Emotion and the Autonomic Nervous System

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Introduction

A glance at some of the classic review papers and chapters on emotion and autonomic nervous system (ANS) physiology reveals a common thread across papers—the evoking of William James' quote on the essential conditions for what should be considered an emotion – "the only emotions I propose expressly to consider here are those that have a distinct bodily expression" (1884, p. 189). It is no wonder that emotion researchers and theorists who consider the biological underpinnings of emotion would use this quote as justification for looking "under the skin" at bodily responses as a window into affective and emotional states.

James' perspective is but one of many factors that sets the stage for examining how ANS responses change during emotion states. Autonomic nervous system responses and emotion reactions share similar temporal features; Emotion responses are described as short-lived, punctuate experiences that typically last seconds to a couple of minutes. This temporal window aligns well with typical ANS changes as opposed to neural activation often measured in milliseconds or neuroendocrine and immunological changes measured over hours or days. Additionally, emotion responses are perceived as being "felt" in the body and folk language implicates bodily changes in these processes. Feeling sick to your stomach when experiencing disgust, a racing heart when walking down a dark, deserted street, or hot sweaty palms when filled with fury, seem to effortlessly couple the emotional state and the bodily change. Given this apparent natural coupling it is not surprising that a large literature has amassed examining the relation between emotion experiences and ANS changes.

There are, however, many factors that modulate the *emotion—physiology link* that limit the straightforward conclusion that a discrete emotion experience is reliably and universally associated with specific changes in ANS responses. Rather than viewing the many factors that can moderate the emotion-ANS link as obstacles, it may be more useful to consider the

moderators as opportunities to understand how emotions are manifested in the brain and body, and how these contextual factors extend our knowledge about emotion. In this chapter, I provide an overview of research examining links between emotion and peripheral physiology; ignoring neuroendocrine and immune responses, which are covered in Chapter # (Prather) and neural activation, covered in Chapter # (x). First, I review research that examines relations between emotion and peripheral physiology, and then address the moderators that can alter the emotion-physiology link, specifically, context, developmental factors, and socio-cultural environments. Due to space constraints, the literature reviewed is illustrative rather than comprehensive. The chapter begins with a primer on psychophysiological theory and autonomic nervous system functioning that serves to both orient the reader to the most commonly measured physiological systems used in the study of emotion and identifies some of the limitations inherent in examining physiological responses to understand emotion and emotion processes.

Peripheral Physiologic Systems

A number of biological systems have been implicated in emotional experiences, including sympathetic and parasympathetic nervous systems, hemodynamic, enteric, neuroendocrine, immune, and neural. A common feature of these biological systems is that their *primary* functions have that little, if anything, to do with emotions. The sympathetic nervous system (SNS) is designed to provide oxygenated blood to the brain and body to support movement; the parasympathetic system can co-regulate SNS responses and supports homeostasis during sleep; the gastrointestinal system breaks down food for energy and excretes waste. These biological systems can change during emotion experiences—providing the foundation for these systems to be examined in emotion research—but the presence of

changes in any of these systems does not indicate that an emotional experience occurred, and the reverse is true as well—a lack of response does not indicate the emotion did not occur.

As described in the first chapter of the *Handbook of Psychophysiology* (Cacioppo, Tassinary, & Berntson, 2000; 2007) inferring mental states from physiological changes poses several challenges, including the idea that *many* mental states can influence specific physiological changes and that a specific mental state is related to *many* physiological responses. In adopting a biological systems approach to understanding emotions, the literature is clear that one-to-one invariants of emotional states and physiological changes that exist across contexts and people are rare, if not non-existent (e.g., Cacioppo, et al., 2007; Kreibig, 2010; Siegel, et al., 2015). The pursuit of unearthing invariants between emotion and psychophysiology might be a noble one—the entire field would benefit if a single channel of physiological responses changed predictably and precisely with the presence of an emotional state, regardless of context, culture, or character—but it is also likely misguided. Patterned physiological responses– looking across a variety of physiological changes – linked to emotion states provides a step in the right direction (e.g., Kreibig, 2010; Levenson, 2014; Stemmler, et al., 2001) particularly if the panel of physiological responses are not strongly correlated with each other. In addition to examining across a variety of physiological responses, a deep understanding of the individual differences, cultural, and contextual factors that influence emotion along with an appreciation of the developmental, physical, and environmental factors that affect physiology can enable researchers to augment their understanding of the emotion-physiology relationship.

At the broadest level, relations between peripheral physiology and emotion can be construed in terms of their *sensitivity* and *specificity. Sensitivity* is the extent to which the physiological responses reliably change as a function of shifts in emotion states with the idea that subtle shifts would affect highly *sensitive* measures, but measures that are lower in

sensitivity would take more intense emotion states to observe changes. Skin conductance, for example, is highly sensitive because very subtle and low level changes in emotion can affect skin conductance levels. In contrast, blood pressure changes are less sensitive given the emotional experience needs to be fairly intense to alter blood pressure levels (Mendes, 2009).

Specificity refers to how physiological responses are related to discrete mental states, with low specificity indicating that a physiological response is related to many mental states and high specificity indicating a physiological response is related to fewer or (possibly) a single mental state. Using skin conductance again as an example, though it is highly sensitive it is not specific. Many affective states, even emotions with different valence like anger and enthusiasm, can engender skin conductance increases (e.g., Kreibig, 2010; Shiota, et al., 2011).

The constructs of sensitivity and specificity are crucial to understanding and predicting associations between emotions and peripheral physiological responses, though these relationships can be modified by context. Staying with the example of skin conductance (SC), if the context is constrained such that a smaller array of emotions are likely to be experienced then one might be on firmer ground to conclude that the physiological response is a reasonable measure of the emotional experience. For example, the threat of experiencing an electric shock reliably increases skin conductance, and while some people might interpret the increased SC as synonymous with the experience of *fear*, others might conclude SC responses are tracking threat detection, general arousal, or intensity (e.g., LeDoux, 2014). Importantly, though, it is unlikely that increased SC in the electric shock context indicates an emotion like happiness or disgust. Thus constraining the context can improve the specificity of the emotion-physiology relationship by limiting the number of likely emotional states that can be experienced.

Autonomic Nervous System

The ANS comprises two major branches: sympathetic and parasympathetic nervous systems (SNS and PNS), both of which are commonly examined in studies on emotion and

physiology, and many measures represent hybrid responses that are influenced by both systems simultaneously. Indeed, the division of the systems is more didactic than functional given the vast number of bodily changes influenced by the *combination* of these systems and the extent to which the SNS and PNS influence each other, which can be reciprocal, co-inhibited, co-activated or orthogonal (Berntson, Cacioppo, & Quigley, 1993).

The SNS functions, in part, to mobilize oxygenated blood from the heart to peripheral sites such as arms, hands, legs, feet, and the brain. The greatest change in SNS responding occurs with physical exertion, like sprinting or intense aerobic exercise. But this system also activates in *non-metabolically demanding* situations, ones that do not by necessity require an increase in oxygenated blood. Measures that tap aspects of SNS that are commonly used in emotion research include heart rate/interbeat interval, skin conductance, finger pulse transit time, blood pressure, skin temperature, pre-ejection period, stroke volume/cardiac output, and local/global blood flow measures (pulse amplitude, total peripheral resistance). Most of these measures tend to be highly correlated with each other suggesting that studies that examine multiple SNS measures to look at patterns of physiological responses might be unwittingly inflating type 1 error if not accounting for the common variance in the measures.

The PNS is typically assessed with heart rate variability (HRV) measures such as cardiac vagal responses. Initially, HRV—the time interval between each heart beat—was believed to be a measurement artifact or nuisance, but further exploration into spontaneous changes in the timing of the heart cycle proved to be psychologically and physiologically meaningful. Though there are still disagreements on the specifics related to measurement, quantification, and psychological meaningfulness of HRV, these measures are often used by emotion psychophysiologists given its putative sensitivity to valence and links to social engagement processes (Larsen, et al., 2008; Porges 2007).

Porges' polyvagal theory (e.g., Porges, 2007) is commonly evoked in studies examining emotional states associated with HRV/vagal changes. Polyvagal theory argues that primates uniquely have vagal nerve modulation (but see Grossman & Taylor, 2007), which has evolved as part of the *social engagement system*. Thus one of the primary postulates of polyvagal theory is that social factors (affiliation, social engagement), personality factors (optimism, bonding, attachment) and emotional states (positive emotions, compassion) can modulate cardiac vagal responses. Thus, higher resting vagal tone is suggested to serve as an index of adaptive regulation and responsiveness to the social environment.

The vast majority of studies examining peripheral physiological responses and emotion focus on one, some, or all of these responses identified above. To a lesser extent emotion researchers have examined responses like electrogastrography (EGG), respiration, or muscle tension. Some of the less commonly examined responses will be reviewed below.

Debate on ANS Specificity of Emotion

Even though peripheral physiological responses are widely integrated in emotion theories, there remain hotly debated theoretical perspectives on how best to conceive of emotions and consequent physiologic responses. These arguments include, whether there exists a specific identifiable physiological pattern that underlies distinct, "basic" emotions; if physiologic patterning maps onto more dimensional aspects of emotion, like approach/avoid tendencies and positive/negative valence; if subtypes of discrete emotions have patterned physiology; if contexts trigger core psychological states (i.e., "ingredients") that engender physiological reactions that are then labeled with emotion words (e.g., Barrett, 2006; Cacioppo, Berntson, Larsen, Poehlmann, & Ito, 2000; Kreibig, 2010; Levenson, 2014).

One of the enduring perspectives argues that "basic emotions" have a specific patterning of physiological responses that differentiates anger, fear, disgust, sadness and happiness (e.g.,

Ekman, Levenson, & Friesen, 1983). The strong version of this argument is that patterned

physiological responses to basic emotions occur across human and non-human animals,

persists across the life span, and is unmodified by context (Ekman, 1993). Over the past few

decades, much has been written in support of and against this strong version of autonomic

specificity of emotions (see Lang, 2014; Levenson, 2014; Norman, Berntson, & Cacioppo, 2014,

for a recent discussion).

Evidence generally in favor of the strong view of autonomic specificity of emotions comes

from cross-cultural studies and literature reviews (e.g., Levenson, 2003). For example,

Levenson and colleagues (1992) traveled to West Sumatra, a large island in Indonesia, and

measured a panel of physiological responses from the Minangkabau during the "directed facial

action" task, which requires the movement of facial muscles to create a configuration tied to a

discrete emotion while seven peripheral physiological responses were obtained: heart rate,

finger transit time, finger temperature and skin conductance, finger amplitude, respiration

period, and respiration depth. They also obtained measures from a US sample using the same

paradigm. Although the mean responses for heart rate, finger temperature, and finger pulse

transit time were greater in the US sample than the Minangkabau for all five emotions

examined, the patterning of the responses were similar—for example, heart rate and finger

temperature were higher during experiences of anger compared to disgust. The authors

concluded that the two cultures "evidenced patterns of emotion-specific ANS activity that were

similar" though they followed this with the point that these data did "not [establish] universality"

(page 983).

More recently, Kreibig identified 134 studies utilizing ANS measures and concluded that

there were "considerable ANS response specificity in emotion when considering subtypes of

distinct emotions" (page 394) but also pointed to the need to incorporate ANS measures beyond

ones that are the easiest to obtain – e.g., HR and SC. Echoing this point, Levenson identified

rarely studied physiological responses in emotion research that might be more reliably related to

emotions such as visible changes in coloration, moisture and secretion, protrusions, and appearance of eyes, which are all ANS-mediated (Levenson, 2003; Levenson, 2014). In sum, claims that specific emotions show ANS patterning comes from 1) cross cultural research showing similar patterned responses to basic emotions; and 2) reviews supporting similar directional changes in physiology as a function of the emotion experienced. Finally, it may be the case that emotion psychophysiologists have simply fallen prey to focusing on responses that are the easiest to measure—akin to looking for lost keys under the light, rather than where they were dropped (Levenson, 2003).

Evidence against the strong view of patterned physiological responses mapping onto discrete emotions comes from meta-analytic approaches which suggest that physiologic patterning might relate to more basic *ingredients* of emotions (e.g., Barrett, 2006). For example, in the meta-analyses that appeared in two editions of the *Handbook of Emotion* (Cacioppo et al, 2000, Larsen et al., 2008), the authors concluded that motivational tendencies embedded within emotional states show some consistent ANS patterning. Specifically, approach-oriented emotional states in which there is an expectation for the need to mobilize energy are more likely to activate sympathetic nervous system (SNS) than emotional states in which no expectation of energy reserves is expected. This is consistent with the biopsychosocial model of challenge and threat, which relies on cardiovascular reactivity to differentiate general *approach* (or challenge) orientation from *avoidance* (or threat) orientation (Blascovich & Mendes, 2010; Mendes & Park, 2014). Also aligned with this perspective is the overlap between fear and defensive/threat responding. LeDoux's animal work on how the brain detects threats and the consequent identification of neural "fear systems" was called "a mistake that has lead to much confusion" by LeDoux himself (2014, p. 2871). Instead, LeDoux argues that animal research shows reflexive motivational responses linked to threat detection more akin to defensive responding than "fear" as an emotional state.

In a recent meta-analysis of over 300 articles using multivariate pattern classification, no consistent evidence was found for autonomic signatures of discrete emotions (Siegel, et al, under review). Instead, the authors observed autonomic patterning that was more closely tied to the experimental context than the emotional state, though the authors acknowledged that the extant literature was biased in such a way that context and emotion were often confounded. These meta-analytic findings are consistent with the perspective that the *context* in which emotions are examined can alter the physiological responses more than the specific emotion experienced (Lang, Bradley, & Cuthbert, 1997).

Underscoring the heterogeneity of physiological responses that has been observed when examining discrete emotions, some studies have shown different patterns of physiologic responses to presumably the same emotion category. Shenhav and Mendes (2014) examined gastrointestinal, SNS, and PNS changes during different types of disgust experiences. Participants were randomly assigned to watch one of three different collections of videos: one condition showed individuals suffering painful-injuries and accidents in which legs and arms were contorted beyond natural mobility, but no breaking of the body envelope occurred (e.g., no spilling of bodily fluids or blood); a second condition showed individuals with breaking of the body envelope with emissions of blood, puss, and vomit, and people consuming disgusting things; the third collection consisted of neutral stimuli, landscapes, landmarks, animals, and people in rural and urban areas. Participants in the first two conditions labeled the emotion they were feeling as "disgust" more than any other emotion label provided and showed greater activation of the levator labii (i.e., the muscle region surrounding the nose previously linked to *disgust*) relative to participants viewing neutral stimuli. However, participants watching breaking of the body envelope videos showed decreases in gastrointestinal activity and HR acceleration, whereas viewing painful-injuries was associated with no changes in gastrointestinal responses, HR deceleration, and HRV increases. Thus two instantiations of the same emotion, disgust, using the same medium (watching videos) produced similar self-reported and facial

expressions, but different physiological patterning of the enteric and sympathetic/parasympathetic nervous system. Together these perspectives suggest greater variability in physiological patterns within the same emotion category, and provide support for a perspective on the "ingredients" of emotions or core motivational properties more likely to share similar physiological patterning – with body envelope breakage engendering more avoidance responses and other's pain experiences more approach-oriented responses (Barrett, 2006; Mendes & Park, 2014).

Emotion researchers often ask, what type of data would be needed to resolve the debate of ANS-specificity of emotional states? Researchers have suggested organization of peripheral responding along evolved neural circuitry might provide a stronger basis for examining emotion-physiology relations (Lang, 2014). Other researchers have noted the paucity of work examining ANS-mediated changes in bodily expressions that might be more closely tied to emotion experiences that manifest in observable bodily changes: for example, piloerections (goose bumps), blushing, sweating, salivating, tearing, and bulging or twinkling eyes (Levenson, 2014) and by examining these downstream responses one might be able to draw sharper boundaries around different emotion categories vis-à-vis physiological changes. Still others have urged researchers to take seriously the social and cultural context, individual differences, and developmental factors that alter how emotions are manifested in the body (Barrett, 2006; Mendes, 2010; Mendes & Park, 2014). Whether any of these approaches resolve this debate remains to be seen, but it is likely that most emotion-physiologists would agree that multiple measures, that are not dually regulated, and attention to temporal, contextual and developmental factors are more likely to lead to better insight into the nature of emotion-physiology relations.

Effects of Emotion on Peripheral Psychophysiology

Many articles and chapters have reviewed the literature examining physiological responses stemming from emotion states, in some cases very thoroughly (e.g., Cacioppo, et al., 2000; Larsen, et al., 2007; Kreibig, 2010). To provide added value here, I use a different organizing principle than what is typically used—the typical organizing feature focuses at the level of the emotion category. Instead, the review here is organized by physiological systems. The intention here is to show how easy it is to over-infer emotion states as having a distinct physiological signature if the organizing principle is at the level of the specific emotion. Instead, if the organizational structure is sorted by physiological responses, it becomes apparent how multiple mental states, not just emotional states, but also stress, cognition, and motivation can trigger the same physiological response.

Sympathetic Nervous System

SNS increases have been linked to a variety of emotional states, including ones that differ in valence, and other mental states including effort, motivation, cognition, salience, and stress. Changes in SNS can be measured in a variety of ways with the most common measures being skin conductance, heart rate/interbeat interval, pulse transit time, and preejection period. These aforementioned responses are not perfect proxies for each other, with each one characterized by different underlying physiologic processes (e.g., skin conductance increases are innervated by acetylcholine, whereas cardiac increases by epinephrine). These responses also differ in the extent to which they are dually innervated by the SNS and PNS versus solely influenced by SNS. Preejection period, for example, which is a chronotropic measure based on the time from the left ventricle contracting to the opening of the aortic valve, is one of the few non-dually innervated measures representing solely SNS activation. However, measurement of PEP, most typically measured using impedance cardiography, tends to be more involved than

measuring other responses like skin conductance or electrocardiography, and is more costly and requires considerable expertise.

Heart rate and skin conductance changes are the most commonly used peripheral measures in emotion research. As described earlier it is not surprising that these measures are ubiquitous given these responses are sensitive to a variety of internal and external information, and have a predictable, short-lived response that mirrors common emotional reactions. Emotions as varied as fear, amusement, anger, sadness, and disgust reliably bring about HR and SC changes (Kriebig, 2010; Larsen, et al., 2007), but so do mental states like effort (Wright & Kirby, 2001), acute stress (Dickerson & Kemeny, 2004; Fredrickson & Matthews, 1990; Jacobs, et al., 1994), mind wandering (Smallwood, O'Connor, Sudbery, &Obonsawin, 2007), active coping (Obrist, 1981), attention (Pribram & McGuinness, 1975) and rumination (Brosschot, Gerin & Thayer, 2006) (see Figure 1). Because these measures, especially, are sensitive to so many mental states it is best to conceive of these responses as primarily indicating larger categories of mental states such as mental demand, saliency, general arousal, or effort (Dawson, Schell, & Filion, 2000). This leaves emotion researchers in a difficult position because if the hypothesis is, for example, that a HR response is larger in one discrete emotion than a different emotion the onus is on the researcher to equate the intensity of the emotion experiences from the different contexts used to induce the emotion. That is, if one wanted to compare HR responses in fear to anger one would have to resolve the problem of equating the intensity of the emotional stimuli. Would the fear of a spider presented to someone with arachnophobia be as intense as a derogatory racist insult leveled at a marginalized minority? Because the variety of contexts that engender emotions varies greatly and those contexts differ in many ways, the question of which emotion elicits greater HR or SC can be a frustrating and non-fruitful endeavor.

Does moving to a measure of SNS that is solely innervated solve this problem? Changes in preejection period (shorter PEP indicates greater SNS activation) have been observed during anger inductions (Herrald & Tomaka, 2002; Mauss, et al, 2007; Mendes, et al, 2008) relative to emotions like shame or motivational states like threat. Though, PEP decreases have also been associated with emotions like joy, disgust and embarrassment (Kriebig, 2010). Considering other mental states, PEP decreases are associated with active coping (Obrist), and motivational states of threat *and* challenge (Blascovich & Mendes, 2010; Mendes, 2009; Seery, 2012). Much less work includes measurements obtained from impedance cardiography so it is unclear whether this type of measurement will reveal more emotion specificity than measures that are dually innervated (see Norman et al., 2014 for a discussion on why these "purer" measures might reveal more reliable associations).

Though I have treated these SNS measures as separate entities, it is not uncommon to combine these measures to form a composite index (Cole, et al., 2001; Murphy, Steele, & Gross, 2007; Roberts, Levenson, & Gross, 2008). The value of doing so is to optimize the common signal across measures and minimize noise inherent in each measure. On the one hand this approach can be useful because it might reduce *researcher degrees of freedom* which might be exploited if one collected many measures and then reported just the one(s) that was significant (Simmons, Nelson & Simonsohn, 2011). On the negative side of the ledger though is that many of the measures have distinct underlying physiologic processes and by combining the measures we might end up learning less about the underlying physiologic responses. Composite measures also make it very difficult to conduct meaningful meta-analysis since there are not agreed upon standards of what determines the composite measure.

Parasympathetic Nervous System

There are several measures of PNS that can be reliably obtained using fairly inexpensive technology and without a lot of experimenter or participant burden (see Allen, 2002). One of the most common measures of PNS used by emotion researchers is high frequency heart rate variability (HF/HRV), also commonly referred to as respiratory sinus arrhythmia (RSA). It is not surprising that emotion researchers rely on RSA given its putative links to relevant affective states like attachment and social engagement. Cardiac vagal tone (or resting HRV) has been associated with dispositional emotional styles (Demaree & Everhart, 2004; Oveis, et al., 2009; Sloan, et al., 2001). For example, individuals with greater hostile tendencies have lower cardiac vagal tone at baseline, during an emotional induction task, and at recovery than those low in hostility (Demaree & Everhart, 2004; Sloan, et al., 2001). Similarly, but on the brighter side, Oveis and colleagues (2009) found that those higher in optimism had higher vagal tone. Accumulating evidence suggests that vagal tone might be a reasonable physiological response to index general positive and negative affect with the caveat that particularly high levels of vagal tone might be detrimental; Kogan and colleagues observed a quadratic relationship between cardiac vagal activity and prosocial behavior such that extremely high levels of vagal tone were associated with less prosocial emotions and traits (Kogan, et al., 2014).

A variety of emotions have been associated with HRV decreases and increases that show some valence differences – negative emotions more likely linked to decreases in HRV, whereas positive emotions might be linked with increases in HRV (Figure 2). In support of a valence interpretation of HRV, in a study examining the benefits of implicit goal setting students were interviewed about their grades while HRV was obtained. Those who exaggerated their obtained GPA during the interview subsequently earned a higher GPA in a later semester. Critically HRV changes mediated the relationship between exaggeration and improvement such

that the greater the HRV decreases the *less* students improved and this effect was corroborated by behavioral coding supporting the idea that participants with greater HRV decreases appeared *more* anxious during the interview (Gramzow, Willard, & Mendes, 2008). Evidence showing HRV increases can be linked with positive outcomes include a recent study showed that induced compassion, compared to other positive emotion inductions (like pride or inspiration), was associated with higher levels of HRV (Stellar, Cohen, Oveis, & Keltner, 2015). But again the directional HRV effects associated with valence is far from invariant. For example, in the Shenhav and Mendes (2014) study looking at different types of disgust, the condition in which participants watched videos of individuals suffering injuries and experiencing twisted limbs was associated with an *increase* in HRV relative to those watching videos with body-envelope breakage. Interestingly there are commonalities in the stimuli across the "compassion" study and the "disgust" study. In the Stellar, et al, paper the stimuli included photos of starving children, homeless individuals, and injured animals (Study 2), which shares many features with the disgust condition from Shenhav & Mendes (2014) which used stimuli of people also suffering and potentially experiencing grave and unfortunate outcomes like falling off buildings and extreme sports accidents. Thus HRV reactivity might be associated with fundamental features of the emotion experience that are not best described by the emotion categories (disgust, compassion, anxiety) but instead by interest, attention, and motivational states, like approach and avoid.

Like SNS activation, PNS changes have been linked to mental states that are viewed as part of the stress response or are more cognitive or motivational. Indeed, cognitive psychophysiologists use HRV decreases to index attention and mental effort (Tattersall & Hockey, 1995), and Porges (e.g., 2007) uses the example of target-shooting as a reliable task that is associated with HRV decreases. In one study relying on this interpretation, Kassam, et al. (2009) examined HRV decreases during a judgment and decision-making task and found that

greater HRV decreases were associated with more accurate performance, specifically more accurate responding on an anchoring and adjustment task. Following this logic, HRV on average decreases reliably during a visual tracking task (Cavanagh & Alvarez, 2005) and individual differences in the amount of HRV decreases predicts social perception accuracy and social sensitivity (Muhtadie, Koslov, Akinola, & Mendes, 2015).

Some studies have used emotional and cognitive interpretations to explain the same effect. In a stereotype threat study, Croizet et al (2004) examined changes in HRV and found that participants primed with threatening stereotypes of their group showed decreases in HRV during a test of "intellectual diagnosticity" and poorer performance than those in the non-stereotyped threat group and the greater the decrease in HRV the worse participants performed on the test. However, in the non-stereotyped group, HRV also decreased during the "intellectual test" but the greater the decrease in HRV the *better* participants performed on the test (though this path was short of significance), which was interpreted as indicated more effort. This work underscores how presumably different mental states (distress compared to mental effort) are associated with a similar physiological response (decrease in HRV) but can have different influences on behavior and performance.

Hemodynamic Responses

Blood pressure (BP) and precursors of blood pressure, like total peripheral resistance (TPR), have been used by health psychologists for decades given their putative role in disease etiology like essential hypertension and cardiovascular disease. Given this link, BP is probably more closely identified with acute *stress* than emotional states. Hemodynamic changes are slower to respond than SNS activation and can be more challenging to measure continuously, which might also prevent emotion researchers from including these measures in their protocols (Mendes, 2009). Even with less accumulated evidence, reviews report increased BP across a

variety of emotions and not necessarily tied to only negative emotional states, such as anger, fear, amusement, but also happiness and amusement (Kreibig, 2010).

Research stemming from motivational theories often examines changes in blood pressure. Wright and colleagues offer their effort mobilization theory, which relies on BP changes (typically systolic blood pressure, SBP) and HR increases to index motivational effort (e.g., Wright & Kirby, 2001; Wright et al., 2007). In this perspective SBP increases linearly with effort, which is consistent with the broader interpretation of SNS activation. Offering a nuanced perspective of motivational states is *challenge and threat* theory (Blascovich & Tomaka, 1996; Blascovich & Mendes, 2010) which proposes that in active, goal-relevant contexts, appraisals of demands and resources interact to produce either general approach motivation, *challenge*, or avoidance orientation, *threat.* One of the physiological changes that best differentiates these psychological states is TPR. In threat states TPR increases, which represents a tightening of the arterioles so blood travel to peripheral sites is impaired, whereas challenge states are associated with increased blood flow to peripheral sites (Mendes, 2009).

In the broader stress literature, there tends to be little nuance in terms of what increases in BP indicates at a psychological level, and instead the broadest, catch-all label "stress" is applied to increased BP responses (e.g., Matthews, Woodall & Allen, 1993; Guyll, Matthews, & Bromberger, 2001). If emotion research can be characterized for forcing too many distinctions between discrete/specific emotions—that is, *splitting*—stress research suffers from the opposite error of collapsing across possibly distinct mental states—that is, *lumping.* The differences between emotion and stress research is most obvious when comparing experimental protocols using many of the measures reviewed here from papers claiming to be studying *stress* compared to those studying *emotion.* In many cases the paradigms are similar, even if the interpretations of the mental states are different, likely leading to the common expression: stress is what is studied in medical schools; emotion is what is studied in psychology departments.

Moderators of the Emotion-Physiology Link

The previous sections may present what seems like an unwieldy literature on ANS responses to emotional states, but a different way to interpret these data is to consider the moderators that may reliably explain the variance in physiological responding across different studies. Thus far, the review of physiological responses associated with emotional states show that these relations are far from invariant. Adopting an approach that relaxes strong essentialist constraints provides a view of emotion that is flexible in terms of how emotions states are manifested in the brain and body. Attending to these moderators may be as important, or even more important, than the emotion category itself. Here, I outline key moderators that can alter the association between emotion and its physiological concomitants. Specifically, moderators such as context including environment and bodily states (positioning of the body), individual differences, cognitive states like labeling, developmental factors and socio-culture factors can affect how emotions are manifested in the body. These factors can influence emotional experience, physiological responses to emotion, and the consequent behavior and feeling states that occur, which underscores the perspective that the emotion-physiology link is flexible and can be altered by top-down *and* bottom-up influences.

Context

Psychological science is replete with examples of how subtle features in the environment or minor tweaks of perspective can alter an emotional state. From holding a pen with one's teeth versus lips leading to more humorous reactions to comic strips (Strack, Martin, & Stepper, 1998) to clutching a warm cup of coffee influencing judgments of others' personality (Williams & Bargh, 2008), there are many demonstrations that bottom-up influences can alter emotion states, often without conscious awareness.

Bottom-up influences that directly affect the body and/or change the interpretation of the event can alter physiological responses of emotional states. An extensive body of non-human animal research work has explored "defensive" responses using rats that were classically conditioned to experience "fear" using acoustic responses and shocks. In one study, Iwata and LeDoux (1988) placed rats in either a cage where they were unrestrained, which allowed free movement, or restrained, which forced immobility. When exposed to an aversive signal, rats that were restrained had a different profile of physiological responses than rats that were unrestrained. Specifically, rats that were unrestrained showed greater heart rate acceleration relative to restrained rats. This study elegantly demonstrates the influence of context in modulating physiological outcomes to the (presumably) same emotion/affective state. If "fear-conditioned" rats have different physiological responses based on the *context* rather than the specific emotional state then it is difficult to argue that fear invariably leads to a predictable physiological response. Instead, this finding shows that the context in which an emotion or affective state is experienced can shape the physiological pattern. One interpretation is that when rats' behavioral options are interpreted in terms of its potential to escape or not, the physiological responses provide functional support. When escape is possible, an increase in cardiac responses would allow for more oxygenated blood to innervate peripheral muscles, whereas when no escape is possible a reduction in sympathetic responses facilitates freezing and, in the case of a predator attack, the lower SNS reaction would reduce blood loss if attacked.

Context and body positioning interact in humans as well. In one study using electroencephalographic (EEG) responses, participants were seated either upright or supine while they experienced insults from a confederate, intended to engender an anger state (Harmon-Jones & Peterson, 2009). Those who were upright showed a shift in left frontal cortical activation that occurs during anger and general *approach-oriented* states, whereas those who were supine did not show a shift in left frontal cortical activity. Self-reported anger *did not differ*

by body position underscoring that physiological changes are often subtle and may be below conscious awareness. Importantly, like LeDoux's restrained rats, putatively the same emotional state experienced in different contexts – in this example, in different body positions – have a different profile of physiological responses. Because anger is typically conceived as an approach-oriented emotion (Carver & Harmon-Jones, 2009) the conclusion was that an incongruent body position, leaning back when feeling angry, blunts a physiological response that co-occurs with the emotional state.

We recently extended this question by exploring if a body position could *potentiate* an affective state and, as a consequence, influence moral judgments. In a recent study, we examined whether manipulated body positions would interact with experienced affective states to influence moral judgments (Park & Mendes, 2015). Participants were randomly assigned to experience anger or shame and were orthogonally assigned to one of three body positions: leaning forward, leaning away and upright/control. When participants were induced to experience anger and were in an approach (leaning forward) body position, they were more likely to endorse utilitarian judgments—pushing a person out of a sinking lifeboat to save more lives. Similar to the EEG study above, this study demonstrates that emotional states are malleable and can be altered by body positions.

Cognitive factors

How one identifies or cognitively interprets an emotion experience provides insight into how top-down influences shape emotion-physiology relations. Self-disclosure or expressive writing has long been suggested to be associated with better health possibly due to its ability to make sense of a traumatic event possibly reducing negative cognitive processes like rumination and preservative thinking (Frattaroli, 2006; Pennebaker, 1997). Following this line of reasoning *labeling* experienced emotions have been linked to reduced amygdala responding to frightening or aversive stimuli (Lieberman et al., 2007). However, if labeling or disclosure occurs soon after

the event it might cement associations which bond the aversive label with the event. For example, Seery and colleagues used a nationally representative sample (more than 2,000 respondents) and queried them about their feelings and thoughts regarding Sept 11, 2001 within 24 hours of the attacks and then followed them for several years to assess their physical and mental health trajectories (Seery, et al., 2008). Those who expressed their thoughts and feeling immediately after the attacks had *worse* health outcomes than those who did not. Thus reflection and cognitive activity around emotions may create more maladaptive binding of the cognitive components of the emotion and the downstream consequences.

To test the idea that immediate reporting of an emotional experience could change a subsequent physiological response, Kassam & Mendes (2013) randomly assigned participants to an emotion task designed to induce either external negative emotions (anger) or internal negative emotions (shame) and measured cardiovascular reactivity throughout the task (specifically, preejection period, cardiac output, and total peripheral resistance). In addition to the emotion manipulation, participants were assigned to either a *reporting* condition or *no reporting* condition. Quite simply this manipulation consisted of participants in the reporting condition to self-report their experienced emotion throughout the study. Indeed, this condition mimicked most lab-based emotion studies that rely on self-reported emotions as the primary outcome variable. In contrast, the *no reporting* condition did not have participants report on their emotions at any time during the study, and instead used self-reports of technology use as the instruments replacing self-reported emotions. If the act of self-reporting on an emotion state changes the experience of an emotion then the physiological response might differ between the reporting and no-reporting conditions. Consistent with this prediction emotion-reporting changed physiologic reactivity, but only when participants were assigned to the *anger* induction. When reporting on emotions and assigned to the anger induction participants on average showed greater hemodynamic changes – increased peripheral resistance/increased blood pressure, whereas participants who did not report on their emotional state showed greater cardiac

increases and lower hemodynamic responses. Thus, the simple act of reporting on an emotional state changed the pattern of physiologic responses even though the emotional induction did not differ. In contrast, among participants in the shame condition, reporting or not on emotional states did not differentially influence physiologic reactions – shame was associated with increased cardiac reactivity and increased vascular resistance regardless of the reporting condition. The conclusion of this work was that self-conscious emotions, like shame, are not modified by deliberate and conscious appraisal of the emotional state, but emotions that might be highly contextualized, like anger, might be more modifiable by conscious processes.

Developmental Factors

Much of modern psychophysiological research assumes reliable mind-body connections—changes in emotional states influence bodily responses and the biological milieu can shape experienced emotions. However, connections between mental states and physiological changes are not static across the life course; at different developmental periods processes like *interoception, proprioception,* and *reactivity* can alter how emotions are experienced in the body.

As we age cognitive declines such as deterioration in short term memory, reaction times, and attention occur even in the absence of neurological diseases (e.g., Levy, 1994). In the body, loss of muscle mass, deficiencies of growth hormones, hardening of the vasculature, and blunted activation reduces the flexibility of responding to different environmental demands (e.g., Epel, Burke, & Wolkowitz, 2007; Matthews, 2005). These bodily changes can alter how emotions are experienced. Most critically for understanding the role of the ANS in emotions is that aging bodies have greater difficulty mounting larger SNS increases, which may alter the emotional experience.

Consider the roles of proprioception and interoception in emotion experience and across the life span. Proprioception, the awareness of *external* body position during static and dynamic movement, and interoception, the awareness of *internal* bodily changes, both decline with old age. Khalsa and colleagues (2009) examined interoception using a heart beat detection paradigm with participants ranging in age from 22 to 63; older subjects showed poorer detection of their heart beats than younger and middle aged adults, and the overall bivariate correlation between age and accurate heart beat detection across two time points was approximately $r = -.47$. Similarly, proprioceptive impairments with age occur along varied dimensions of static and dynamic body positions (see Goble, et al., 2009, for a review).

Declines in interoception and proprioception are not the only physiologic changes that occur in aging that is relevant to emotional states. As people age there is a degrading and loss of flexibility of key physiological systems, like the SNS. For example, Levenson and colleagues found lower heart rate responses for anger, fear, and sadness in older adults compared to younger adults during a directed facial action task (Levenson, et al., 1991). In some cases younger adults had twice as large SNS increases as older adults (a finding that mirrors physical exercise).

Importantly, in research with older adults, high arousal emotions, like anger, did not engender increases in skin temperature that has been observed in younger adults (Levenson, et al., 1991). Changes in the flexibility of the vasculature especially in the peripheral regions— arms and hands; legs and feet—are typically affected by neuropathy that occurs with aging and the extremities tend to be affected first. The lack of skin temperature increase during anger is especially interesting given that anger is characterized as having an approach orientation (Carver & Harmon-Jones, 2009) and has been associated with greater dilation of the arterioles allowing more blood to get to the effector muscles and periphery, which is one of the likely physiological changes that increases skin temperature during anger (Mendes, et al., 2008). However, it is important to note that the flexibility of the vasculature is compromised in an

asymmetrical manner with age – vessels can still constrict easily but are harder to dilate. Therefore, emotional states that have approach functions may be compromised before states of emotions with withdrawal or avoidance feature, which might become the default response in older age.

Evidence of declines in sensory perception of the body with age and how this decline can interrupt the mind-body connection has been used as evidence of *maturational dualism*, a phenomenon that suggests that the bodily changes that often co-occur with the aging process can influence the experience of affective states in specific ways (Mendes, 2009). Thus for older adults, intentions, motivations, and emotions may be experienced in the mind (and brain) but not be embodied in the same way as they are in younger adults. The weakening of the mind-body connection in older adulthood is primarily due to a loss of peripheral perception and blunted physiological reactivity and may blunt the ability to use internal states to guide decisions and behavior.

The consequence for this loss in mind-body connections with age has implications for emotion-physiology relations. In a study examining the somatic marker hypothesis, older adults used bodily information to a lesser extent than younger adults (Denburg, Tranel, & Bechara, 2004). In previous papers, the somatic marker hypothesis posited that bodily states outside of conscious awareness can influence behavior (Bechara, Damasio, Tranel, & Damasio, 1997). To test this hypothesis, participants (brain damaged and control) were presented with four decks of cards with various gains and losses associated with the cards. Two of the decks resulted in overall losses – large gains, but large losses as well – whereas the other two decks resulted in smaller gains, but also smaller losses. They found that as participants turned over cards from the various decks, changes in skin conductance co-occurred with choices from the riskier decks. Importantly, these bodily changes *preceded* conscious reporting of which decks were risky by approximately 40 trials. Thus, the somatic marker hypothesis claims that bodily changes can indicate psychological or mental states prior to conscious reporting. In the original article,

25

normal participants were compared to patients with ventral medial lesions. While normal participants consciously reported which decks were risky by about the 40th trial, lesion patients were not able to learn this pattern.

In the extension of this earlier study, older adults (56 to 85 years old) did not show preferences for the advantageous decks (Denburg, et al., 2004). When examining individual responses, the authors reported that among the younger group, 37 out of 40 participants eventually picked from the advantaged deck, among the older group, only 15 out of 40 showed this same "unimpaired" pattern. The remaining older participants either showed more preference for the disadvantaged deck or no preference. It is unclear whether older participants had blunted physiological responses during the task, which limited their ability to sense internal states or the physiologic response was intact and as strong as that experienced by younger participants, but the ability to sense the bodily changes—interoceptive awareness—was diminished (Khalsa, 2009) or there was some neural impairment.

An implication of the loss in mind-body connections is that older individuals might have to rely more on the external environment to determine their internal states, and possibly their emotional experience. This is consistent with Cartensen's socio-emotional selectivity theory, which describes a positivity effect in older adults including a shifting away from negative stimuli toward more positive stimuli (Cartensen, 2006). Another implication is that older participants would be more susceptible to suggestions of an emotional state since they might have to rely more on their external world to provide information about their internal states. Although theory and evidence suggest that environmental cues can strongly influence affective states and meaning (Barrett, 2009) the loss of ability to detect internal states might make older participants more susceptible to environmental cues. Future studies exploring these ideas would be imperative to determine boundary conditions of mind-body relations.

Culture

The shaping of emotion via cultural displays and norms is a vibrant area of inquiry and several thorough reviews highlight critical features in how emotion is experienced and displayed across cultures (see Shweder et al., 2007). Among many things, culture provides rules of appropriate and inappropriate expression (i.e., display rules) and this cultural context can shape how the body responds to emotional experiences. For example, expressions of anger may have different meanings in different cultures. In a Western culture, anger expression might indicate blocked goals and be aligned with feelings of frustration (e.g., Berkowitz, 1989). In East Asian cultures there is a strong normative prohibition to expressions of anger and tends to be reserved for those in high status or dominant positions (Park et al., 2013). Recently, Kitayama and colleagues (2015) examined two large related datasets from the US and from Japan to compare anger expression and consequent physiologic and biological health responses with the idea that because anger has different cultural rules around its expression, bodily changes associated with anger expression in the US would be more detrimental than anger expression in the Japanese context. Relying on more than 1000 US participants and more than 500 Japanese participants, Kitayama and colleagues found that the interaction between anger expression and culture was significant in predicting physiologic outcomes. Specifically, anger expression among Japanese was associated better biological health, including lower resting blood pressure, whereas in the U.S. context anger expression was associated with poorer health and higher blood pressure.

Summary

      The goal of this chapter was to review literature and theory relating to emotion and peripheral psychophysiology. If one adopted an essentialist, natural origin perspective on emotion, physiologic responses stemming from emotion would be predictable across the life span and resistant to ephemeral changes in the environment, sturdy to changes in language and labeling, and not modifiable by something as subtle as body positioning, yet across different research programs employing multiple methods there is evidence that there is flexibility in how emotions are manifested in the body. Taken together these data suggest that any emotion category for which common language applies, such as *anger, sadness, or shame*, result in a wide variety of physiological and behavioral consequences. Importantly, one should not conclude that emotion labels at this level of understanding are useless, they certainly are not, but rather that there are critical cognitive, bodily, and developmental moderators that influence the link from emotion to physiological responses. Attending to these moderatos may be as important, or even more important, than the emotion category itself.

Figure Captions

Figure 1. Sympathetic nervous system (SNS) activation associated with multiple mental states: emotional, motivational, cognitive, and acute stress.

Figure 2. Parasympathetic nervous system (PNS) changes are associated with multiple mental states: emotional, motivational, cognitive, and acute stress. Arrows indicate the direction of the PNS activation.

References

Allen, J. J. (2002). Calculating metrics of cardiac chronotropy: A pragmatic overview. *Psychophysiology*, *39*, S18

Barrett, L. F. (2006). Are emotions natural kinds? *Perspectives on psychological science*, *1*, 28-58.

Bechara, A., Damasio, H., Tranel, D., & Damasio, A. R. (1997). Deciding advantageously before knowing the advantageous strategy. *Science*, *275*(5304), 1293-1295.

Berntson, G. G., Cacioppo, J. T., & Quigley, K. S. (1993). Respiratory sinus arrhythmia: autonomic origins, physiological mechanisms, and psychophysiological implications. *Psychophysiology*, *30*(2), 183-196.

Blascovich, J. & Mendes, W. B. (2010). Social psychophysiology and embodiment. In: S. T. Fiske, D. T. Gilbert, G. Lindzey, (Eds.). *The handbook of social psychology, 5ᵗʰ Edition* (pp. 194-227). New York, NY: John Wiley & Sons Inc.

Blascovich, J., & Tomaka, J. (1996). The biopsychosocial model of arousal regulation. *Advances in experimental social psychology*, *28*, 1-51.

Cacioppo, J. T., Berntson, G. G., Larsen, J. T., Poehlmann, K. M., & Ito, T. A. (2000). The psychophysiology of emotion. *Handbook of emotions*, *2*, 173-191.

Cacioppo, J. T., Tassinary, L. G., & Berntson, G. G. (2000). Psychophysiological science. *Handbook of psychophysiology*, *2*, 3-23.

Cacioppo, J. T., Tassinary, L. G., & Berntson, G. (Eds.). (2007). *Handbook of psychophysiology*. Cambridge University Press.

Carstensen, L. L. (2006). The influence of a sense of time on human development. *Science*, *312*(5782), 1913-1915.

Carver, C. S., & Harmon-Jones, E. (2009). Anger is an approach-related affect: evidence and implications. *Psychological bulletin*, *135*(2), 183.

Cavanagh, P., & Alvarez, G. A. (2005). Tracking multiple targets with multifocal attention. *Trends in cognitive sciences*, *9*(7), 349-354.

Cole, S. W., Naliboff, B. D., Kemeny, M. E., Griswold, M. P., Fahey, J. L., & Zack, J. A. (2001). Impaired response to HAART in HIV-infected individuals with high autonomic nervous system activity. *Proceedings of the National Academy of Sciences*, *98*(22), 12695-12700.

Croizet, J. C., Després, G., Gauzins, M. E., Huguet, P., Leyens, J. P., & Méot, A. (2004). Stereotype threat undermines intellectual performance by triggering a disruptive mental load. *Personality and Social Psychology Bulletin*, *30*(6), 721-731.

Dawson, M. E., Schell, A. M., & Filion, D. L. (2007). 7 The Electrodermal System. *Handbook of psychophysiology*, *159*.

Demaree, H. A., & Everhart, D. E. (2004). Healthy high-hostiles: Reduced parasympathetic activity and decreased sympathovagal flexibility during negative emotional processing. *Personality and Individual Differences*, *36*(2), 457-469.

Denburg, N. L., Tranel, D., & Bechara, A. (2005). The ability to decide advantageously declines prematurely in some normal older persons. *Neuropsychologia*, *43*(7), 1099-1106.

Ekman, P., Levenson, R. W., & Friesen, W. V. (1983). Autonomic nervous system activity distinguishes among emotions. *Science*, *221*(4616), 1208-1210.

Epel, E. S., Burke, H. M., & Wolkowitz, O. M. (2007). The Psychoneuroendocrinology of Aging: Anabolic and Catabolic Hormones.

Gramzow, R. H., Willard, G., & Mendes, W. B. (2008). Big tales and cool heads: academic exaggeration is related to cardiac vagal reactivity. *Emotion*,*8*(1), 138.

Gross, J. J. (2002). Emotion regulation: Affective, cognitive, and social consequences. *Psychophysiology*, *39*(3), 281-291.

Grossman, P., & Taylor, E. W. (2007). Toward understanding respiratory sinus arrhythmia:

    relations to cardiac vagal tone, evolution and biobehavioral functions. *Biological*

    psychology, *74*(2), 263-285.

Guyll, M., Matthews, K. A., & Bromberger, J. T. (2001). Discrimination and unfair treatment:

    relationship to cardiovascular reactivity among African American and European

    American women. *Health Psychology*, *20*(5), 315.

Harmon-Jones, E., & Peterson, C. K. (2009). Supine body position reduces neural response to

    anger evocation. *Psychological Science*, *20*(10), 1209-1210.

Herrald, M. M., & Tomaka, J. (2002). Patterns of emotion-specific appraisal, coping, and

    cardiovascular reactivity during an ongoing emotional episode.*Journal of Personality and*

    Social Psychology, *83*(2), 434.

Iwata, J., & LeDoux, J. E. (1988). Dissociation of associative and nonassociative concomitants

    of classical fear conditioning in the freely behaving rat. *Behavioral Neuroscience*, *102*(1),

    66.

James, W. (1884). II.—What is an emotion?. *Mind*, (34), 188-205.

Kassam, K., Koslov, K., & Mendes, W. B. (2009). Decisions under distress: Stress profiles

    influence anchoring and adjustment. *Psychological Science, 20*, 1394-1399.

Kassam, K. S. & Mendes, W. B. (2013). The effects of measuring emotion: Physiological

    reactions to emotional situations depend on whether someone is asking*. PLoS ONE,* 8,

    e64959*.*

Kogan, A., Oveis, C., Carr, E. W., Gruber, J., Mauss, I. B., Shallcross, A., ... & Keltner, D.

    (2014). Vagal activity is quadratically related to prosocial traits, prosocial emotions,

    and observer perceptions of prosociality.

Kreibig, S. D. (2010). Autonomic nervous system activity in emotion: A review. *Biological*

Psychology, 84, 394-421.

Lang, P. J. (2014). Emotion's response patterns: The brain and the autonomic nervous system.
E*motion Review, 6,* 93-99.

Lang, P. J., Bradley, M. M., & Cuthbert, B. N. (1997). Motivated attention: Affect, activation, and
action. *Attention and orienting: Sensory and motivational processes*, 97-135.

Larsen, J. T., Berntson, G. G., Poehlmann, K. M., Ito, T. A., & Cacioppo, J. T. (2008). The
psychophysiology of emotion. *Handbook of emotions*, *3*, 180-195.

LeDoux, J. E. (2014). Coming to terms with fear. *Proceedings of National Academy of Sciecne,*
111, 2871-2878.

Levenson, R. W. (1992). Autonomic nervous system differences among
emotions. *Psychological science*, *3*(1), 23-27.

Levenson, R. W. (2003). Blood, sweat, and fears. *Annals of the New York Academy of*
Sciences, *1000*(1), 348-366.

Levenson, R. W. (2014). The autonomic nervous system and emotion. *Emotion Review, 6,* 100-
112.

Lieberman, M. D., Eisenberger, N. I., Crockett, M. J., Tom, S. M., Pfeifer, J. H., & Way, B. M.
(2007). Putting feelings into words affect labeling disrupts amygdala activity in response
to affective stimuli. *Psychological science*, *18*(5), 421-428.

Matthews, K. A., Woodall, K. L., & Allen, M. T. (1993). Cardiovascular reactivity to stress
predicts future blood pressure status. *Hypertension*, *22*(4), 479-485.

Mauss, I. B., Cook, C. L., Cheng, J. Y., & Gross, J. J. (2007). Individual differences in cognitive
reappraisal: Experiential and physiological responses to an anger
provocation. *International Journal of Psychophysiology*, *66*(2), 116-124.

Mendes, W. B. (2009). Assessing the autonomic nervous system. In: E. Harmon-Jones and J.S.
Beer (Eds.) *Methods in social neuroscience*, (pp.118-147). New York, NY: Guilford
Press.

Mendes, W. B. (2010). Weakened links between mind and body in older age: The case for

    maturational dualism in the experience of emotion. *Emotion Review, 2,* 240-244*.*

Mendes & Park (2014). Neurobiological concomitants of motivation states. In: *Advances in*

    Motivational Science. Academic Press (pp. 233-270).

Muhtadie, L., *Koslov, K., *Akinola M., & Mendes, W. B. (2015). Vagal flexibility: A

    physiological predictor of social sensitivity. *Journal of Personality and Social Psychology.*

Murphy, M. C., Steele, C. M., & Gross, J. J. (2007). Signaling threat how situational cues affect

    women in math, science, and engineering settings. *Psychological Science*, *18*(10), 879-

    885.

Norman, G. J., Berntson, G. G., & Cacioppo, J. T. (2014). Emotion, somatovisceral afference,

    and autonomic regulation. *Emotion Review*, *6*(2), 113-123.

Obrist, P. A. (1976). The cardiovascular-behavioral interaction—as it appears

    today. *Psychophysiology*, *13*(2), 95-107.

Oveis, C., Cohen, A. B., Gruber, J., Shiota, M. N., Haidt, J., & Keltner, D. (2009). Resting

    respiratory sinus arrhythmia is associated with tonic positive emotionality. *Emotion*, *9*(2),

    265.

Park, J.& Mendes, W. B. (2015). *Body positioning potentiates emotional responses on moral*

    decision making. Manuscript in preparation.

Porges, S. W. (2007). The polyvagal perspective. *Biological psychology*, *74*(2), 116-143.

Roberts, N. A., Levenson, R. W., & Gross, J. J. (2008). Cardiovascular costs of emotion

    suppression cross ethnic lines. *International Journal of Psychophysiology*, *70*(1), 82-87.

Seery, M. D. (2013). The Biopsychosocial Model of Challenge and Threat: Using the Heart to

    Measure the Mind. *Social and Personality Psychology Compass*, *7*(9), 637-653.

Shenhav, A. & Mendes, W. B. (2014). Aiming for the stomach and hitting the heart:

    Dissociable triggers and sources for disgust reactions. *Emotion, 14,* 301-309.

Shiota, M. N., Neufeld, S. L., Yeung, W. H., Moser, S. E., & Perea, E. F. (2011). Feeling good: autonomic nervous system responding in five positive emotions. *Emotion*, *11*(6), 1368.

Siegel, E. H., Cannon, M., Condon, P., Chang, Y., Dy, J., Quigley, K. S. & Barrett, L. F. (under review). *A meta-analytic search for autonomic signatures of emotion.*

Simmons, J. P., Nelson, L. D., & Simonsohn, U. (2011). False-positive psychology undisclosed flexibility in data collection and analysis allows presenting anything as significant. *Psychological science*, 0956797611417632.

Sloan, R. P., Bagiella, E., Shapiro, P. A., Kuhl, J. P., Chernikhova, D., Berg, J., & Myers, M. M. (2001). Hostility, gender, and cardiac autonomic control. *Psychosomatic Medicine*, *63*(3), 434-440.

Stellar, J. E., Cohen, A., Oveis, C., & Keltner, D. (2015). Affective and physiological responses to the suffering of others: Compassion and vagal activity. *Journal of Personality and Social Psychology, 108*(4), 572-585.

Stemmler, G., Heldmann, M., Pauls, C. A., & Scherer, T. (2001). Constraints for emotion specificity in fear and anger: The context counts. *Psychophysiology*, *38*(2), 275-291.

Strack, F., Martin, L. L., & Stepper, S. (1988). Inhibiting and facilitating conditions of the human smile: a nonobtrusive test of the facial feedback hypothesis. *Journal of Personality and Social Psychology*, *54*(5), 768.

Williams, L. E., & Bargh, J. A. (2008). Experiencing physical warmth promotes interpersonal warmth. *Science*, *322*(5901), 606-607.

Wright, R. A., Junious, T. R., Neal, C., Avello, A., Graham, C., Herrmann, L., ... & Walton, N. (2007). Mental fatigue influence on effort-related cardiovascular response: Difficulty effects and extension across cognitive performance domains. *Motivation and Emotion*, *31*(3), 219-231.

Wright, R. A., & Kirby, L. D. (2001). Effort determination of cardiovascular response: An

      integrative analysis with applications in social psychology.
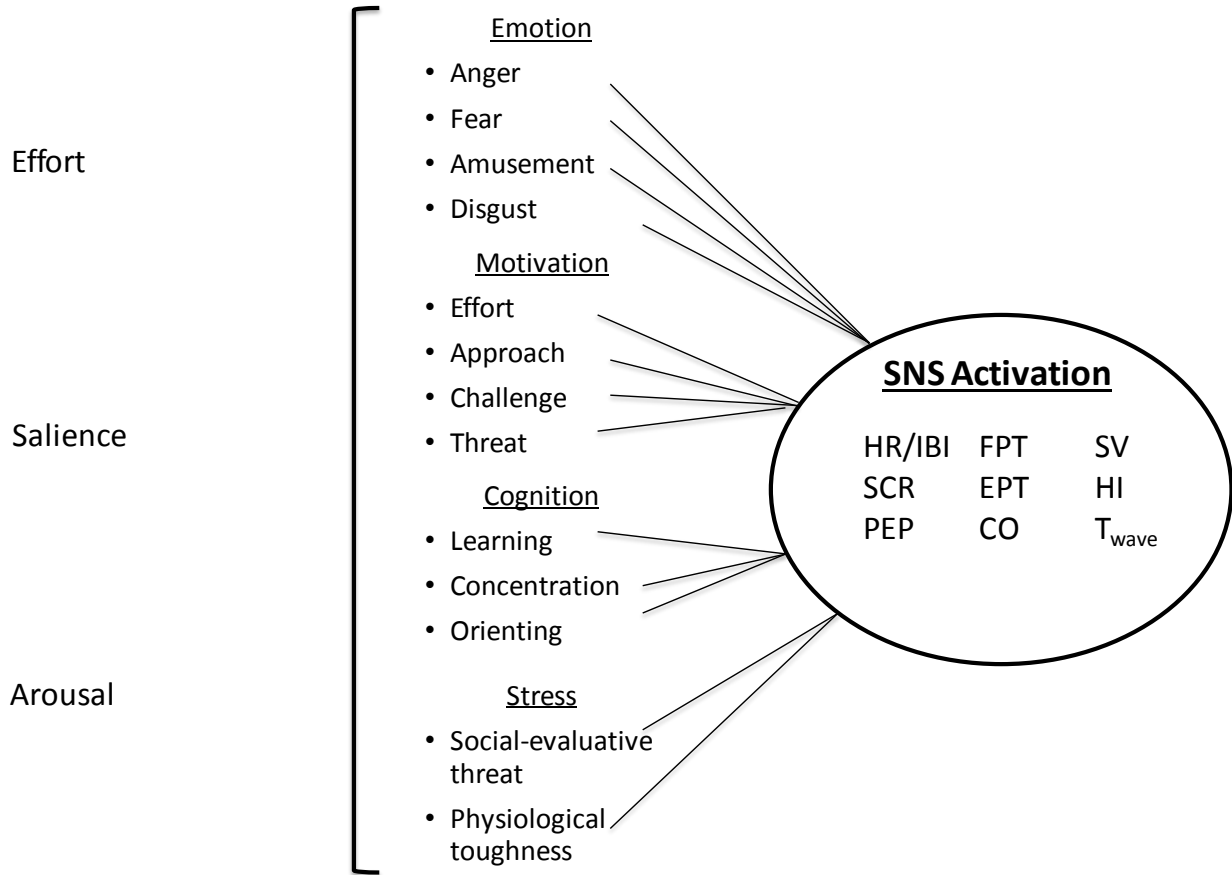
Figure 1.

Figure 2.

Attention

Effort

Relaxation

Emotion
• Anger ↓
• Compassion ↑
• Fear ↓
• Disgust ↑/↓

Motivation
• Effort ↓
• Approach ↓
• Challenge ↓
• Threat ↓

Cognition
• Attention ↓
• Mental Demand ↓
• Vigilance ↓

Stress
• Stress ↓
• Relaxation ↑

PNS Changes

HRV