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>> Version of Record - Mar 7, 2014

What is This?

The Autonomic Nervous System and Emotion

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Abstract

In many evolutionary/functionalist theories, emotions organize the activity of the autonomic nervous system (ANS) and other physiological systems. Two kinds of patterned activity are discussed: (a) coherence (i.e., emotions organize and coordinate activity within the ANS, and between the ANS and other response systems such as facial expression and subjective experience), and (b) specificity (i.e., emotions activate different patterns of ANS response for different emotions). For each kind of patterning, significant methodological obstacles are considered that need to be overcome before empirical studies can adequately test theories and resolve controversies. Finally, links that coherence and specificity have with health and well-being are considered.

Keywords

autonomic nervous system, coherence, methodology, specificity

When it comes to emotion, all roads lead to the autonomic nervous system (ANS). Whether it is the generation, expression, experience, or recognition of emotion, the role of the ANS is critical. In the six decades since Ax first applied modern laboratory-based psychophysiological methods to determine whether anger and fear produced different patterns of attendant ANS activity (Ax, 1953), the centrality of the ANS in emotion has inspired large bodies of research devoted to different aspects of the ANS–emotion relationship. Regrettably, despite many heroic attempts, these literatures are still characterized more by enduring controversies than by consensual views. Among the many controversies, two of the most long-lived and most passionately debated both concern the extent of patterning of the ANS in emotion. The first of these focuses on the degree of ANS *coherence* in emotion and the second on the degree of ANS *specificity* in emotion.

With coherence, the core issue is the extent to which the ANS response in emotion is organized and coordinated. Research in this domain has addressed two kinds of coherence: (a) coherence within the ANS (e.g., among cardiac, vascular, and electrodermal responses), and (b) coherence between the ANS and other emotion response systems (e.g., among cardiovascular responses, facial expressions, and subjective emotional experience). With specificity, the core issue is the extent to which ANS responses differ for particular emotions. With both, different theorists, empiricists, and literature amalgamators often reach quite disparate conclusions about the extent of patterning.

In this article, I will be considering both coherence and specificity, sources of ANS patterning in emotion that have usually been considered separately. My intent is not to provide yet another review of the relevant literatures. A number of these reviews already exist, some selective and others more exhaustive, some quite dispassionate and others more polemic, and none producing a sense of emerging consensus. Rather my premise is that the lack of consensus is highly symptomatic of underlying challenges in navigating between theories and empirical tests. Thus, I plan to revisit the theoretical underpinnings of coherence and specificity, discuss what studies would look like that would truly test and provide opportunities to disconfirm these ideas, and consider some of the significant methodological obstacles that will need to be overcome if such research is going to be pursued. I believe that all serious researchers working in this area (regardless of their theoretical preconceptions) would benefit from thoughtful dialog about how these ideas can best be tested in the laboratory and in the field, how to improve the replicability of findings, and how to reach greater consensus as to whether there really is any patterned ANS activity in emotion, and, if so, what kind and how much.

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Patterned ANS Activity: Possibility or Oxymoron?

Any discussion of the extent of patterned ANS activity in emotion must address concerns that are often raised as to whether the ANS even has the *capacity* for differentiated action. Clearly, if the ANS is structurally or functionally incapable of multiple patterns of activation, then the search for patterned ANS activation in emotion is doomed. For this reason, it may be useful to review briefly some of the structural and functional features of the ANS that support patterned activation as well as those that work against it.

Structure

Is the ANS even capable of patterned activity? In one influential view, the ANS can produce only one pattern of activation, a pattern best characterized as diffuse and undifferentiated arousal (Cannon, 1927). If correct, then the number of discernable ANS patterns is limited to two (i.e., not activated and diffusely activated). Cannon's "all-or-none" view of ANS activation derived support from several structural features of the ANS. For example, there are large ganglia located near the spinal chord where almost all of the fibers of the sympathetic nervous system (SNS) are routed after leaving the thoracic and lumbar segments of the spinal chord. In these ganglia, preganglionic SNS neurons connect with the postganglionic neurons that travel to target organs (e.g., heart, lungs). Having so many SNS neurons in such close proximity is conducive to cross-talk and coactivation between sympathetic nerves. Diffuse action is also facilitated by norepinephrine being the primary neurotransmitter for postganglionic SNS neurons when they synapse with their target organs. Because norepinephrine is released by the medulla of the adrenal glands during SNS activation, circulating norepinephrine can sustain and broaden ANS activation.

Cannon's view of the ANS continues to be influential. It played an important role in several highly influential cognitive theories of emotion (Mandler, 1975; Schachter & Singer, 1962) and is often cited in arguments against ANS patterning in emotion. There is no question that the state of diffuse SNS that Cannon described does exist. However, it is more accurate to view it as but one of a number of patterns of activation the ANS is capable of producing. Within the SNS, contemporary studies reveal a number of different types of receptors (e.g., alpha and beta receptors and their various subtypes), each of which has a different "tuning" (i.e., maximal sensitivity to different neurotransmitters) and a different "geography" (i.e., differential distribution throughout the SNS).

The other branch of the ANS, the parasympathetic nervous system (PNS), provides additional potential for differentiated action. The structure of the PNS is quite different from that of the SNS. In the PNS, preganglionic fibers exit from the brainstem and sacral segments of the spinal chord and synapse with postganglionic fibers close to the target organs without passing through common ganglia. Because neurotransmission (both presynaptic and postsynaptic) in the PNS is via acetylcholine, circulating norepinephrine released by the adrenal medulla does not cause diffuse PNS activation.

In thinking about the potential for multiple patterns of ANS activation, it is important to consider coactivation in target organs that are served by *both* SNS and PNS fibers (e.g., the sino-atrial node of the heart, pupils of the eyes). With these organs, the interplay of SNS and PNS action allows for additional patterns of activation. For example, heart rate is one of the most commonly used ANS measures in the specificity and coherence literatures. Heart rate at any given moment in time is a function of the action of three neural influences: (a) intrinsic pacemaker cells in the sino-atrial node (which would cause the heart to beat at approximately 100 beats per minute; Jose & Collison, 1970), (b) PNS fibers (which act to slow the rate), and (c) SNS fibers (which act to speed the rate). At rest, heart rate is under vagal restraint, slowed by PNS action (via the vagal nerve) to its typical resting rate of approximately 70 beats per minute. Thus, increases in heart rate during an emotional episode may reflect reduced PNS influence or increased SNS influence.

These and other structural features of the ANS certainly provide an adequate basis for patterned action in emotion. Of course, asserting that the ANS has the *capacity* for patterned action is still a long way from establishing coherence or specificity of ANS in emotion.

Function

Using descriptors such as "vegetative" and affording minimum coverage in many neuroscience, neurology, and physiology texts suggests that the ANS is but a simple, crude, and minor part of the nervous system. The reality, however, is quite different. The ANS coordinates and manages a complex, highly differentiated network of nerves, organs, and biological sensors that is distributed throughout the human body. Importantly, the ANS plays a critical role in determining the quality of our lives in both the short and long terms. In the short term, the ANS constantly monitors conditions and makes adjustments that enable us to deal with a host of internal and external demands. In the long term, the ANS assumes major responsibility for tracking and controlling a wide range of functions that determine our health, illness, vigor, and thriving, and that ultimately determine whether we survive or perish.

Functionally, the ANS plays a number of different roles, serving as regulator, activator, coordinator, and communicator. As regulator, the ANS is responsible for homeostasis, maintaining our internal bodily milieu within strict limits so as to minimize damage and maximize functioning. As activator, the ANS facilitates short-term deviations away from homeostasis that allocate bodily resources in ways that enable us to deal effectively with significant challenges and opportunities. As coordinator, the ANS manages a rich, continuous bidirectional flow of data that makes critical information about bodily states and activities available to both evolutionarily ancient and newer brain structures. As communicator, the ANS produces visible appearance changes that have high signal value for conspecifics.

These multiple functions, the large number of component elements involved, the complexity of efferent and afferent neural transmissions, and the need to consider influences both within the individual and in others results in an extremely high noise-to-signal ratio that creates significant challenges for researchers searching for patterned ANS activity.

To illustrate this challenge, consider the search for ANS "signatures" associated with particular emotions. The ANS is by design a slave to many masters, with emotion being just one of the many. Thus, at any given moment, a change in ANS activity that is detected in the laboratory is more likely to result from the action of a nonemotional master rather than an emotional one. Let's suppose that there is, in fact, an ANS signature associated with a particular emotion that includes increased pupil dilation, decreased tonus of the smooth muscles surrounding the fine airways in the lung, and increased cardiac contractile force. And further, let's suppose that these ANS functions are monitored and quantified continuously during a given day in the life of an individual. Throughout that day, we can expect numerous occurrences of these ANS changes, sometimes in isolation and sometimes together. But, when they do occur, they are far more likely to result from more prosaic homeostatic demands rather than emotion. Thus, changes in pupillary diameter are most likely to result from changes in ambient light levels, changes in airway tonus are most likely to result from metabolic factors that alter oxygen demands, and changes in cardiac contractility are most likely to result from the need to alter hemodynamics to support changes in posture. Simply stated, on most of the days of most of our lives, standing up and turning toward the light is a much more likely and parsimonious explanation for this particular configuration of ANS changes than being in the throes of an emotion such as "anger" or "fear."

These biological realities create formidable challenges for attempts to characterize the ANS changes associated with particular emotions, requiring careful sifting through the ongoing flow of behavior to separate emotional moments from nonemotional ones. Just as these realities work against efforts to identify physiological concomitants of emotions, they create even more daunting problems for attempts to infer emotion and other psychological states on the basis of observed patterns of ANS activity. As examples of the latter, it seems particularly imprudent to conclude ipso facto that a person whose respiratory sinus arrhythmia increases is in a state of positive emotion or is a compassionate person.

Three Common Misconceptions about the ANS and Its Role in Emotion

In this article, I will be claiming that many of the problems that plague the literatures on ANS coherence and specificity in emotion are methodological in nature. However, no consideration of the role of the ANS in emotion would be complete without taking note of some of the common assertions about ANS functioning that simply go against neural realities, can lead to misinformed conclusions about underlying neural mechanisms, and, thus, complicate interpretations of findings and add a certain degree of confusion to the literature.

The first misconception is that the SNS is the "go," "activating," or "energizing" system, and the PNS is the "braking," "calming," or "resting" system. Although this metaphor might fit the heart (see previous discussion of ANS control of heart rate), in other parts of the ANS it is the PNS that is clearly the activating system. Importantly, these PNS-activated systems include many of the target organs that are critically involved in emotion. Thus, for example, the PNS causes *increased* activation in salivary glands (salivation), tear ducts (crying), and the gut (e.g., stomach and intestinal activity).

The second misconception is that measures of heart rate variability (including respiratory sinus arrhythmia) are indicators of activity of the entire vagus nerve or, even worse, the entire parasympathetic nervous system. Measures of vagal influence on the heart are just that. It is highly unlikely that they serve as proxy measures of the action of the vagus on other important target organs (e.g., the stomach, liver, small intestine, kidney). Moreover, it is even less likely that they serve as proxy measures of the action of other PNS nerves (e.g., the sacral nerve, which serves the colon, rectum, bladder, and genitalia, or the seventh cranial nerve, which serves salivation and crying).

The third misconception is that the ANS primarily serves to increase and decrease activity in target organs (i.e., efferent functions). The reality is quite different. For example, the majority of neural traffic in the vagus nerve is not efferent in nature, but rather afferent, with vagal fibers providing a neural highway that transports critical information about the state of the bodily milieu back to the brain. These afferent functions are extremely important when theorizing about the role the ANS plays in emotion, especially when thinking about so-called "bottom-up" influences (e.g., the influence of emotional arousal on cognition) and peripheralist models that stress the influence of visceral feedback in emotion (e.g., in creating subjective emotional experience).

Why Patterning? The Evolutionary/ functionalist Model

Many of us grew up in an era dominated by cognitive models of emotion (Lazarus, 1991; Lazarus, Averill, & Opton, 1970; Mandler, 1975; Schachter & Singer, 1962). This "top-down" view, which envisions emotions as resulting from the computations of higher order brain centers, continues to be quite vibrant. This can be seen, for example, in appraisal theories of emotion (Scherer, 1982; Smith & Ellsworth, 1985), which articulate a set of cognitive operations that lead to different emotions. The top-down view also assumes an important role in modern conceptualizations of how emotions are regulated (Gross, 1998; Ochsner & Gross, 2005; Shiota & Levenson, 2009), with emphasis placed on the capacity of higher order appraisals (e.g., reframing, distancing) to alter the activation, intensity, and duration of emotions. In these cognitive models, patterning plays an important role in the thoughts and appraisals that lead to and modulate emotions, but patterning in attendant ANS activation is generally not as critical (for an appraisal model that allows for patterned ANS activity, see Scherer, 1984).
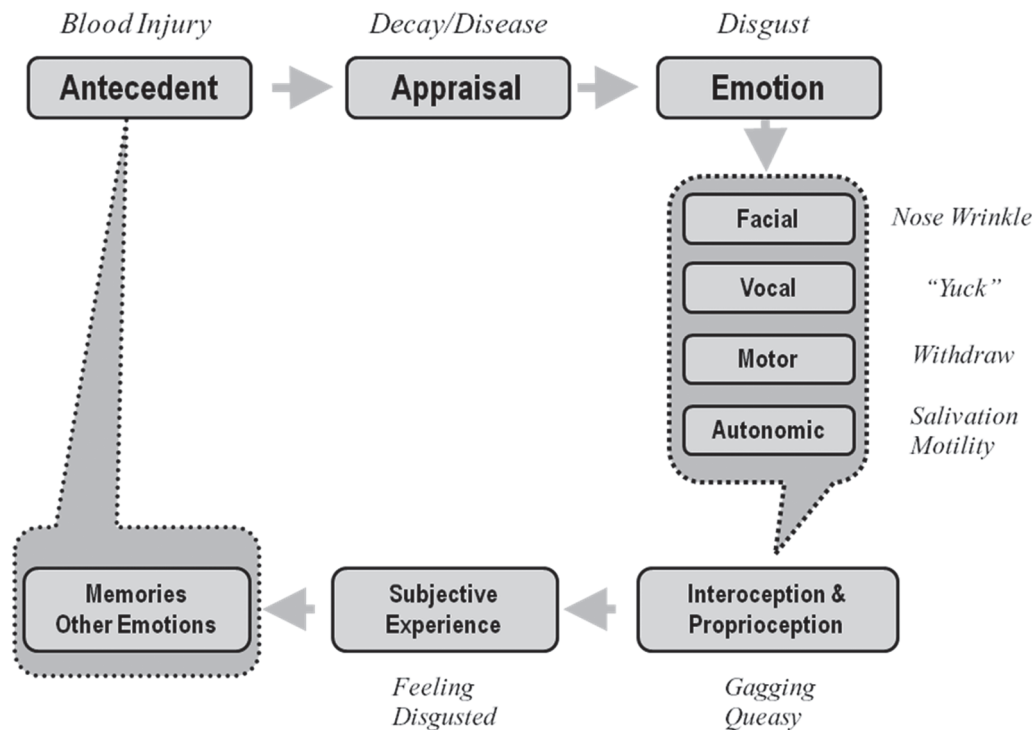
Figure 1. Schematic model of emotion elicitation.

Evolutionary/functionalist models are quite different in their view of the role of the ANS in emotion. In part because of their interest in features of emotion that show continuity across species, they are less likely to view higher level thought processes as necessary precursors and initiators of emotion. Instead, they typically endorse a "bottom-up" view, with ANS and other peripheral responses shaping the subjective experience of emotion (at least in humans) and influencing cognitive functioning (James, 1884; Levenson, 1999, 2011). A defining feature of evolutionary/functionalist models is the belief that different emotions were preserved in evolution because they provided generalized solutions to common problems (Tooby & Cosmides, 1990). Because the problems that different emotions address are quite different, so are the solutions. These different solutions, each involving particular behavioral activities with their attendant biological support, provide the conceptual underpinnings for the specificity hypothesis, which predicts that different emotions will be associated with different patterns of biobehavioral activity. This logic can be seen in the schematic model of an emotion presented in Figure 1.

The figure illustrates how exposure to a blood injury leads to the emotion of disgust. Inputs from organs of sensation are monitored continuously by phylogenetically ancient brain centers (e.g., amygdala) in a rapid appraisal process that is designed to detect a small number of well-defined patterns of sensory input that are particularly relevant for the organism's survival and well-being (e.g., visual, sensory, and olfactory cues that denote disease and decay). When one of these patterns is detected, an emotion (in this case, disgust) is activated. Emotions

such as disgust represent highly generalized solutions that are most likely to enable the organism to deal effectively with these common challenges or opportunities most of the time. These emotions have the capacity to "interrupt" ongoing activity throughout the peripheral and central nervous system and reallocate resources to the problem at hand. They create patterned activation within the ANS and between the ANS and other biological systems (e.g., motor programs, vocalization, facial expression) that is both coherent and specific. This patterned ANS activation is optimal for supporting adaptive behaviors and for communicating critical information to conspecifics. Thus, in the case of an encounter with disease and decay, the emotion of disgust rapidly prepares the individual to withdraw from, shut off, and expel the undesirable substance. Along the way, associated changes in vocalization ("yuck" and gagging sounds), expression (nose wrinkling), and posture (pulling back) also provide valuable signals to conspecifics that can activate their emotions and mobilize and guide their behaviors.

In many evolutionary/functionalist views, subjective emotional experience is not a core feature of emotion, but rather arises after information becomes available from biological sensors that detect changes in temperature, pressure, posture, tonus, and movement (Levenson, 1999). This proprioceptive and interoceptive information is integrated in subcortical brain centers such as the anterior insula (Craig, 2009) and made available to higher brain centers. To the extent that different emotions have different patterns of associated somatic and visceral activity, they "feel" differently to us (e.g., the subjective experience of disgust is quite different than the subjective experience of

sadness). These different feelings create links to memories of other related experiences (e.g., other encounters with blood injuries), motivate coping/regulatory behaviors (e.g., to reduce the unpleasant visceral sensations), and may stimulate additional emotional responses (e.g., evoking amusement over having had a strong emotional reaction in a situation that proved to be benign rather than threatening).

These additional emotional responses are important to account for in studies of ANS specificity in emotion. For example, contemporary research participants, raised with massive exposure to "gross-out" humor, are highly likely to laugh when exposed to disgusting stimuli (in fact, they often laugh when merely seeing another person assume a facial display of disgust). For a study purporting to examine ANS activity associated with disgust, when many or most subjects are laughing, it is easy to end up studying the ANS activity associated with the emotion related to the laughter (e.g., embarrassment, amusement, unfelt happiness, etc.) rather than the target emotion of disgust.

ANS Patterning in Emotion: Multiple Variants

The evolutionary/functionalist model of emotion I have outlined suggests that two major variants of ANS patterning should exist in emotion, coherence and specificity. Moreover, each of these variants should be manifest in several different ways. With coherence, emotions are seen as increasing the level of organization: (a) within the ANS, and (b) between the ANS and other response systems. With specificity, particular emotions are seen as being associated with different patterns of ANS activity, which should be manifest in: (a) ANS functions that are not readily visible (e.g., changes in heart rate); (b) ANS functions that are readily visible and have high communicative value (e.g., blushing, piloerection, crying); and (c) physical sensations derived from ANS activity that are experienced subjectively (e.g., sensations of heat and pressure). In the following sections, I will discuss ANS patterning in emotion in terms of both coherence and specificity. For each kind of patterning, I will discuss the theoretical foundations, the obstacles that need to be overcome to conduct sound empirical studies, and the current state of the associated empirical literatures.

Coherence

Philosophical and psychological traditions tracing back to Plato and Freud have depicted emotions as the antithesis of rational thought. Viewed from this vantage point, emotions produce chaos rather than order, interfere with the conduct of planned action, and lead to maladaptive consequences. Evolutionary/functionalist models envision a dramatically different landscape in which emotions impose order and coherence across disparate bio-behavioral systems (Darwin, 1872; Ekman, 1992; Frijda, 1986; Levenson, 1994; Tomkins, 1962), support effective action, and lead to adaptive consequences. In the evolutionary/functionalist view, emotions are the royal road to coordinated,

effective responses to challenges and opportunities. Rational thought, in extremis, can interfere with the natural flow of emotional responding, leading to chaotic and maladaptive action.

Along these lines, I have noted that "the essential function of emotion is organization" (Levenson, 1994, p. 124), describing this organizational function as follows: "Physiologically, emotions rapidly organize the responses of different biological systems including facial expression, muscular tonus, voice, autonomic nervous system activity, and endocrine activity to produce a bodily milieu that is optimal for effective response" (Levenson, 1994, p. 124) and

> Response coherence implies that emotions organize and synchronize different response systems … such that when we are in the throes of a strong emotion, our subjective, behavioral, and physiological responses should track each other more closely than when we are at rest. (Sze, Gyurak, Yuan, & Levenson, 2010, p. 803)

As noted before, it is important to consider coherence both *within* the ANS and *between* the ANS and other response systems. Examining data obtained during an episode of relatively intense emotion may help illustrate these two kinds of coherence. Figure 2 depicts two aspects of ANS responding (cardiovascular and electrodermal) and facial responding (behavioral coding of disgust expressions) measured continuously from an individual participating in a study in our laboratory. This participant was shown an excerpt from an industrial safety film ("It Didn't Have to Happen") that portrays a factory worker severely cutting his hand on a saw blade.

Although this film often elicits amusement in addition to disgust in contemporary subjects, this particular subject reported primarily feeling disgust with no amusement. Moreover, careful coding of his facial behavior using the facial action coding system (FACS; Ekman & Friesen, 1978) revealed three episodes of facial behavior during the film, all consistent with high levels of disgust (e.g., high intensity nose wrinkling [FACS Action Unit 9]). This participant showed no facial expressive signs of amusement or any other emotion.

Figure 2 presents: (a) second-by-second averages of the participant's normalized heart rate (solid black line), (b) second-by-second averages of normalized skin conductance (grey line), and the apex (i.e., the moment of maximal muscle contraction) of each of the three disgust expressions (black disk superimposed on the heart rate line). During the first 35 seconds of the film (seconds 55–90 on the X axis), the characters in the film engage in various fairly benign activities. During this time, the subject sat quietly and watched the film as instructed (his eyes were open and his head position was straight ahead). Examining the physiological activity during this period, there is little coordination or similarity visible in the pattern of activity in the two ANS measures (heart rate and skin conductance), nor is there any visible emotional facial behavior. This state of affairs is typical of the low coherence that exists both within the ANS and between the ANS and facial expression when no emotion is present. If a statistical measure of the degree of association were applied (e.g., a within-subject time-lagged correlation), the relationship would be near zero.
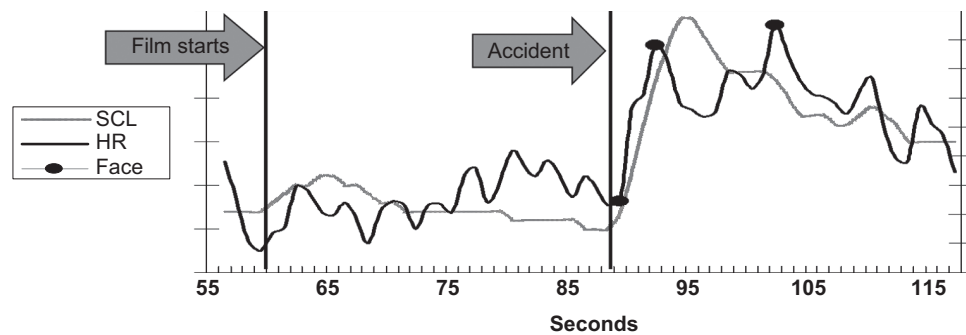
Figure 2. Autonomic and facial responses to industrial accident film.

In the 27-second period starting with the depiction of the accident (seconds 88–115 on the X axis) things change dramatically. Within the first second following the accident, heart rate and skin conductance both increase sharply (skin conductance increases more slowly, which is consistent with the temporal dynamics of these ANS systems). This parallel coactivation is the first sign of within-ANS coherence. Moreover, if you mentally smooth out the faster perturbations, both ANS functions show a similar underlying "arc" of activation and deactivation over the ensuing 25 seconds. Focusing on the faster perturbations, there are cycles of rise and fall that occur every 8–10 seconds in both heart rate and skin conductance. These likely reflect the participant's rapid and deep breathing in response to the accident scene. Thus, in a number of different time domains, there is strong visual evidence of coordinated activation and deactivation of these two ANS functions after the accident occurs. If we were to apply a statistical measure of coherence to the ANS data during this emotional period following the accident, it would produce much higher values than during the non-emotional period prior to the accident.

Examining the ANS and facial behavior during the period following the accident illustrates coherence between these two different response systems. The first disgust expression occurs in the first second after the accident occurs, coinciding with the onset of the sharp increases in heart rate and skin conductance. The second disgust expression occurs at the first peak in heart rate. Immediately following that facial expression, heart rate drops to a lower level and then starts to increase again. The third disgust expression occurs at the next peak in heart rate (the highest level it reaches during the film). Again, immediately following the expression, heart rate begins to drop. Thus, during this period of intense emotional response, bursts of facial expression are associated with both the initial onset of ANS responding (in heart rate and skin conductance) and with its peaks (particularly in heart rate).

These data are meant to be illustrative. They come from a single subject chosen because he had a strong disgust response to the film in self-report and facial expression (he was chosen completely blind to his physiology and to the relationship between his physiology and facial behavior). Thus, there are certainly legitimate issues that can be raised concerning generalizability. However, I believe there is considerable heuristic value in this kind of careful within-subject analysis of coactivation of multiple response systems before and during the occurrence of a strong emotion. It hopefully makes much clearer what coherence within the ANS and between the ANS and another response system looks like. If this example does, in fact, capture the essential nature of these two kinds of coherence, then it has profound implications for the kinds of experimental designs, manipulation checks, and data analytic techniques that are necessary to provide an adequate empirical test of the coherence hypothesis.

Obstacles. Progress in determining whether emotions do, in fact, organize and produce coherence within the ANS and between the ANS and other response systems has been hampered greatly by the lack of studies using experimental designs that are sensitive to the kinds of coordination within and across systems that are portrayed in Figure 2. To be able to assess and quantify these kinds of coherence, a study would need to meet three criteria: (a) subjective, behavioral, and physiological responses need to be measured continuously over time within individuals; (b) different temporal characteristics of various response systems need to be accounted for; and (c) levels of coherence must be measured when subjects are actually in the throes of a strong emotional experience. In a recent review of the literature on coherence (Sze et al., 2010), we found only one study that had assessed coherence in ways that met all three of these criteria.

Most of the existing research on coherence has failed to meet the first criterion, choosing a between-subjects rather than a within-subjects approach. In the between-subjects approach, subjects typically are exposed to an emotion elicitor, and their responses (averaged over some unit of time) are derived for at least two measures. Between-subjects correlations are then determined. Thus, if the film-viewing study used in the within-subject design portrayed in Figure 2 were used in a between-subjects design, a group of subjects would watch the accident film and their mean heart rate, mean skin conductance, and average intensity of disgust expressions would be determined for the 27-second period following the accident. Then the correlation between heart rate, skin conductance, and disgust intensity would be computed across subjects.

The between-subjects correlation derived from this kind of study essentially tests whether individuals who have relatively

larger heart rate responses (as compared to other subjects) also have relatively large (or relatively small) skin conductance and disgust facial expression responses. This is a very interesting research question in its own right, examining an individual difference that might have important relationships with health and well-being (e.g., Kring & Neale, 1996; Weinberger, Schwartz, & Davidson, 1979). However, this kind of between-subjects study does not provide a test of coherence as envisioned in evolutionary/functionalist theories or as illustrated in the previous within-subject example.

Although not the focus of the present article, it is worth noting that the literature using the between-subjects/individual difference approach has not yielded consistent findings, with studies reporting positive relationships (Lanzetta, Cartwright-Smith, & Kleck, 1976), no relationships (Mauss, Wilhelm, & Gross, 2004), and negative relationships (Buck, Miller, & Caul, 1974; Notarius & Levenson, 1979) among response systems. The latter findings, usually taking the form of a negative correlation between physiological and facial response has often been interpreted as providing support for classic "hydraulic" or "discharge" models of emotion (i.e., when emotions are expressed strongly through one response channel, they exhaust the available energy and are expressed weakly through other channels; Notarius & Levenson, 1979). Again, albeit highly interesting and theoretically rich, studies using these between-subjects designs should not be interpreted as testing the capacity of emotion to increase coherence within and between response systems within individuals over time.

Empirical support. As noted earlier, in our recent review of the coherence literature, we found only one prior study that met all three of the criteria stated before. This was a study from our research group (Mauss, Levenson, McCarter, Wilhelm, & Gross, 2005) that utilized: (a) continuous measures of ANS physiology, expressive behavior (observational coding of video recordings), and subjective-emotional experience (using a rating dial methodology; Gottman & Levenson, 1985); (b) within-subject time-lagged correlations that allowed for different temporal dynamics across responses to characterize coherence; and (c) verification that subjects were in the targeted emotional state. This study found quite strong evidence for coherence across response systems. For example, during a film that targeted sadness, the within-subject lagged correlation (averaged across participants) between self-reported emotional experience and facial behavior was $r = 0.74$ and between facial behavior and skin conductance level was $r = -0.52$. In addition to being statistically significant, these fall in the range of what are generally considered to be large effect sizes (Cohen, 1977). This is particularly impressive given that in this kind of experimental design the measures of emotional experience, behavior, and physiology share minimal common method variance.

We recently completed another study using this methodology (Sze et al., 2010). This second study explored possible contributors to individual differences in the coherence between physiology and subjective emotional experience. We found that the average within-subject coherence between physiology and

subjective experience was greater among subjects who had extensive experience with Vipassana meditation (which has a strong focus on attending to visceral states) compared to those who had extensive dance experience (which has a strong focus on attending to somatic states) and controls. Again, the evidence for coherence was quite strong. Examining the average within-subject lagged correlations between self-reported emotion and heart period among the meditators revealed that these correlations were statistically significant and fell into the range of medium to large effect sizes (i.e., the average correlation for the film that produced the greatest coherence across subjects was $r = .50$; the average across all four films that were used was $r = .35$).

Despite these findings, I expect that many emotion researchers share the conclusion found in recent reviews of the literature (Barrett, 2006; Mauss & Robinson, 2009) that coherence across emotion response systems is quite low. However, it is important to note that almost none of the studies included in these reviews use what I have argued is a minimally adequate research design for testing the kinds of coherence envisioned in the evolutionary/functionalist theories. Moreover, as noted before, the few studies that have used appropriate designs suggest a quite different conclusion, with moderate to high levels of coherence occurring when individuals are in the throes of emotion. Given the important role that coherence plays in many theories of emotion and its possible relationships with health and well-being, this is clearly an area that would benefit from additional research using the most appropriate methods possible.

Specificity

The idea that different emotions have different patterns of attendant ANS activity grows directly out of a central tenet of the evolutionary/functionalist model. In this model, emotions help the organism deal effectively and efficiently with a set of common problems that are critical for species survival. Examples of these problems include: defending what is ours, avoiding harm, recruiting support from conspecifics, and restoring calm (Levenson, 2003a; Tooby & Cosmides, 1990). Consistent with this view, to the extent that these solutions involve different kinds of behaviors and that these behaviors require different configurations of ANS activation to provide optimal support, then eliciting these emotions should produce different patterns of ANS activity.

Although the focus of this article is on the role of the ANS in emotion, it is important to realize that this argument for ANS specificity can readily be applied to the other response systems depicted in Figure 1. This notion is consistent with the view that each emotion has an affect program (Tomkins, 1962), with "subroutines" that control the action of different response systems. Thus, different emotions should be associated with different patterns of facial expressions (Ekman, 1984; Ekman, Friesen, & Ellsworth, 1972), vocalization (Scherer, 1989), and motor activity (Frijda, 1986; James, 1884). As with ANS specificity, the literatures that have arisen around specificity in facial expression, vocalization, and motor activity have often been fraught with controversy (e.g., Ekman, 1994; Russell, 1994).

Obstacles.   Humans have emotions all the time and physiological recording equipment is widely available and relatively inexpensive. Thus, one might think that research on ANS specificity would be quite easy to conduct. To the contrary, there are a number of significant obstacles and challenges that need to be overcome if research on ANS specificity in emotion is to advance beyond its current state and if clarity is to replace controversy.

Verifying emotional states.   Evolutionary/functionalist models posit that patterned activity in bio-behavioral response systems will occur when the individual is in the throes of a particular emotion. Thus, actually *having* a particular emotion is a necessary condition for testing this model. In an earlier era before human subjects protections were in place, subjects were typically placed in situations that powerfully created the antecedent conditions thought to produce particular emotions. For example, in a classic study of fear and anger (Ax, 1953), participants were either placed in a situation of high threat (thinking they were about to be electrocuted by faulty equipment) or high frustration (being forced to repeat menial tasks and exposed to high levels of criticism by the experimenter) to produce fear and anger respectively. These *in vivo* situations were well aligned with classic views of the antecedent conditions that produce fear (i.e., imminent bodily harm) and anger (i.e., unjust treatment and frustration). In contrast, subjects in contemporary studies of emotion are more likely to be asked to: (a) view still or moving images of emotionally significant objects (e.g., guns, gore, puppies) or that depict people in emotional situations (e.g., being in danger, engaging in revolting acts, doing adorable things); (b) remember or imagine times when they felt emotions; (c) hear or view lists of emotional words; (d) listen to music or other emotionally evocative sounds; or (e) make facial expressions or watch others make emotional facial expressions. Consistent with this, a recent review of 134 published studies of ANS specificity (Kreibig, 2010) found that films were the most common emotion elicitors used, followed by personalized memories, and then by real-life manipulations.

In decades of trying to induce emotion in the laboratory using almost every one of these methods, one verity that has emerged for me is that *there is no guarantee that any particular stimulus will produce any particular emotion in any particular individual at any given time*. Thus, no matter how carefully the emotion elicitor is designed and delivered, for studies considering whether particular emotions produce different patterns of ANS activity, there must be some independent verification that a participant is actually having the emotions of interest. This is particularly important in contemporary studies; with milder emotion elicitors there is even greater likelihood that individual participants will respond to experimental manipulations in emotionally different ways. Thus, a study purporting to compare the ANS activity associated with fear and anger, for example, may include many participants who do not experience one or the other of these emotions at any reasonable level of intensity, others who experience quite different nontargeted emotions (e.g., amusement, embarrassment), and yet others who experience complex sequences of emotion that may or may not include the emotions of interest.

How should emotional state be verified? Following the tenets of evolutionary/functionalist models of emotion, the best evidence that an emotion has been elicited will come from careful examination of multiple emotion response systems. In studies of ANS specificity, to avoid circularity, verification must be based on response systems other than the ANS (e.g., facial, motor, vocal responses). Because there are reasonable arguments that can be raised against endowing any particular response system with "gold standard" status (Mauss & Robinson, 2009), it is useful to seek convergent evidence across multiple response systems to establish which emotions have been elicited and when (see following section on the importance of establishing the timing of emotion onset and offset). What about verification by self-report? In models such as the one presented in Figure 2, self-reported emotional experience is not considered part of the initial emotional response but rather is constructed after the fact (Levenson, 1999, 2011). Nonetheless, self-report may provide an additional level of convergent evidence for verification when available.

This leads to the important question of what to do with verification data once collected. Strikingly, many studies in the ANS specificity literature did not verify emotion at all, depending on a priori assumptions about what emotions were being evoked. Among those that did verify, it has been common to use these data as an overall manipulation check to show that condition A did in fact produce more of emotion X, and condition B did in fact produce more of emotion Y. Most commonly, having established this, the researcher then analyzes data from all participants on all trials. This approach maximizes usable data but undercuts the rationale for verification. A fair test of ANS specificity of emotion requires it be tested only on trials where there is good evidence that the target emotion (and no other emotion) has occurred.

The importance of verification for testing the hypothesis of ANS specificity in emotion can be illustrated with an example from our own research. In this study, we (Levenson, Ekman, & Friesen, 1990) tested ANS specificity using a directed facial action task in which participants were given muscle-by-muscle instructions that, if followed, would produce prototypical facial expressions of six different emotions (Ekman & Friesen, 1975). In the verification stage of the analysis, we used FACS coding of facial behavior to establish the extent to which the target emotion (and no other) was present on the face. In a subject-by-subject analysis of four ANS differences among anger, fear, disgust, and sadness facial configurations, we found that ANS differences occurred at greater than chance levels on trials on which facial configurations met the highest verification standards, but at less than chance levels on trials where the verification standards were not met. Thus, conclusions about ANS specificity in this study would be completely different if based on the nonverified rather than verified data.

Intensity.   In the canonical examples of emotion that accompany the evolutionary/functionalist model, the world is cruel and

brutish; antecedent conditions are powerful, unambiguous, and quick to onset; appraisal is fast and automatic; and bio-behavioral responses are large in magnitude and involve multiple response systems (e.g., a tiger jumps from its hiding place, the person immediately experiences intense, full-blown fear with racing and pounding heart, frightened vocalizations, classic facial display of fear, and runs as fast as possible for safety). However, as we move away from these prototypical emotion elicitors into the kinder and gentler laboratory variants, antecedent conditions are typically more ambiguous, less prototypical, and slower to develop. Moreover, appraisals are less automatic and more prone to be quickly modified by reappraisals that serve emotion regulatory goals. The emotions that result in these latter situations are likely to be much lower in intensity, more fleeting (perhaps segueing into other emotions), and more likely to produce measurable activity in some but not all response systems. Finding elicitors that produce reasonably high-intensity emotions without triggering human subjects concerns can be challenging, but is essential for studying ANS specificity.

If high-intensity emotions are critical for providing a fair test of ANS specificity, low-intensity emotions are also important for understanding the relationship between patterned ANS activity and emotional intensity (Levenson, 1988). It may be that ANS differentiation increases linearly as emotional intensity increases, but other relationships are certainly possible. For example, there may be a threshold of intensity below which patterned ANS activity does not occur, and a threshold above which ANS activity becomes more diffuse and undifferentiated. Having data available to test these linear and nonlinear models will require developing emotion elicitors that are effective for producing a range of intensity levels and characterizing the degree of ANS specificity at different intensity levels.

Broadly assessing ANS functions.   Most research on ANS specificity has focused on ANS measures that are fairly easy to obtain and quantify, primarily heart rate and skin conductance/resistance (Kreibig, 2010). Although these measures represent aspects of cardiovascular and electrodermal processes that are important in emotion, they are insufficient for characterizing the full gamut of ANS responses in emotion. Respiration, for example, plays a critical role in preparing the organism for adaptive action in emotion, but it often is not assessed in studies of ANS specificity. The activity of the gastrointestinal system in emotion has been studied even less, which is ironic given how common references to "gut feelings" are and how frequently gastrointestinal activity appears in metaphors associated with particular emotions (e.g., butterflies in the stomach during fear; stomach turning during disgust). Perhaps because of their rareness, gastrointestinal measures were not included in a recent cataloging of measures in the literature on ANS specificity (Kreibig, 2010). Such studies do exist, but they are rare (e.g., Baldaro, Gattacchi, Codispoti, & Tuozzi, 1996; Harrison, Gray, Gianaros, & Critchley, 2010; Vianna & Tranel, 2006), perhaps reflecting some of the challenges involved in detecting and quantifying gastrointestinal activity (Stern, Kock, Stewart, & Vasey, 1987).

One of the great ironies in research on ANS specificity has been the almost exclusive focus on the least visible forms of ANS activity and the near complete neglect of the most visible signs of ANS activity. This is particularly ironical because the high levels of specificity might be expected to occur in ANS measures that have the greatest signal value for conspecifics. I believe that one reason for this neglect is that, when it comes to visible, socially informative signs of emotion, the facial musculature has been the "alpha dog." This is, of course, understandable. With its 40-plus muscles, ideal location (at eye level) for viewing by others, and dual enervation that allows for both voluntary and involuntary action (Rinn, 1984), the face is an enticing target for researchers interested in specificity in the visible signs of emotion.

Without diminishing the important role the facial muscles play in conveying information about specific emotional states, it is important to note that the ANS also is a rich source of such information. Several years ago, I (Levenson, 2003b) compiled a list of visible changes that are mediated by the ANS and that might be linked to specific emotions (see Table 1). Compared to studies of the less visible forms of ANS response, studies of these more visible forms have been quite rare. This is not due to measurement difficulty; many of the most highly visible ANS changes can be measured using common psychophysiological transducers (e.g., blushing via photoplethysmography; Shearn, Bergman, Hill, Abel, & Hinds, 1990) or direct observation (e.g., crying; Gross, Fredrickson, & Levenson, 1994). Moreover, for those who believe in ANS specificity, these visible ANS-mediated changes arguably provide some of the lowest hanging fruit available for testing this view (e.g., is blushing more common in embarrassment than in fear, is blanching more common in fear than in anger, or is crying more common in sadness than in disgust?). This is clearly an important area for future research and one that could prove very informative in evaluating the extent of ANS specificity in emotion.

To detect ANS differences among a set of several emotions, obviously there needs to be more than a single measure. But rather than just adding additional measures based on convenience, it would be useful to select measures more thoughtfully. Selection criteria for measures could include a desire to sample broadly from major ANS response systems (e.g., cardiac, vascular, electrodermal, gastrointestinal, etc.) or could be shaped by ideas about associated behaviors (e.g., what are the most relevant ANS systems for supporting and signaling freezing/fleeing, fighting, or withdrawing/expulsion in a study comparing fear, anger, and disgust).

Fully characterizing the activity of particular autonomic systems.   Psychophysiological measurement in research on ANS specificity needs to strive for a richer and more complete characterization of the important operating parameters of the target organ systems. For example, consider the cardiovascular system. As noted earlier, measures of heart rate are the single most common measure in studies of ANS specificity in emotion (Kreibig, 2010). Heart rate provides useful information on the frequency of cardiac contractions and is highly reactive to changes in muscle activity (Obrist, Webb, Sutterer, & Howard, 1970). Moreover,

Table 1.   Visible ANS-mediated changes in emotion (adapted from Levenson, 2003b)

Type	Change	ANS-mediated Basis	Emotion
Coloration	Reddening	Vasodilation, increased contractility	Anger
	Blushing	Vasodilation	Embarrassment
	Blanching	Vasoconstriction	Fear
Moisture and secretions	Sweating, clamminess	Sweat glands	Fear
	Salivating, drooling	Salivary glands	Disgust
	Foaming	Salivary glands	Anger
	Tearing, crying	Lacrimal glands	Sadness
	Lubricating	Mucus membranes	Sexual arousal
Protrusions	Piloerection	Muscle fibers at base of hair follicles	Fear, anger
	Genital erection	Vasodilation	Sexual arousal
	Blood vessels bulging	Vasodilation	Anger
Appearance of eyes	Constriction	Pupils	Anger
	Dilation	Pupils	Fear
	Bulging eyes	Eyelid muscles	Anger, fear
	Drooping lids	Eyelid muscles	Sexual arousal
	Twinkling	Lacrimal glands plus contraction of orbicularis oculi	Happiness

changes in muscle activity are critically involved in behavioral adjustments (e.g., fighting, fleeing, freezing, fondling) thought to distinguish among emotions in the evolutionary/functionalist view. However, heart rate only represents the tip of the iceberg when it comes to characterizing the activity of the cardiovascular system. A comprehensive assessment of cardiovascular functioning in emotion would include measures of other cardiac functions such as the force of contractions (cardiac contractility) and the amount of blood leaving the left ventricle on each contraction (cardiac output). It would also include multiple measures of vascular functioning such as the amount of blood flow in multiple areas of the body important in emotion (e.g., hands, feet, face) and changes in the resistance of the vascular system. Moreover, emotion researchers have become increasingly interested in specifying the relative activity of the parasympathetic and sympathetic branches of the ANS. As noted earlier, because it is influenced by both of these branches, heart rate cannot, by itself, reveal their relative activation. To do so requires more complex analyses such as spectral analysis of heart rate variability (Akselrod et al., 1981) computation of respiratory sinus arrhythmia (Grossman, van Beek, & Wientjes, 1990), or using more specialized methods of detecting and quantifying cardiovascular activity (e.g., impedance cardiography; Sherwood et al., 1990).

Timing.   Based on facial expressions, emotions appear to last less than 5 seconds (Ekman, 1984). Longer emotional episodes certainly do occur, but they often are made up of multiple bursts of facial expression (e.g., the three bursts in Figure 2). Given the view presented earlier that most of the time, the ANS is not acting in the service of emotion, it is critical to assess ANS activity during those moments when it actually is under the influence of emotion, not when the reigns of the ANS are in the hands of its other masters.

Viewed from this perspective, the history of research on ANS specificity has been plagued by problems related to the timing of measured ANS response. In an earlier review of this literature (Levenson, 1988), I discussed this issue in some detail and noted how many of the classic studies in the ANS specificity literature (e.g., Funkenstein, King, & Drolette, 1954; Schachter & Singer, 1962) had gone to considerable lengths to elicit emotion, but that the measurement of ANS activity did not occur until well *after* the elicitation procedure was over.

The timing of ANS measurement may be even more important in the contemporary era, where the emotion elicitors are typically less powerful and the emotions they produce are less intense and more fleeting. In the most recent review of the literature on ANS specificity, Kreibig (2010) did not evaluate studies in terms of whether they ensured that the timing of ANS responses matched the onset and duration of emotion, but did assess the length of measured ANS response. The most common response duration was 60 or 30 seconds, and other common averaging intervals included 2, 3, and 5 minutes. Thus, even if the onset of ANS measurement was closely matched to the onset of emotion (established by some independent criteria such as the onset of facial activity, which is still unfortunately rare), the duration of ANS measurement in these studies was bound to include large stretches of nonemotional ANS activity.

Assessing physical sensations.   The role that physical sensations (i.e., information from the viscera and muscles) play in emotion has long been of interest. In James's (1884) influential view, these sensations constituted the essential building blocks for emotion. This notion has stimulated several waves of research. Early research focused on assessing individual differences in awareness of visceral information using questionnaires (Mandler, Mandler, & Uviller, 1958). In search of more

objective measures, researchers later developed elaborate laboratory tasks that assessed the ability to discern small changes in ANS functions such as heart rate (Brener & Jones, 1974; Katkin, Blascovich, & Goldband, 1981; Whitehead, Drescher, Heiman, & Blackwell, 1977). The general conclusion from this latter work was that most individuals were not very accurate in perceiving these small changes in heart rate. However, the relevance of these tests for the visceral perception that occurs during emotion was not clear.

A revival of interest in the role of physical sensations came with work that was less concerned with the accuracy of perceptions and more with the psychological processes that influenced visceral awareness and the reporting of physical symptoms (Pennebaker, 1982). This was followed by a series of cross-national studies that showed consistency in the associations between particular sensations and particular emotions (Scherer & Wallbott, 1994), linguistic studies of the physiological content of emotional metaphors (e.g., heat and pressure; Lakoff, 1987), and work that showed that activity of the facial muscles (presumably via feedback mechanisms) could produce (Levenson et al., 1990) and modulate (Strack, Martin, & Stepper, 1988) subjective emotional experience. Most recently, the important role that visceral information plays in emotion and the ways this information is organized in the brain have become active areas of inquiry in neuroscience research using both patient and activation models (e.g., Craig, 2009; Critchley, 2005). Thus, the stage may now be set for a new round of systematic examinations of the degree of specificity of ANS and other bodily sensations in different emotions.

Reintroducing the study of bodily sensations into research on ANS specificity provides an opportunity to search for convergence across different ways of assessing ANS activity. For example, in our studies of ANS specificity using the directed facial action task (Ekman, Levenson, & Friesen, 1983; Levenson et al., 1990), one of the reliable differences between emotions was higher levels of finger temperature associated with anger compared to fear. A very similar ANS difference has also been reported in studies of the temperature-related metaphors people use to describe their emotions (Lakoff, 1987) and in cross-national studies of self-reported physical sensations associated with different emotions (Scherer & Wallbott, 1994; Wallbott & Scherer, 1988).

A cautionary note regarding ANS specificity in the fMRI era. ANS data are increasingly being collected as part of fMRI studies of the brain activation that occurs during emotion. It is not difficult to envision a new generation of data relevant to ANS specificity in emotion that comes from these kinds of studies. Because movement artifacts are very troublesome in fMRI studies, many scanner paradigms use extremely weak emotion elicitors, often more related to emotion recognition than emotion generation. If the ANS data obtained from these studies are to be helpful in addressing fundamental issues concerning ANS patterning in emotion (both coherence and specificity), it is critical that these data be held to the same standards of verification, intensity, comprehensiveness, and timing that

are being proposed here for studies that take place outside of the magnet.

Empirical support. Debate on ANS specificity in emotion has a rich intellectual history, tracing back to the diametrically opposing views of James (1884), who argued for ANS specificity, and Cannon (1927), who argued against. In the ensuing decades a large number of empirical studies have been conducted addressing this issue (134 in the most recent comprehensive review; Kreibig, 2010). Despite this sizeable body of work, the controversy endures, with different authors coming to dramatically different conclusions as to the degree of ANS specificity that exists in emotion (e.g., Barrett, 2006; Cacioppo, Klein, Berntson, & Hatfield, 1993; Kreibig, 2010; Levenson, 1992, 2011; Mauss & Robinson, 2009; Zajonc & McIntosh, 1992).

Although it is probably fair to say that far more published studies have reported evidence of ANS differentiation between emotions than have not, significant questions can be raised about the reliability of these findings across laboratories, ANS measures, methods of elicitation (Stemmler, 1989), particular emotions (Kreibig, 2010), particular models of emotion (e.g., discrete emotions or emotion dimensions; Mauss & Robinson, 2009), and emotion intensities.

I have speculated that ultimately there will be compelling evidence for ANS specificity among four to six of the more "basic" emotions (Levenson, 2011). Having said this, I can fully understand the conclusion of those who see the existing literature as being far from definitive. As I have tried to indicate in the foregoing sections, there are enormous obstacles that need to be overcome if a body of research is going to be created that adequately tests the hypothesis of ANS specificity in emotion. As long as the bulk of existing research (both that hypothesizing specificity and that predicting the opposite) is plagued by problems related to unverified emotion elicitation, low emotional intensity, narrow assessment of ANS functioning, incomplete characterization of the activity of autonomic systems, and poor temporal matching of ANS measurement to emotion occurrence, it will be impossible to reach well-founded, data-based conclusions about the extent of ANS specificity in emotion.

ANS Patterning in Emotion: Concluding Thoughts

ANS patterning in emotion remains an area of great scientific interest. It has profound implications for understanding the nature of emotion and for testing predictions derived from different theories of emotion. In addition, high-quality studies of ANS patterning, both those that examine coherence and those that examine specificity, hold promise for revealing important downstream consequences of emotion. These include the influences of emotion on other psychological processes (e.g., attention, cognition, learning, memory) and the role that emotion plays in mental health, physical health, and well-being.

The dramatic advances in methodologies for measuring brain structure and function that have occurred in recent years

(e.g., structural and functional MRI, magneto-encephalography, multichannel electroencephalography) might have eclipsed interest in the role the ANS plays in emotion. Ironically, the opposite has occurred, and there are now rich new theories and understanding of how the brain and ANS interact in generating, regulating, recognizing, and responding to emotion. Along the way, there have also been significant advances in the ways that ANS activity can be detected and quantified. New hardware and software makes it possible to measure an expanding array of ANS functions in increasingly detailed and temporally fine-grained ways. Applying these methods to the study of ANS coherence and specificity in emotion would go a long way toward addressing some of the shortcomings of the existing research in terms of the issues such as the comprehensiveness of ANS measurement and its temporal matching with the occurrence of emotion. Much of the remaining needed improvement will be much more low-tech, focusing on the quality of paradigms used for eliciting and verifying emotional states and finding ways to produce emotional states that are of sufficient intensity, so that the associated emotional ANS activity can emerge as detectable signal amidst the vast sea of nonemotional ANS activity.

As debate over the extent of ANS patterning in emotion enters its second century, there is reason for renewed optimism about the potential for new progress in examining fundamental questions about the extent of ANS patterning in emotion. If we can build a body of sound research that consists of carefully designed, well-executed studies, we will be in a much better position to reach more definitive conclusions about the extent of ANS coherence and specificity in emotion. As with any good science, the goal of such work should not be to find ways to support a particular preconceived position (or discredit another position) at any cost, but rather to provide a body of evidence adequate for determining the conditions under which ANS coherence and specificity exist or for disconfirming these views.

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