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CHAPTER SIX

Neurobiological Concomitants of Motivational States

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Contents

Abstract

Core features of motivational states—approach, avoidance, engagement, and disengagement—may be reliably measured from a variety of neurobiological changes, including autonomic nervous system, neural activity, neuroendocrine systems, and cell biology. The goals of this chapter are to review various biological systems that are concomitant with distinct motivational states, and to examine overlap with and distinctions between conceptual cousins of motivation, namely emotion and stress. We then turn to moderators of the link between motivational states and neurobiology, such as context, thought processes, developmental factors, and sociocultural environments. In so doing, we offer important constraints to links between motivation and neurobiology.

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1. INTRODUCTION

Motivational states often have a fundamental feature of *action-readiness,* a behavioral response of an organism to coordinate biological systems to move towards or away from a stimulus. To accomplish these behavioral responses, multiple neurobiological systems are activated and coordinated, which include fast-acting systems such as neural activation and the autonomic nervous system (occurring within seconds); slower-acting systems like the neuroendocrine, immune, and enteric systems (taking minutes to hours); and even slower responses that reflect chronic activation such as changes in oxidative stress and cellular structure (developing over months to years). Our goals here are to review and present an integrative systems model of motivation that incorporates the neurobiology that undergirds motivational states and examine how the underlying biology of motivational states is constrained and influenced by context, thought processes, developmental changes across the life span, and sociocultural environments (Figure 1). The goals of this type of review and integration are certainly bold, and we admittedly do not come close to achieving the complexity of integrating an exhaustive biological systems approach to the neurobiology of motivation. However, we hope this review and integration provides a primer to those in motivational science to consider how best to integrate

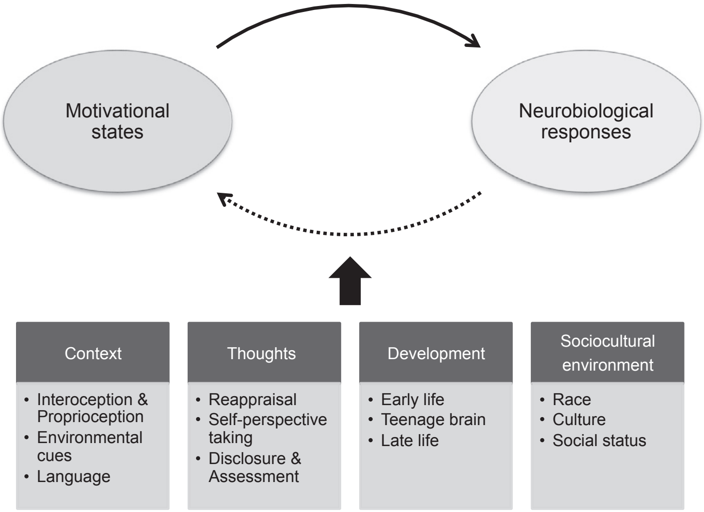

Figure 1 Links from motivational states to neurobiological changes are moderated by context, thoughts, development, and sociocultural environment. Solid line indicates stronger evidence of linking motivational states to neurobiological responses than the dotted line leading from neurobiological responses to motivational states.

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neurobiology within motivational models and theories, and advances the discussion regarding what motivation science learns from a biological systems approach.

Motivational states—like approach, avoid, engage, and disengage—are core processes apparent across the animal kingdom, observable early in development, and retained across the life span. Motivational responses run the gamut from reflexive actions that require little or no conscious involvement to more deliberate, consciously controlled responses that are planned and executed. Considering both the reflexive and controlled responses, many theories consider how core motivational states can be detected and differentiated with a variety of neurobiological responses. Even with this vast literature examining motivational states and their concomitant neurobiological responses, it is rare to find theories that attempt to integrate different biological systems to chart the neurobiology of motivation and the various boundary conditions and moderators of the relations between motivational states and biological responses. This is particularly surprising given the large literature in two fields closely related to motivation, specifically emotion and stress, which tend to consider biological responses as *sine qua non* to the affective states.

Here, we consider affect as an umbrella term that encompasses motivation, stress, and emotion (cf. Gross, in press). Noted theorists have offered extensive thoughts on how these constructs are distinct and when they are overlapping (e.g., Carver & Harmon-Jones, 2009; Lang, 2014), and we will not revisit these boundary conditions extensively here. Rather, we use the starting point that these affective constructs have both distinct and overlapping features, and when neurobiological responses converge or diverge across these constructs, it can advance our understanding of these affective states.

1.1 Emotion and Neurobiology

A perusal of some of the classic review papers and chapters on emotion and neurobiology reveals a common thread: the evoking of William James' quote on the boundary condition 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 emotional states.

Even though neurobiological responses are widely integrated in emotion theories, there remain hotly debated theoretical perspectives on how best to conceive of emotions and concomitant neurobiology: 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 there are contexts that trigger core physiological responses and this combination of core responses (i.e., "ingredients") comprises larger constructs that are then labeled with emotion words (e.g., Barrett, 2006; Cacioppo, Berntson, Larsen, Poehlmann, & Ito, 2000; Kreibig, 2010; Levenson, 2014). Specifically, emotion researchers have long disputed the existence of autonomic specificity, which is the idea that discrete emotions, especially the "basic emotions," have a specific patterning of physiological responses that differentiate states like anger, fear, disgust, sadness, and happiness (e.g., Ekman, Levenson, & Friesen, 1983; Kreibig, 2010). The strong version of this argument is that patterned physiological responses to an emotional experience occur across human and nonhuman animals, persist across the life span, and are unmodified by context. Over the past few decades, much has been written in support of and against this strong version of the autonomic specificity of emotions (see Lang, 2014; Levenson, 2014; Norman, Berntson, & Cacioppo, 2014; for a discussion).

Evidence against this view comes from meta-analytic approaches showing support for autonomic nervous system (ANS) relations to broader dimensions like valence, intensity, and motivational states rather than discrete emotion categories (Cacioppo et al., 2000; Larsen, Berntson, Poehlmann, Ito, & Cacioopo, 2008). Additionally, there are empirical data that show different patterns of physiological responses to presumably the same emotion category. For example, we (Shenhav & Mendes, 2014) randomly assigned participants to watch two different videos: one video showed individuals suffering painful injuries and accidents in which legs and arms were twisted or contorted, but no breaking of the body envelope occurred (e.g., no blood); the other video showed individuals with body envelope violations, eating disgusting things, emissions of blood, puss, and vomit. Participants in both groups labeled the emotion they were feeling as "disgust" more than any other emotion, and significantly more than the control participants. However, participants watching body envelope violations showed decreases in electric gastric changes and heart rate acceleration, whereas the painful injuries were associated with no changes in gastrointestinal responses and heart rate deceleration. Consistent with this, the *context* in which emotions are examined can alter the physiological responses more than the specific emotion experienced (Bradley & Lang, 2007; Lang, Bradley, & Cuthbert, 1997).

Arguably, what does seem to emerge in most meta-analytic approaches is support for broader categories showing physiologic patterning. 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 the general motivational tendencies embedded within emotional states showed 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 the sympathetic nervous system (SNS) than emotional states in which no expectation of energy reserves is expected. This perspective is evident in animal research as well. LeDoux's previous work on how the brain detects threats and the identification of "fear systems" has been called "a mistake that has led to much confusion" by LeDoux (2014, p. 2871) himself. Instead, LeDoux argues that his work shows reflexive motivational responses linked to threat detection and defense responses more akin to motivation than emotion states.

One way to draw sharper distinctions between emotion and motivation is the concept of *active* versus *passive* situations. Emotions are often *active,* happening to the individual, but emotions also can be experienced vicariously or in response to another's suffering, and as such, emotions can be *passive* (i.e., observed rather than experienced). Paralleling this point, it is common for emotion researchers to study emotion experiences using passive stimuli—watching videos to evoke emotion, looking at still facial expressions of emotions in photographs, observing someone else's emotion (Gross & Levenson, 1995). In contrast, it is rare for researchers to study motivation in a passive setting. Instead, simulated or actual testing conditions are more likely used to assess performance behaviors associated with certain motivational processes. (e.g., Elliot & Church, 1997; Hulleman & Harackiewicz, 2009; Tauer & Harackiewicz, 2004). As we will review later, active situations are more likely to trigger system-wide biological changes and thus may lead to affective states that are easier to differentiate with neurobiological responses.

1.2 Stress and Neurobiology

Stress research also relies on biological responses as a primary source of measurement, and many theories use biological systems as the starting point to understand stress experiences (Epel, McEwen, & Ickovics, 1998; McEwen, 2006; Sapolsky, 1996). For example, two biological systems—the hypothalamic pituitary adrenal (HPA) axis and the sympathetic adrenal medullary axis—are referred to as the two primary *stress* systems even though these systems activate and are responsive to many internal and external changes that have little, and sometimes nothing, to do with the affective state of *stress*. Although not as bold (or as controversial) as the search for the neurobiological specificity of emotions, stress researchers have attempted more sophisticated approaches to examining the neurobiology of stress by adapting two approaches that are relevant to the review here: (1) differentiating "positive stress" from "negative stress" and (2) creating a combined index across biological systems to better estimate the effects of stress, which provides a glimpse into the multiple systems approach to understanding integrated neurobiology.

The concept of "positive stress" was offered by the scientist often considered to be the father of stress research, Hans Selye, who noted that *eustress,* a positive outcome resulting from environmental stressors, could confer protective health benefits (Selye, 1974). The idea of a positive side of stress is apparent in most major stress theories even if it is far less studied than the damaging effects of stress. Epel and her colleagues, for example, suggested that chronic stress, which can result in severe mental and physical health ailments, might, in some cases, result in *thriving* or improved physiologic responses and health (Epel et al., 1998). These perspectives suggest that when examining acute and chronic responses associated with stress responses, a comprehensive approach is to look at both catabolic and anabolic hormones. Catabolic hormones, like cortisol, break down muscle and tissue, whereas anabolic hormones are associated with growth and rebuilding. Along these lines, researchers now are more commonly including anabolic hormones, adrenal steroids and counter-regulatory hormones, like insulin-like growth factor, growth hormones (GH), dehydroepiandrosterone (DHEA/DHEAs), testosterone (T), and neuropeptide Y (NPY), to provide a more complete examination of how individuals respond to stressors (see Epel et al., 1998; Southwick, Vythilingam, & Charney, 2005 for reviews). For example, basal states (homeostatic or resting levels of circulating hormones) have been associated with resilience in both field and lab studies. In one study of special force soldiers during extreme training stress, those with higher levels of NPY showed better psychological and physical performance throughout their intense training regime (Morgan, Cho, Hazlett, Coric, & Morgan, 2002). In a laboratory study of young adults, lower baseline levels of DHEAs showed heightened vulnerability to experiencing negative affect in the context of threatening social situations involving social rejection (Akinola & Mendes, 2008). Thus, by considering different classes of hormones beyond catabolic ones, researchers can gain traction on when (or for whom) stressful contexts can result in improved health and performance.

Another approach to examining "biological stress" incorporates a cross-systems approach to obtain a composite score of chronic stress—*allostatic load* (Geronimus, Hicken, Keene, & Bound, 2006; McEwen, 2006; Seeman et al., 1997). Conceptually, the idea behind allostatic load is that multiple biological systems interact and respond to chronic stress and that higher levels of allostatic load indicate problems with the body maintaining *allostasis*—the benign response the body has to maintain homeostasis. Allostatic load is measured with 10 (relatively) independent biological measures and a single composite score is calculated from: resting systolic and diastolic blood pressure, body mass index, glycated hemoglobin, albumin, creatinine clearance, triglycerides, c-reactive protein, homocysteine, and total cholesterol. The purported value of this type of composite is that when widespread alterations of biology occur from extended stress or individuals' perceived stress, the total amount of damage is indicated by a higher total index.

Motivation science sits at the nexus of the emotion and stress literature and may provide the bridge that profitably links these affective states to neurobiology. For example, if we consider the extremes of "lumping" and "splitting," stress science has too easily "lumped" all physiological reactions into a unidimensional construct of *stress* often ignoring the beneficial responses that can occur. In contrast, emotion science has too readily "split" emotional states and searched for unique neurobiology for each specific emotion, when they might benefit from grouping them based on their shared core processes (e.g., Barrett, 2006). Like Goldilocks and exemplar theory, motivational states might then represent the "just right" level of analysis to relate neurobiological responses.

2. BIOLOGICAL SYSTEMS UNDERLYING MOTIVATIONAL STATES: MOOD RINGS, TEA LEAVES, AND PSYCHOPHYSIOLOGY

Imagine you could read people's minds. Without having to ask them how they feel or discern the meaning of their body position or facial expression, you could accurately detect the affective state of a person. Is the person disengaged, paralyzed, exhilarated, intrigued, or bored? This mind reading would extend to affective states that the person is currently unaware that he or she is feeling. In part, this is the promise of using neurobiological measures to detect mental states unobtrusively and continuously with great precision. Additionally, the physiologic changes that occur might explain (mediate) the behavior stemming from the motivational state or relate to important distal outcomes like mental or physical health. But just like mind reading, tea leaves and mood rings, there is plenty of rightful skepticism regarding the precision of psychophysiological methods and what exactly the changes in physiology refer to at the psychological level. Does a specific physiological change always indicate the presence of a mental state? Does a mental state always produce the specific change in physiology? Although the literature, as well as common sense, suggest the answers are "no" to these questions, the challenge is to determine *when* and *how* neurobiology can advance the study of motivation. We consider these questions as we review psychophysiological theory of inference and the extant data on the neurobiology of motivation.

To begin to consider the relation between motivational states and neurobiological responses, it is useful to first consider how psychophysiological inferences are made and the principles regarding how to infer motivational states from physiological responses. A more in-depth discussion can be found in each edition of the *Handbook of Psychophysiology* (Cacioppo et al., 2000, p. 2010); here, we review the critical features of psychophysiological inference as it relates to motivation science.

Psychophysiological theory is built around the *identity thesis*—that thoughts, feelings and intentions are *embodied*—which is to say that an affective state results in some detectable change in the body. This is a general statement with no specificity with regard to the direction of the change, how long the change needs to occur, whether the mental state needs to be consciously perceived or can be below conscious awareness, or which physiological system or systems are activated. Given this, how does one begin to use neurobiology to infer motivational states?

There are many obstacles inherent in psychophysiological inference. For example, there are different kinds of mental states that result in the same change in neurobiology. HPA activation can occur during tasks with sustained mental effort, events that are important and intense, or in tasks that are socially evaluative and threatening (Dickerson & Kemeny, 2004; Lovallo & Thomas, 2000). Similarly, SNS activation can occur in motivational states that are approach-oriented, but threat and avoidance can also activate an SNS response (Blascovich & Mendes, 2010). Even affective states like love and hate, that is, diametrically opposed states, can engender similar SNS increases. Parasympathetic withdrawal can index negative affect, but it can also result from mental effort and attention (Demaree & Everhart, 2004; Kassam, Koslov, & Mendes, 2009). Our point is that just because one finds evidence that a psychological state co-occurs with a certain physiological response does not mean that the presence of the physiological change indicates that the psychological state occurred (what neuroscientists refer to as *reverse inference*).

Of course, there are ways to increase inferential precision by measuring a broader net of physiological responses, examining changes over time, and/or constraining the context in which the affective state is examined. Examining the direction of change (increase or decrease) and the temporal trajectory (fast onset with slow habituation, slow onset with fast habituation, etc.) across different biological systems (SNS, PNS, HPA, etc.) can provide greater inferential precision. With more attention to the intensity of responses, temporal trajectories, and multiple responses, it might be possible to isolate the suite of responses that are more consistently associated with a specific motivational state.

A number of biological systems have been implicated in motivational states, including the SNS and PNS, hemodynamic, enteric, neuroendocrine, immune, gonadal, and, of course, neural systems[1] (Table 1). A common feature of these biological systems is that their *primary* functions have little, if anything, to do with motivation. The SNS is designed to provide oxygenated blood to the brain and body to support movement; the parasympathetic system provides coregulation of the SNS and supports homeostasis during sleep and helps digest food, and the gastrointestinal system breaks down food for energy and excretes waste. A mammal's heart rate might slow down when freezing in response to detecting a predator, vagal withdrawal might occur when engaged in sustained attention, or gastrointestinal contractions might decrease when exposed to a substance that signals avoidance, but the presence of any physiological changes by themselves do not indicate that a motivational state has occurred. Biological systems *can be* co-opted by motivational tendencies, which provide the foundation for these systems to be examined with a psychophysiological lens, but the presence of changes in any of these systems does not indicate that an organism is experiencing a specific motivational state (and the reverse is true as well). The constraints

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[1] We limit our review to neural responses collected with EEG technology, rather than also considering imaging research, in order to keep the chapter to a reasonable length. An excellent review of imaging studies linked to motivational states can be found in Beer (2012).

Table 1 Summary of neurobiological responses associated with motivational states

	Approach	**Avoid**	**Effort**
Synonyms/Related constructs	Challenge Activation Appetitive	Threat Inhibition Withdrawal Defensive	Attention Mental demand Engagement Vigilance
Basal/Resting state			
Autonomic nervous system		• lower HRV (cardiac vagal tone)	
Neuroendocrine	• higher T • higher T & lower cortisol	• lower DHEAs	
Immune/cell biology	• longer telomeres • more telomerase		
Neural responses	• greater left frontal cortical activation	• greater right frontal cortical activation	
Reactivity			
Autonomic nervous system	• large increases in SNS (HR, PEP, SC)	• Immediate SNS decreases • Delayed moderate increases in SNS • decreased HRV	• moderate increases in SNS (HR, SBP) • decreased HRV
Neuroendocrine	• moderate cortisol increases • increased T • increased anabolic hormones	• increased cortisol	• moderate cortisol increases • moderate T increases
Immune/cell biology	• longer telomeres • more telomerase	• increases in TNF-α • shorter telomeres	
Neural responses	• shifts to more left vs. right frontal	• error-related negativity	

HRV, heart rate variability; SNS, sympathetic nervous system; HR, heart rate; T, testosterone; DHEAs, dehydroepiandrosterone; SBP, systolic blood pressure.

on psychological inference from physiological states is neither a new nor a resolved problem that has plagued psychophysiology from its inception, and can, in some cases, greatly limit the value of using physiology to understand motivation.

We do not mean to set a pessimistic tone; in stark contrast, we believe the literature indicates that there is tremendous value in examining physiological responses to motivational states. However, in adopting the biological systems approach, we acknowledge upfront that one-to-one invariants (i.e., a motivational state that results in a change in a physiological response that exists across cultures, contexts, and people) of psychological states and physiological changes are rare and, possibly, nonexistent. The pursuit of invariants between motivation 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 and intensity of a motivational state, regardless of any situational or individual difference factor—but it might be futile. Instead, a deep understanding of the myriad factors that influence physiological responses to motivational states, along with an appreciation of the developmental, physical and environmental factors that influence physiology can enable researchers to augment their understanding of how neurobiology and motivation are related.

2.1 Autonomic Nervous System

The ANS comprises two major branches: sympathetic and parasympathetic nervous systems (SNS and PNS), both of which are relevant to motivational states, although measures used to assess changes in these systems often represent hybrid responses that are influenced by both systems simultaneously. 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 related ones: enteric, vascular, and hemodynamic. In this section, we review common ANS measures used to index motivational states and the current state of theoretical and empirical development that can be brought to bear to understand how and why this wide-ranging peripheral system is so intimately tied to motivational states.

As noted above, the SNS functions 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 can occur with physical exertion, like sprinting or aerobic exercise. But this system also activates in *nonmetabolically demanding* situations (ones that do not, by necessity, require an increase in oxygenated blood). One of the most influential theories examining how

SNS responses (and HPA activation) relate to motivational states comes from Richard Dientsbier's work on physiological toughness (1989). Arguing against the zeitgeist of the time—that increases in SNS arousal were fundamentally maladaptive and associated with poor cognitive and behavioral performance—Dientsbier reviewed decades of non-human animal and human studies supporting the claim that strong increases in SNS responses during active tasks were related to better physical and cognitive performance. For example, in studies of school aged children in Scandinavian counties who were about to take a standardized test, the larger the increase in epinephrine the better the performance (Johansson, Frakenhaeuser, & Magnusson, 1973; Rauste-von Wright, von Wright, & Frakenhaeuser, 1981). Thus, greater SNS mobilization was linked to better cognitive performance, directly contradicting the inverted-U arousal-performance link popularized by the Yerkes–Dodson model (1908), which argued that at higher levels of arousal[2], performance was impaired. Dientsbier concluded his review of the positive linear relation between SNS arousal and test performance by stating "despite the high difficulty level of…these tasks…these data indicate *no curvilinear relations*; naturally evoked peripheral catecholamines *never seem to be too high* for optimal performance" (emphasis added, p. 86).

2.1.1 Cardiovascular Theories

Challenge and threat theory is a direct descendent of Dientsbier's theory of physiological toughness; its origin is in motivational theory (Blascovich & Mendes, 1999, 2010; Blascovich & Tomaka, 1996; cf. Wright & Kirby, 2003), though it has been applied to both stress (Mendes et al., 2007a O'Donovan et al., 2012) and emotion research (Herrald & Tomaka, 2002; Kassam & Mendes, 2013; Mendes et al., 2008). The basic premise of this theory is that appraisals of situational demands and personal resources to cope with such demands combine to engender a general motivational state of *challenge,* an approach-oriented response, or *threat,* an avoidant response. These motivational states can be differentiated with cardiovascular reactivity, and, possibly, neuroendocrine changes.

The context to observe these motivational states is highly specific and has been labeled *motivated performance situations,* which are defined as *active* tasks that require instrumental cognitive responses, and are self- or goal relevant.

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[2] The inverted-U function may be apparent in other biological systems. For example, at very high levels of HPA activation the low affinity receptors in the hippocampus bind to glucocorticoids, which can impair memory.

This specification excludes situations that are passive (watching a video or vicarious responses) and situations in which people are not invested in the task or are not personally relevant. To determine if the situation constitutes a motivated performance situation, task engagement is determined by examining whether SNS activation occurs, which requires testing SNS increases from a resting state to during the task. Once task engagement is confirmed, the differentiation between *challenge* and *threat* follows.

Psychologically, *challenge* states occur when personal resources are perceived to outweigh situational demands, and the concomitant physiological changes include greater heart efficiency (increased cardiac output) and decreased vascular resistance (declines in peripheral resistance). In contrast, *threat* states are concomitant with a cardiovascular profile of less heart efficiency (increased SNS, but no changes in heart blood flow) and increased vasoconstriction, which reduces the amount of oxygenated blood in the periphery (Mendes, 2010).

Research over the past two decades has shown that antecedents of *challenge* and *threat* states include (respectively) downward and upward social comparisons with similar others (Mendes, Blascovich, Major, & Seery, 2001), interactions with in-group compared to out-group racial partners (Blascovich, Mendes, Hunter, Lickel, & Kowai, 2001; Mendes et al., 2008), social interactions with typical versus atypical partners (Mendes et al., 2007b), oxytocin compared to placebo manipulations prior to a stressful task (Kubzansky, Mendes, Appelton, Block, & Adler, 2012), manipulations of high power versus low power (Akinola & Mendes, 2014; Scheepers, de Wit, Ellemers, & Sassenberg, 2012), and positive compared to negative social feedback (Kassam et al., 2009; Mendes et al., 2008). Furthermore, individuals who are characterized by resilient personality profiles are more likely to experience *challenge* than *threat* when confronted with novel "stressful" situations. For example, individuals with higher stable self-esteem (Seery, Blascovich, Weisbuch, & Vick, 2004) and those with greater belief in a just world (Tomaka & Blascovich, 1994) are more likely to exhibit a profile of cardiovascular responses consistent with *challenge* states than *threat* states.

Another motivational theory relying on cardiovascular reactivity is effort mobilization theory (Wright & Kirby, 2001), which integrates principles from Brehm's motivational intensity theory (Brehm & Self, 1989) and hemodynamic responses. This theory maintains that effort will increase monotonically with task difficulty and can be indexed by SNS activation (typically measured with systolic blood pressure and to a lesser extent heart rate changes). However, as task difficulty approaches and then exceeds ability, disengagement occurs and effort will no longer be exerted. Considerable evidence has amassed supporting the effort mobilization perspective (Wright & Kirby, 2001). Taken together, these theories underscore the value of examining cardiovascular responses as indexes of task engagement and effort, as well as identifying general approach and avoidance motivational states.

2.1.2 Heart Rate Variability

A typical adult human heart beats about 80 times per minute, but the heart does not beat like a metronome; instead, the interval between each heart rate is variable. Initially, heart rate variability (HRV)—the time interval that occurs between each heart beat—was believed to be a measurement artifact, 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 the measurement, quantification, and psychological meaningfulness of HRV, these variability measures might prove to be especially important for motivational scientists interested in indexing mental effort and, possibly, other motivational states (see *Biological Psychology, 2007, volume 74*).

Though most work has focused on resting/baseline HRV (cardiac vagal tone) and its links to dispositions and socioemotional contexts, research examining HRV reactivity (changes in cardiac vagal tone) is especially relevant to motivation science. One theory that has received much attention in terms of the inferences one can draw from HRV is Porges' polyvagal theory (Porges, 2007). This theory argues that primates uniquely have cardiac vagal nerve modulation (cf. Grossman & Taylor, 2007), which has evolved as part of the social engagement system. One of the primary postulates of polyvagal theory is that social factors (affiliation, social engagement) or personality factors (optimism, bonding, compassion) can modulate cardiac vagal responses. Specifically, Porges argues that greater HRV can be used as an index of adaptive regulation and responsiveness to the social environment.

Adding some complexity to interpreting HRV changes, however, is the context. In highly stressful situations or tasks that require mental attention or effort, the vagal brake withdraws, resulting in lower HRV. Indeed, cognitive psychophysiologists have used HRV decreases to index attention and vigilance (Tattersall & Hockey, 1995). 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 better performance on a decision making task. Decreases in

HRV have also been interpreted with regard to mental effort with a negative valence—specifically, mental load. For example, Croizet et al. (2004) examined changes in HRV during a stereotype threat paradigm and reported that participants assigned to a stereotype threat prime evidenced greater decreases in HRV and poorer performance than those in the control condition, and the HRV decreases mediated the relationship between stereotype threat and performance.

HRV decreases are also interpreted as stemming from negative affect or distress. This interpretation was applied to study implicit goal setting in an academic environment. In previous studies, participants who exaggerated reports of their grade point average (GPA) tended to improve their GPA in subsequent semesters more than those who did not exaggerate (Willard & Gramzow, 2008). However, an open question was whether exaggeration was benign and serving a type of implicit goal setting or instead exaggeration was a form of anxious repression. To examine this question, participants first relaxed so their resting HRV could be obtained (with electrocardiography and respiration). Participants then reported their GPA and course grades in private, and then met with an experimenter to review their academic history (Gramzow, Willard, & Mendes, 2008). Differences in HRV between the resting baseline and the interview were calculated. Participants who exaggerated their GPA during the interview showed greater HRV increases from baseline to the interview, suggesting that these individuals were not necessarily anxious about exaggerating their achievements. Additionally, these individuals, who had greater increases in HRV when discussing their GPA, tended to improve their GPA in a subsequent semester. Converging evidence from nonverbal behavior coded during the interview also suggested that exaggerators appeared composed rather than anxious, supporting the interpretation that greater increase in HRV while discussing one's GPA was associated with equanimity rather than anxiety.

The difficulty in inferring what psychological states lead to changes in HRV is further compounded because the contexts in which researchers measure HRV often include a mix of features (e.g., attention, valence) leading to what Lang bemoaned as a "moving target" in psychophysiological research (Lang, 2014). In a recent study, we attempted to avoid this contextual confounding by measuring HRV changes using a purely attentional task—a visual tracking task—that was devoid of any social or emotional content (Muhtadie, Koslov, Akinola, & Mendes, in press). We then calculated difference scores reflecting the ability to withdraw the vagal brake to capture an individual difference in *vagal flexibility*, and used that measure to predict social and emotional functioning. Across four studies, this work showed that vagal flexibility is a reliable individual difference biobehavioral index that can be elicited consistently in the laboratory, occurs reliably within-individuals over time, and provides unique and socially specific information beyond that provided by vagal tone. Furthermore, we found that vagal flexibility was associated with more accurate detection of social-emotional cues in still facial images, and predicted greater awareness of, and more sensitive affective, behavioral, and physiological responding to social cues during a dynamic interpersonal interaction. Thus, individual differences in the ability to show sustained attentional effort (as indexed by vagal flexibility) were related to greater social and emotional sensitivity.

2.2 Neural Activity: Electroencephalogram

Neural processes associated with motivational processes are commonly measured via electroencephalogram (EEG)—the recording of electrical activity along the scalp produced by the firing of neurons within the brain (Niedermeyer & da Silva, 2005). Due to its high temporal resolution, EEG enables more rapid, online observation of neural responses underlying motivational processes than is possible with traditional behavioral measures or other neuroscience techniques such as functional neuroimaging. In the following section, we discuss two notable themes of motivational processes measured with this technique: (1) approach motivation measured as relative left frontal cortical activation, and (2) defensive motivational responses assessed with error-related negativity (ERN).

2.2.1 Relative Left Frontal Activity and Approach Motivation

Three decades of past work has suggested that asymmetry in frontal cortical activation is meaningfully associated with individual differences in psychological tendencies. Much of this work has focused on the relations between relative left or right frontal cortical activation and emotional experience. Broadly speaking, findings from this line of work initially converged to suggest that relatively greater left frontal activity was related to positive affect, whereas relatively greater right frontal activity was related to negative affect (see Coan & Allen, 2004; Davidson, 2000; Fox, 1991 for reviews).

However, an alternative point of view emerged to explain the asymmetry findings, which directly implicated motivational states of approach-avoidance. The catalyst for this view stemmed from the observation that previous studies linking emotional experiences to differential patterns of frontal activity confounded the valence of emotion (positive or negative) with its motivational orientation (approach or avoidance) such that the positive emotions examined in prior work involved approach motivation (e.g., joy, pride), whereas the negative emotions involved avoidance motivation (e.g., fear, guilt) (Harmon-Jones & Harmon-Jones, 2011). Thus, to tease apart the effects of emotional valence and motivational orientation on asymmetrical frontal cortical responses, it was critical to examine emotional and motivational states orthogonally.

By considering anger, a negatively valenced but approach-oriented emotional state (Berkowitz, 1999; Ekman & Friesen, 1975; Harmon-Jones, 2003), researchers were able to overcome the valence-motivation confound. In a series of studies, Harmon–Jones and colleagues found that both trait and state anger were related to increased left (vs right) frontal activation, measured with EEG (based on power in alpha band; 8–13 Hz), thereby supporting the view that asymmetry in frontal activation better reflects approach vs avoidance motivation rather than positive vs negative affect per se. Specifically, they found that self-reported trait anger was positively correlated with increased left frontal activity during a resting baseline (Harmon-Jones, 2004; Harmon-Jones & Allen, 1998), and this effect replicated when state anger was experimentally induced. Specifically, when participants received negative feedback from an evaluator on their essays, they showed greater relative left frontal activity compared to those who received neutral feedback (Harmon-Jones & Sigelman, 2001; Harmon-Jones, Vaughn-Scott, Mohr, Sigelman, & Harmon-Jones, 2004). Moreover, the increased relative left frontal activity following the anger manipulation was positively correlated with self-reported feelings of anger (Harmon-Jones & Sigelman, 2001).

Extending this work, we examined how healthy individuals who showed more left frontal activity at rest would respond to an acute social evaluative stressor (Koslov, Mendes, Patjas, & Pizzagalli, 2011). If greater left frontal cortical activation was associated with more general approach tendencies, then this biobehavioral individual difference might confer adaptive responses when confronted with a novel, acute stressor. We measured resting EEG prior to completing a standardized social stressor that included giving an impromptu speech to a panel of stoic evaluators followed by a question and answer session, while we measured cardiovascular indicators of *challenge* and *threat* motivation (cardiac output and total peripheral resistance). As expected by the motivational interpretation of frontal cortical asymmetry, participants who showed greater relative left frontal activation at rest were more likely to show a pattern of *challenge* responses during the acute stressor, whereas those with greater relative right frontal activation showed more *threat* responses. These data provide suggestive evidence that for healthy adults, left asymmetry may confer psychological benefits by its association with more adaptive physiological responses during stress.

In this section we reviewed research that suggests that asymmetry in frontal cortical activation is a useful neurophysiological index of motivational states associated with approach or avoidance, independent of emotional valence. This motivational model of frontal cortical asymmetry has been supported by several lines of research, linking greater relative left frontal activity to anger experience, behavioral activation system activity, and challenge (vs threat) motivation. Next, we turn to another important motivational process—defensive motivational response—indexed by ERN.

2.2.2 Error-Related Negativity and Defensive Motivational Responses

ERN is a response-locked event-related brain potential involved in error processing (Falkenstein, Hohnsbein, Hoormann, & Blanke, 1991; Gehring, Goss, Coles, Meyer, & Donchin, 1993), which originates from the anterior cingulate cortex (Debener et al., 2005). It is observed as a negative voltage deflection that is maximal at fronto-central electrode sites and peaks approximately 50–100 ms following erroneous responses in choice response time tasks. Although the ERN is commonly conceptualized as reflecting cognitive processing, such as response mismatch (Bernstein, Scheffers, & Coles, 1995), conflict monitoring (Botvinick, Braver, Barch, Carter, & Cohen, 2001), or reinforcement learning (Holroyd & Coles, 2002), recent investigations suggest that it also reflects affective or motivational responses to unfavorable outcomes such as perceived threat (Hajcak, 2012; Weinberg, Riesel, & Hajcak, 2012). For example, Weinberg, Riesel, & Hajcak (2012) recently proposed that errors are motivationally salient events that can pose a threat to individuals, and the ERN is a neurophysiological signal of the defensive motivational system that is activated in response to such threat.

Consistent with this model, one recent study shows that the size of the ERN is positively associated with defensive startle reflexes, a common bodily reaction to threat (Hajcak & Foti, 2008). Similarly, individual differences in defensive reactivity modulate the magnitude of the ERN. People who are more vigilant and sensitive to threat-related cues, such as those with high trait anxiety (Hajcak, McDonald, & Simons, 2003; Pourtois et al., 2010) or high negative affect (Hajcak et al., 2004; Luu et al., 2000), those with greater behavioral inhibition system sensitivity (Boksem et al., 2006), and patients with obsessive-compulsive disorder (Endrass et al., 2008; Gehring et al., 2000), show enhanced ERN compared to those who are less sensitive to such cues.

Increasing evidence also suggests that not only trait-level but also state-induced defensive motivational reactivity modulates the ERN. That is, when errors are increased in their threat value or aversiveness, ERN magnitude is also increased. One study demonstrated this effect by showing that task instructions that emphasized accuracy over quickness enhanced the size of ERN (Gehring et al., 1993). More recent work found that when the motivational significance of errors was manipulated by rewarding participants with different amounts of incentives across trials (i.e., earning 5 vs 100 points), errors made on the trials associated with high (vs low) monetary reward produced larger ERNs (Hajcak et al., 2005). Likewise, experimentally inducing stereotype threat by asking minority students to perform an "intelligence test" significantly increased ERN only among those who were highly identified with academics and thus more vulnerable to stereotype threat (Forbes et al., 2008). Similarly, performing a computer task under social evaluative threat enhances the size of the ERN, especially among socially anxious, interdependent individuals who are more vigilant to such type of threat (Park and Kitayama, 2014).

Conversely, given the link between heightened defensive reactivity and enhanced ERN, it may be anticipated that the magnitude of the ERN will be attenuated after manipulations designed to provide a sense of security or safety. This prediction was tested in recent studies by Inzlicht and colleagues. For example, when primed with religious beliefs, which is likely to reduce threat perception, people show smaller ERN (Inzlicht and Tullet, 2010). Similarly, when participants were given an opportunity to misattribute the source of negative arousal/threat arising from error commission to a benign external factor, the size of their ERN was significantly reduced (Inzlicht and Al-Khindi, 2012). An increasing body of work then suggests that the ERN not only reflects cognitive processing such as response mismatch or conflict monitoring, but also reflects neural responses to the motivational salience of errors that are significantly modulated by defensive reactivity varying across both individuals and situations.

2.3 Neuroendocrine

Two neuroendocrine systems, the HPA and the hypothalamic–pituitary–gonadal axis (HPG) represent the most typically examined neuroendocrine systems in motivation science. The HPA system is typically measured with its end product, cortisol, and is obtained reliably from blood, saliva, and urine. The underlying biological pathway starts with signals received at the hypothalamus that triggers the release of corticotrophin releasing hormone (CRH). CRH then triggers the pituitary to release adrenocorticotropic hormone which stimulates the adrenals to release hormones, including cortisol. Cortisol is commonly examined by stress researchers who compare cortisol levels during a resting state to cortisol levels following exposure to an affectively-charged event. A meta-analysis of 208 studies examining cortisol reactivity identified the antecedents that most reliably led to a cortisol increase (Dickerson and Kemeny, 2004). Relevant to motivation science are the findings that passive tasks (like noise exposure or watching scary films) did not reliably increase cortisol responses, but tasks that were active with elements of uncontrollability and/or social evaluation reliably led to increases in cortisol. Although lay perceptions of cortisol conceive of it as the "stress hormone," it is important to point out that cortisol increases do not invariantly relate to negative affect as the "stress" label suggests. Instead, cortisol increases can occur during mentally demanding and active tasks that lead to approach-behavior (or challenge; Dientsbier, 1989; Koslov et al., 2011; Lovallo and Thomas, 2000). Also, the context most often studied among researchers interested in cortisol reactivity is a standardized stressor called the Trier Social Stress Task that requires participants to give a speech and complete a difficult mental arithmetic task in the presence of two stoic evaluators. Thus, the context is a mix of social evaluation, uncontrollability, and one that requires cognitive effort and mental demand. This creates a bit of a puzzle for motivation researchers, because cortisol increases might indicate an experience of uncontrollability, social evaluation, and negative affect, but it might also indicate intense mental effort.

HPG is typically studied in motivation science by examining its end-product, testosterone (T), and to a lesser extent estrogen. Mirroring many of the other neurobiological responses reviewed thus far, early research on basal levels of T and changes in T were often interpreted along emotion lines, specifically that higher T was associated with aggressiveness and anger (e.g., Monaghan and Glickman, 1992). These interpretations often came from animal studies showing animals behaving more aggressively with exposure to T manipulations. As work in this area developed and human research augmented animal research, a wider net of affective and motivational states were found to be concomitant with high T; these states were primarily dominance, higher status, and approach/challenge states (Mazur and Booth, 1998; Mehta and Josephs, 2011). Basal levels of T have been found to moderate responses after victory and defeat with high T associated with more positive responses after wins than losses (Mehta et al., 2008). Similarly, increases in T in response to a stressor have been linked to police officers' social standing, and among young male adults T increases have been correlated with cardiovascular indexes of *challenge* states, greater reductions in HRV, and better performance in a cooperative task (Akinola and Mendes, 2014).

More recent models have considered the contribution of several hormones simultaneously: the dual hormone hypothesis, which examines cortisol and T (Mehta and Josephs, 2010), and anabolic balance, which considers the ratio of DHEAs and cortisol (Mendes et al., 2007a; Southwick et al., 2005). These approaches might provide greater precision toward understanding how motivational states are manifested neurobiologically by providing a wider biological systems approach.

2.4 Cellular Biology

Thus far, we have reviewed neurobiological responses that change based on motivational states and are manifested in the body within seconds or minutes. Much of the underlying neurobiology related to physical health outcomes, however, are altered over months and years, and these cellular based systems can modify motivational states. One cellular structure that appears sensitive to affective states is telomere length (Epel, 2009). Telomeres are the protein caps that sit on top of chromosomes. When cells replicate, telomeres can shorten and when telomere caps are shortened past a critical length, the cell dies (cell senescence). Initial research examining chronically stressed maternal caregivers showed that greater perceived stress and number of years as a caregiver were both correlated with shorter telomere length (Epel et al., 2004). Further examination of this psychobiomarker found that shorter telomere length was associated with more threat appraisals during novel stressors and greater avoidance physiology during stress tasks (Epel et al., 2006; O'Donovan et al., 2012). Other promising measures of cellular biology, like oxidative stress measures (e.g., F2-isoprostanes; 8-OHdG), might offer motivational researchers insight into how biology might potentiate or attenuate motivational responses, and offer exciting avenues for future research (e.g., Forlenza and Miller, 2006; Yager et al., 2010).

3. MODERATORS OF MOTIVATIONAL STATES

Thus far, we highlighted neurobiological responses and their links to different motivational states, but as noted, these relations are far from invariant and, indeed, as we underscored throughout, there are critical moderators of these relations. If one adopted a natural origin perspective on motivational states, neurobiological responses stemming from motivational states would be predictable across the life span and resistant to changes in the environment, impervious to subtle modulation in language and labeling, and not modifiable by something as subtle as changes in body positioning. Adopting an approach that relaxes these natural origin constraints provides a view of motivation that is flexible in terms of how motivational states are manifested in the brain and body. Attending to these moderators may be as important, or even more important, than the motivational category itself.

It may seem obvious how motivation and neurobiology are linked. We perceive a stimulus in our environment; we make sense of its signal properties; depending on these properties, we have a reflexive response to approach or avoid, attend or ignore, and our brains and bodies respond to this motivational state. Often researchers attempt to study the neurobiology of motivation by exposing people or animals to stimuli that would be expected to produce a specific motivational reaction and then reify the consequent neural and physiological responses as a signature of a specific motivational response. For example, researchers may conclude that approach is indicated by an increase in core temperature and avoidance is indicated by a decrease in temperature, but this conclusion is at worst an illusion or, at best, a heuristic; instead, multiple processes affect the stimulus-to-motivational state cascade, which can alter the physiological responses.

In the following section, we explore moderators of the motivation-neurobiology link such as bodily states like proprioception (positioning of the body), cognitive states like reappraisal, developmental factors, and socioculture factors. Each of these factors can influence motivational states, neurobiological responses to motivation, and the consequent behavior and feeling states that occur, which underscores the perspective that motivation is altered by top-down *and* bottom-up influences.

3.1 Context

Psychological science is replete with examples of how body positions or subtle primes can potentiate an affective state, behavior, or neurobiological response. From examples of holding a pen with one's teeth versus lips leading to funnier ratings of comic strips (Strack, Martin, & Stepper, 1998) to clutching a warm cup of coffee influencing judgments of others' likable personality (Williams and Bargh, 2008), there are many demonstrations that bottom-up influences can alter affective states, often without conscious awareness. These studies are popular perhaps because it seems surprising that the subtle changes we experience can alter judgments and behavior. However, to move these theories forward, theoretical models that link brain responses, body responses, and boundary conditions need to be identified. Although the term "embodiment" has been co-opted by researchers paying little attention to the underlying neurobiology that is implicated but often not examined, the large literature of those who take neurobiology seriously has shed light on important moderators that alter links between motivation and neurobiology. Here, we review various contextual factors that can shape motivational responses.

Posture and body positioning can influence motivational experience in non-human animals. As described above, an extensive body of work has explored so-called "fear" responses using rats that are classically conditioned to experience "fear" using acoustic responses and shocks. In one study, Iwata and LeDoux (1988) placed rats in either an unrestrained-home cage, which allowed free movement, or restrained them in a conditioning box, 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 increases relative to restrained rats. This study both poses a challenge to an ANS emotion specificity perspective and shows the importance of context in modulating physiological responses. If "fear-conditioned" rats have different physiological responses based on *context* rather than the specific emotional state, then it is difficult to argue that fear leads to a predictable physiological response. Instead, this finding shows how a motivational interpretation can shed light on a divergent physiological pattern. Specifically, when rats' behavioral options are interpreted in terms of its potential to escape or not, the physiological signatures are what would be expected. 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 might reduce blood loss if attacked.

Motivation and body positioning interact in humans as well. In one study using EEG responses, participants were placed in either an upright seated position or a supine position while they experienced insults from a confederate (Harmon-Jones and Peterson, 2009). Those who were seated upright showed the characteristic shift in left frontal cortical activation that occurs during *approach-oriented* states, whereas those who were supine did not show the shift in left frontal cortical activity. Self-reported emotional states did not differ by condition underscoring the possibility that these neurological changes are often subtle and may be below conscious awareness. This study elegantly demonstrates how an incongruent body position could blunt a neurobiological response that typically co-occurs during *approach* states.

We 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 (Gray et al., 2014). 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 Harmon-Jones study, this finding demonstrates that motivational states are malleable and can be altered by bottom-up influences like body positions.

3.2 Thoughts Alter Motivational States

The flexibility of motivation is also revealed in how thoughts can alter motivational states. Several lines of research converge on the idea that how one remembers or thinks about a situation influences the affective experience and its consequences. Broadly, this work has explored concepts such as self-perspective taking, disclosure and assessment, labeling affective experiences, and reappraisal.

Reappraisal, thinking about arousing or stressful events in a positive light, can influence motivational states and neurobiological changes (Gross, 2002). Across a number of studies, we focused on having individuals reappraise their physiological arousal as beneficial for their performance prior to completing a stressful task. In other words, we explained *challenge* states to participants and encouraged them to think about their physiological arousal as helpful to their performance rather than harmful. Across these investigations, this reappraisal manipulation engendered adaptive physiological responses and improved performance (Jamieson et al., 2013a). In one study, participants were instructed to deliver a speech in the presence of a panel of evaluators for a mock job interview (Jamieson et al., 2012). Just before the speech, participants were randomly assigned to one of three strategies, one of which was a reappraisal strategy and the other two were control conditions. In the reappraisal condition, participants read a (manufactured) newspaper article describing research that found that physiological arousal was functional and improved cognitive performance. The article stated that increases in physiological responses (like heart rate) before a stressful task indicate that people will perform well and that this response is adaptive. It suggested to participants that the best way to cope with a stressor was to remind themselves that increases in arousal are good for the individual. In contrast, one of the control conditions provided a coping strategy that was ineffective at coping with acute stress—ignoring the source of stress. The second control condition did not include any instructions on how to cope with the stressful task, but rather reiterated general instructions. Cardiovascular reactivity obtained during the speech task showed that the reappraisal condition resulted in more beneficial and adaptive stress responses, specifically more efficient cardiac functioning (higher cardiac output) and decreases in vascular resistance (lower total peripheral resistance) compared to either of the two control conditions. Additionally, a measure of attentional bias (Emotional Stroop, MacLeod et al., 2002) showed slower completion times to negative, self-relevant words than control words in the two control conditions, compared to the reappraisal condition. In short, this study demonstrated that appraising bodily changes that occur during stress as adaptive can result in more positive, benign physiological responses, as well as less attentional vigilance for threat in the environment.

Using a similar paradigm, we examined whether reappraisal could benefit test performance. In this study, we recruited students about to take the Graduate Record Examination (GRE) to come to the lab and assigned them to either a condition in which they learned that arousal during an exam helped their performance (reappraisal condition) or a no-information (control) condition (Jamieson et al., 2010). Participants in the reappraisal condition showed a significant increase in SNS responses (consistent with approach-oriented, *challenge* responses) and, more importantly, performed better in the quantitative portion of the GRE. Moreover, when students returned to the lab after they had completed the actual GRE with a copy of their tests reports, participants assigned to reappraise their arousal obtained higher GRE math scores than those in the control condition. When queried about their test-arousal on exam day, compared to control participants, reappraisal participants reported that arousal was more likely to help their performance, and they reported feeling more certain about their test-taking skills.

The importance of these studies is that they underscore how flexible motivational states are. By simply construing one's physiological arousal as adaptive, participants showed more benign physiological functioning, lower threat vigilance, and better test performance. These reappraisal strategies share much in common with *cognitive behavioral therapy*, which uses cognitive re-labeling to alter dysfunctional behavior. Indeed, we tested the effectiveness of a reappraisal intervention for participants with social anxiety disorder (SAD; Jamieson et al., 2013b) and observed that individuals with SAD benefitted from reappraising arousal as functional during a stressful social evaluation lab task, and showed more approach-oriented cardiovascular reactivity than individuals with SAD who were not provided with this intervention.

3.3 Developmental Factors

As we described earlier, much of modern psychophysiological research assumes reliable mind-body connections—changes in motivational states influence bodily responses and the biological milieu can shape motivational states. However, connections between mental states and neurobiology are not static across the life course and at different developmental periods processes like *interoception, proprioception, reactivity,* and *neural maturation* can alter the mind-body connection. Here we review how these bodily processes influence motivation-neurobiology relations, and how developmental factors can advance our understanding by providing boundary conditions to test hypothesized relations.

There is little reason to be optimistic about how the aging process influences our brains and bodies. 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 GH, hardening of the vasculature, and blunted activation reduces the flexibility of responding to different environmental demands (e.g., Epel et al., 2007; Matthews, 2005). How might these bodily changes alter how motivational states are experienced? If approach-oriented responses tend to be associated with larger SNS activation and aging bodies have greater difficulty in mounting larger SNS increases, do these bodily changes modify the type of experiences older people seek? Can bodily changes that result from aging explain the motivational processes of those later in life?

Proprioception, awareness of the body's static and dynamic body position, and interoception, awareness of internal bodily changes, are important for the experience of affective states, but is there evidence that these sensory modalities decline with age like other senses such as taste, hearing, and vision? The short answer is, yes, both proprioception and interoception decline with old age. Interoceptive changes with age, for example, were observed in a study by Khalsa, Rudrauf, Feinstein, & Tranel (2009) using a heart beat detection paradigm with participants ranging in age from 22 to 63. Older subjects showed poorer detection of their heart beats compared to younger and middle aged adults, and the overall bivariate correlation between age and accurate heart beat detection was $r = -0.49$ and $r = -0.45$ at two time points. These effects persisted after controlling for body mass index, sex, and the ability to detect one's own pulse directly from the wrist. With regard to proprioceptive declines with age, a much larger literature exists documenting these effects. Indeed a review article (Goble et al., 2009) provides evidence of proprioceptive impairments with age along varied dimensions of static and dynamic body positions.

Declines in interoception and proprioception are not the only dramatic physiological change that occurs in older age that is relevant to motivational states. As people age there is a blunting of key physiological systems, like SNS responses. 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, anger manipulations did not engender increases in peripheral (finger) skin temperature as 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 and 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 more resistant to dilation. Therefore, motivational states like approach may be compromised before states of threat and withdrawal, which might result in avoidance and withdrawal becoming the default response in older age.

These declines in sensory perception of the body with age and how these changes can interrupt the mind-body connection has been suggested to result in a state of *maturational dualism*, a phenomenon that argues that the bodily changes that 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 primarily due to a loss of peripheral perception and blunted physiological reactivity thus may impair the ability to use internal states to guide decisions and behavior.

What are the possible consequences of loss of mind-body connections in older age for motivation? There are intriguing clues in the literature regarding how the disconnection in older age may influence motivational states. For example, one study examined the somatic marker hypothesis in older adults (Denburg et al., 2005). In previous papers, Damasio and colleagues (e.g., Bechara et al., 1997) described the somatic marker hypothesis, which posited that bodily changes outside of conscious awareness can influence behavior. To test this hypothesis, participants 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 (activity in the eccrine gland, indicating sympathetic activation innervated by acetylcholine) 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 an extension of this study, older adults (56–85 years old) did not show preferences for the advantageous decks (Denburg et al., 2005). 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. There are at least two possible interpretations of these data in light of the ideas presented here: (1) older participants had blunted physiological responses during the task, which limited their ability to sense internal states vis-á-vis the somatic marker hypothesis or (2) the SNS 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). Of course another possibility is that the lack of choice of the advantageous decks was due to a combination of blunted reactivity and loss of interoception.

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

3.4 Sociocultural Environment

As we described above, factors related to aging, context, and bodily perceptions can alter how motivation is manifested in neurobiology. The last moderator we will review considers the sociocultural context in which individuals reside. Cultural and social neuroscience studies offer a unique way of considering how sociocultural environment can influence motivation and its consequent processes. One popular sociocultural context that moderates motivational responses is the intergroup context. Intergroup anxiety and, specifically, the extent to which individuals experience stress and threat when interacting with individuals who differ in race/ethnicity provides an important qualifier for general motivational tendencies. An example of this can be seen in one study where we paired white and black participants with partners (confederates) who were either white or black, to create same race and different race pairings (Mendes et al., 2008). The participants received social evaluations from their partners that suggested either social acceptance or social rejection, and then the dyads engaged in cooperative tasks while we measured their ANS responses. Not surprisingly, when participants received accepting feedback from a same race partner, their physiological responses were consistent with an approach-challenge state during the cooperative interaction, but rejecting feedback resulted in more threat and withdrawal. More interestingly, the cross-race pairs showed more *approach* responses after rejecting feedback, consistent with an anger response following perceptions of discrimination. The important point here is that the social context changed how the feedback was interpreted.

In another line of work, recent cultural neuroscience findings show that errors/mistakes have different motivational value across cultures. In one study, Park and Kitayama (2014) examined cultural differences in the motivational significance of errors that were made under social evaluative threat. To induce evaluation apprehension, participants in this study were briefly exposed to an image of a face (vs control images such as a scrambled face and a house) during a flanker task, as a social cue signaling a potential threat to the self. It may be expected that mere exposure to a watching face like this (i.e., face priming) is sufficient to evoke social evaluative threat, particularly among people who are prone to social anxiety, thereby increasing their ERN as an index of threat response. Consistent with previous findings that Asians experience greater social anxiety than European Americans when other people's evaluations are at issue (Ishii et al., 2011; Norasakkunkit et al., 2012), Asians showed larger ERN on the face priming trials than on the control priming trials. In contrast, there was no effect of face priming among European Americans.

In another study, Kitayama and Park (2014) identified a condition in which Americans' defensive response to errors is enhanced, that is, when their self-interest is at stake. Although the motivation to pursue self-interest (called self-centric motivation here) is often regarded as universal, numerous cross-cultural findings suggest that this motivational drive is stronger among European Americans who are strongly expected to develop the positivity of the self that is detached from social others, compared to Asians who are strongly encouraged to fit in and abide by social expectations even in sacrifice of their own interest (Heine et al., 1999). Kitayama and Park examined a neural basis of this cultural difference in self-centric motivation by asking participants to perform a flanker task to earn reward points either for themselves or for their close, same-sex friend. For half of the blocks, participants performed the task to earn reward points for themselves (i.e., self-blocks) and for the remaining half, they did so to increase reward points for their close friend (i.e., friend-blocks). They were further told that they could use the earned points to choose one gift item for themselves and another gift item for their friend from a list of 15 items (e.g., mug, t-shirt). It would be expected that people may experience errors as more threatening when these errors are made in the task they perform to increase reward points for themselves (vs their close friend), as long as they have a strong motivational concern to maximize self-interest over the interest of their friend. Confirming this prediction, European Americans who are high in self-centric motivation showed larger ERN in the self-blocks than in the friend-blocks. In contrast, there was no such difference in the ERN amplitudes of Asians. Together this work shows the possible moderating effects of sociocultural factors on how motivation is valued and experienced, and the consequent neurobiological changes.

4. SUMMARY

We reviewed classic and contemporary research examining the neurobiology of motivational states and overviewed multiple systems in an attempt to bring several different biological systems under a single umbrella. We also identified similarities and differences between motivation, and emotion and stress processes. Finally, we identified several critical moderators of the motivation-neurobiology link, specifically context, thought processes, development, and sociocultural factors, and highlighted key findings that show how these factors alter motivational states and related neurobiological states. We certainly are not claiming that neurobiological invariants of motivation do not exist, but if invariants are claimed, they should persist across contexts, development, and culture.

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