing in the neural axis. Lowest levels are characterized by more reflexive or bipolar modes of activation. As one moves to higher levels of the neuraxis, activation patterns are capable of more complex bivariate activation patterns. Furthermore, heterarchical projections allow higher levels to bypass intermediate levels and directly modulate lower levels. This pattern allows higher level cognitive and emotional processes to directly influence basic motor responses to create complex behavioral patterns. Right: higher levels of the neuraxis can be categorized as having increasing behavioral complexity, and informational processing capacity. Adapted from Decety, Norman, Berntson, and Cacioppo (2012).
branches. A subset of participants displayed a predominant increase in sympathetic activity, others a predominant parasympathetic withdrawal, and others varying combinations of these responses. Although there were considerable individual differences in the responses, individual response patterns were stable across the three psychological stressors (Berntson et al., 1994). These findings are consistent with a much broader literature (Cacioppo, Tassinary, & Berntson, 2007) highlighting the ability of a physiological system to achieve the same end organ response, heart rate in this case, through the manipulation of different underlying processes (i.e., different patterns of sympathetic and parasympathetic response). Thus, in addition to elucidating some of the complexities of the affect system and its relation to behavior, the notion of rerepresentation of function across the nervous system provides some insight into the dynamic hierarchical regulation of autonomic processes and the inherent difficulty associated with finding strict emotion-specific ANS signatures.

Conclusions

The nature of emotions, their neurobiological foundations and their somatovisceral manifestations continues to be one of the most hotly debated topics in psychology and neuroscience. Much of the debate stems from methodological constraints. Studies typically restrict measurement to a handful of physiological measures, each with different temporal resolution and unique temporal dynamics associated with affective responses. Many such systems are dually regulated by the sympathetic and parasympathetic branches of the ANS which can obscure underlying relationships between affective states and autonomic responses. For instance, aversive conditioned stimuli can produce coactivation of the sympathetic and parasympathetic branches, yielding accelerated, decelerated, or even unchanged heart rate, depending on the relative strength of sympathetic versus parasympathetic activation (see Berntson, Cacioppo, & Quigley, 1991). Additionally, the standard measures used to determine potential patterns of ANS response to discrete emotions (vascular and cardiac functioning, skin conductance) are not necessarily representative of the intrinsic sensory apparatus that conveys somatovisceral information through the nervous system. That is, although our measures are quite sensitive with regards to variables such as skin conductance, heart rate, or blood pressure, they are not necessarily good measures of how that afferent information is transmitted and represented within the brain. In fact, there is considerable evidence that the individuals vary a great deal with regards to their sensory and perceptual representation of somatovisceral states (Critchley & Harrison, 2013).

The fact the field is still asking some of the same questions proposed by Darwin, James, and Cannon, namely, what are emotions and how are they related to somatovisceral processes, could be viewed by some to reflect a lack of general conceptual progress in emotion research. However, it seems more likely that the propositions put forth by the aforementioned authors simply outpaced their ability to test them. Indeed, it has really only been in the last quarter century that our methodological approaches have advanced to the point of even being able to address such questions with anything resembling the appropriate levels of precision and complexity. With regards to answering the questions set forth by Darwin and James, it seems likely that the field is closer to the end of beginning rather than the beginning of the end.

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