Vagal Tone and Vagal Flexibility Reflect Distinct Processes Related to Social Connection

By

Jared D. Martin

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The dissertation is approved by the following members of the Final Oral Committee:
Paula M. Niedenthal, Howard Leventhal WARF Professor, Psychology
Heather Abercrombie, Associate Professor, Psychiatry
Markus Brauer, Professor, Psychology
John Curtin, Professor, Psychology
Judith Harackiewicz, Paul Pintrich Professor, Psychology
Carol Ryff, Professor, Psychology

Abstract

Recent theoretical and empirical evidence suggest that levels of vagus nerve activation track an individual's level of social connection. However, a comprehensive understanding of this relationship remains elusive. To date, there have been two barriers to progress toward a deeper understanding of how vagal activation relates to social connection. First, there are multiple ways to assess levels of vagal activation, with psychophysiologists often quantifying either – but rarely both – vagal tone (i.e., average vagal activation during a resting baseline) or vagal flexibility (i.e., changes in vagal activation in response to a demanding task). Second, theories of the social functioning of the vagus nerve have failed to fully explicate how individual differences in vagal tone and vagal flexibility distinctly relate to social connection. As such, the question of how vagal activation relates to social connection has been obscured by multiple metrics for its quantification and lack of sufficient theoretical clarity to derive and test hypotheses.

In this dissertation, I propose that vagal tone and vagal flexibility distinctly reflect two separable but related psychological constructs involved in successfully connecting with others. I argue that whereas vagal tone reflects the ability to down-regulate physiological activity in the presence of others, vagal flexibility reflects the ability to calibrate physiological activity to the behavioral demands of the environment. These two propositions, in tandem with previous empirical research, lead to concrete predictions regarding the role of vagal tone and vagal flexibility in social connection. First, if vagal tone indeed down-regulates physiological activity in the presence of others, individuals with higher vagal tone should be better at recognizing others' facial expressions, a hypothesis I test in Study 1. Second, if vagal flexibility indeed reflects dynamic up- or down-regulation of physiological activity in a way that allows us to meet the behavioral demands of the situation, then individuals with greater vagal flexibility should exhibit increased social engagement behaviors and more feelings of social connection, a hypotheses I test in Study 2. Third, since social connection is strongly tied to health and well-being, vagal tone and vagal flexibility should predict health and well-being, with the effect of vagal flexibility on health and well-being mediated by levels of social connection, hypotheses I test in Study 3.

Findings from Study 1 show that individual differences in vagal tone predict differentiated patterns of physiological responses to facial expressions presented as social-evaluative feedback, such that individuals with greater vagal tone exhibit more cortisol output in response to negatively, compared to positively, evaluative stimuli. This finding suggests that individuals with greater vagal tone are better able to understand the social meaning of others' facial expressions and may thus be better able to connect with others. Findings from Study 2 indicate that vagal flexibility, but not vagal tone, is a strong positive predictor of feelings, but not behaviors, that indicate social connection. And in Study 3, neither vagal tone nor vagal flexibility predict physical health. Mediation analyses suggest that vagal tone and vagal flexibility both are associated with subjective well-being: vagal tone directly predicts subjective well-being; vagal flexibility indirectly predicts subjective well-being through feelings of social connection.

Overall, findings from this dissertation provide preliminary evidence for the argument that individual differences in vagal tone and vagal flexibility relate to social connection through two distinct abilities. The present findings contribute to a comprehensive understanding of how individual differences in two metrics of vagal activation relate to social connection, and suggest implications for health and well-being related to social connection. In doing so, findings from these studies may ultimately help inform interventions to help us live happier, healthier, and more socially-connected lives.

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Introduction

Social connection is good for our bodies and our minds. Greater social connection—from interactions with close friends to participation in community groups—is linked to higher positive affect, better overall physical and mental health, and up to a 90 percent decrease in all-cause mortality (Bennett, 2005; Cacioppo, Cacioppo, Capitanio, & Cole, 2015; Holt-Lunstad, Smith, & Layton, 2010; McIntyre, Watson, Clark, & Cross, 1991). Despite the clear benefits of connecting with others, the physiological systems that predict an individual's ability to understand and engage with the social environment remain underexplored (Berkman, Glass, Brissette, & Seeman, 2000; Capitanio, 2011; Cohen, 2004; Cohen, Gotlieb, & Underwood, 2000; Marshall & Fox, 2006). The documented health-protective benefits of social connection, coupled with concerns about social isolation among U.S. adults, make understanding the physiological systems that predict social connection critical and timely (Berkman et al., 2000; Cohen, 2004; McPherson, Smith-Lovin, & Brashears, 2006).

All healthy individuals possess body systems involved in interpersonal understanding and social connection (Adolphs, 2002, 2009; Berger & Calabrese, 1975; Burgoon & Hale, 1984). To successfully connect with others, be it at a sporting event or in quiet conversation, we must be able to do at least two things with our bodies. First, we must be able to down-regulate our physiological activation in the presence of others (Hare, Melis, Woods, Hastings, & Wrangham, 2007; Mundy & Acra, 2006). This is because, if our hearts race and our palms sweat whenever we interact with other people, we won't be able to connect with them because even simple social interactions will be physically and psychologically taxing, if not aversive (Coles & Heimberg, 2000; Heerey & Kring, 2007; Leary & Atherton, 2011; Schofield, Coles, & Gibb, 2009). Second, we must be able to calibrate our physiological activity to match the demands of our current environment so as to best prepare an appropriate behavioral response (Bortoletto, Lemonis, & Cunnington, 2011; Coombes et al., 2009; Hajcak et al., 2007; Sherwood, Allen, Murrell, & Obrist, 1988). Being able to dynamically modulate our physiological activity to enact behaviors appropriate to the environment is important for developing rapport and social connection because people like to affiliate with predictable, socially-aware, and efficacious others (Baumeister & Leary, 1995; Bernhard, Fehr, & Fischbacher, 2006; Carver & Scheier, 1982; Leary, 2010; Rofé, 1984). Thus, two abilities—1) down-regulation of physiological activation in the presence of others, and 2) calibration of physiological activity to prepare the body for contextually-appropriate behavior—are involved in successful social connection (Hare et al., 2007; Leary, 2010; Mundy & Acra, 2006).

Although down-regulation of physiological activation and calibration of physiological activity to the behavioral demands of the environment are both key to social connection, there is nonetheless vast inter-individual variability in these abilities (Derryberry, Reed, & Pilkenton-Taylor, 2003; Else-Quest, Hyde, Goldsmith, & Van Hulle, 2006; Rothbart, 2007). Psychologists have long taken advantage of such naturally-occurring individual differences in patterns of biological activity in order to gain insight into psychological processes (DeYoung et al., 2010; Kosslyn et al., 2002; Mischel, 2004). An individual differences approach of this sort prompts the driving question of the present dissertation: are there peripheral physiological signatures that mark individuals who are particularly good at connecting with others? One potential answer to this question lies in activation of the vagus nerve.

Vagal activity: what is it, what does it do, and how is it assessed?

Classically partitioned into two branches, the sympathetic and parasympathetic nervous systems, the autonomic nervous system is involved in relatively automatic biological processes such as sweating, digestion, and salivation (Grundy, 2006; Illigens & Gibbons, 2009; Proctor & Carpenter, 2007; Wang, 2012). One of the core functions of the autonomic nervous system is to prepare the body for quick, adaptive behavioral responses to environmental demands (Kreibig, 2010; Porges, 2001). To do this, the autonomic nervous system simultaneously modulates activity of both its divisions to prepare the body for situationally-appropriate behavior (Berntson, Cacioppo, & Quigley, 1991; Sherwood et al., 1988). Whereas the sympathetic nervous system promotes arousal and mobilizes the body's energy stores for action, the parasympathetic nervous system counters the effects of the sympathetic nervous system and promotes a calm physiological state (Janig, 2006; Moore, Dalley, & Agur, 2014; Vanderah & Gould, 2016)[1]. From vigorously outrunning a rabid dog to peacefully sitting at the dinner table, the two branches of the autonomic nervous system work in tandem to coordinate biological activity in the service of situationally-appropriate behavioral responses.

The vagus, or 10th cranial nerve, is the chief nerve of the parasympathetic branch of the autonomic nervous system (Moore et al., 2014; Vanderah & Gould, 2016). From the Latin for "wanderer," the vagus nerve takes a meandering path from the brainstem to the viscera, projecting afferent (i.e., directed toward target organs) and efferent (i.e., directed from organs) connections from the brainstem to the gut, heart, lungs, and many other internal organs (Moore et al., 2014; Vanderah & Gould, 2016). The vagus nerve is nearly always "on" as evidenced by the fact that the intrinsic human heart rate is upwards of 140 beats-per-minute without the continual down-regulatory effect of tonic vagal activation (Porges, 2003). Aside from its down-regulatory influence when individuals are calm and at rest, levels of vagal activation also shift to meet the

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[1] Although classical conceptions of autonomic nervous system function imply that the sympathetic and parasympathetic branches are in direct functional opposition such that increased activity in one branch necessitates decreased activity in the other, empirical findings show that this is not the case (Berntson et al., 1991). Rather, sympathetic and parasympathetic activity can occur in any combination, including co-activation.

metabolic and behavioral demands of the environment (Kreibig, 2010; Kreibig, Gendolla, & Scherer, 2012; Porges, 2001, 2007). Specifically, augmentation of vagal activation provides "calming" down-regulation of physiological activity, including down-regulation of peripheral effects of sympathetic activity as well as down-regulation of the HPA axis stress hormone cortisol (Janig, 2006; Porges, 2001; Vanderah & Gould, 2016). Furthermore, withdrawal of vagal activation allows the arousing sympathetic nervous system and HPA axis to dominate physiological activity (Janig, 2006; Vanderah & Gould, 2016). In summary, the vagus nerve is by-and-large continually active, providing both tonic down-regulation of physiological activity during resting conditions as well as contextually-appropriate up- or down-regulation of physiological activity to further suit the behavioral and metabolic demands of the individual's current environment.

The two general modes of vagal functioning, tonic down-regulation of arousing physiological activity (sympathetic nervous system and HPA axis) at rest and contextually-appropriate calibration of physiological activity (i.e., up- or down-regulation of physiological activity in response to environmental demands) are reflected in the two predominant metrics for assessment of vagal activation (Allen, Chambers, & Towers, 2007; Beauchaine, 2001, 2015; Berntson, Cacioppo, & Grossman, 2007; Human & Mendes, 2018; Muhtadie, Koslov, Akinola, & Mendes, 2014). Perhaps the most frequently employed metric of vagal activation is *vagal tone,* which reflects an individual's average level of vagal activation during resting conditions (i.e., in the absence of stimuli that require behavioral or metabolic modulation: Allen et al., 2007; Beauchaine, 2015; Berntson et al., 2007). Vagal tone is most commonly assessed by averaging levels of vagal activity during a resting baseline (Task Force, 1996). A second metric of vagal activity is *vagal flexibility* which reflects the degree to which an individual's level of vagal activation flexibly modulates in response to behaviorally-relevant stimuli (Human & Mendes, 2018; Muhtadie et al., 2014). Vagal flexibility is typically calculated by taking the difference between levels of vagal activation at rest and levels of vagal activation during a demanding task (i.e., average task level – average baseline level). A schematic representation of vagal tone and vagal flexibility is presented in **Figure 1.**

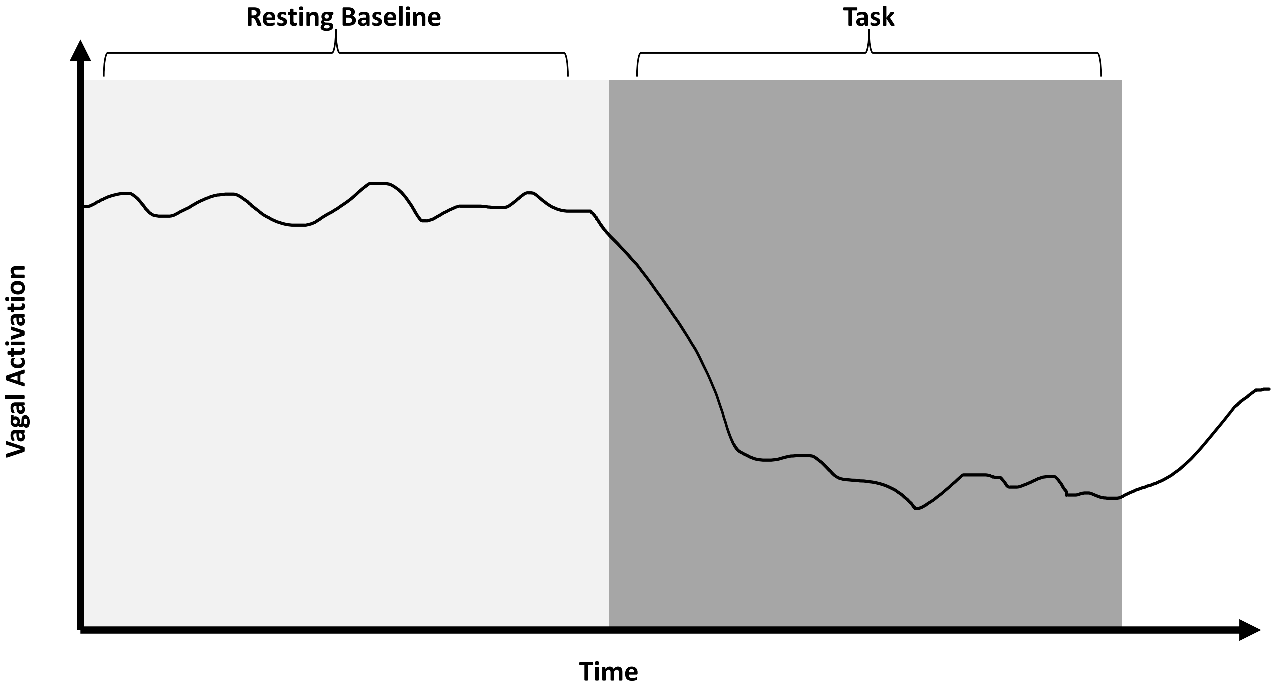

Figure 1: ***Vagal tone and vagal flexibility: two metrics of vagal activation.*** The vagus nerve is nearly always on, providing a down-regulatory influence over physiological activity. In light of its over-time nature, psychophysiologists have adopted two general approaches to quantifying levels of vagal activation. The first, and most common approach, calculates the average level of vagal activation during a resting baseline. This metric is referred to as *vagal tone.* The second metric, growing in popularity, calculates the difference in levels of vagal activation between a resting baseline and a demanding task (i.e., average task level – average baseline level). This metric is known as *vagal flexibility* and reflects the body's ability to modulate its physiological activity to meet the behavioral demands presented by the environment.

By down-regulating physiological activity and calibrating our bodies to the behavioral demands of the present situation, the vagus nerve has been implicated in our ability to understand, behaviorally respond to, and feel connected with others (Beffara, Bret, Vermeulen,

& Mermillod, 2016; Denver, Reed, & Porges, 2007; Geisler, Kubiak, Siewert, & Weber, 2013; Kok & Fredrickson, 2010; Stellar, Cohen, Oveis, & Keltner, 2015). However, theories of the social functioning of the vagus nerve have failed to fully explicate how the two predominant metrics of vagal activation (i.e., vagal tone and vagal flexibility) distinctly relate to individual differences in social connection (Porges, 2001, 2007; R. Smith, Thayer, Khalsa, & Lane, 2017; Thayer & Lane, 2000). In this dissertation, I argue that two separable but related psychological constructs involved in successfully connecting with others are differentially reflected by individual differences in vagal tone and vagal flexibility. I propose that 1) vagal tone reflects the overall ability to down-regulate physiological activity in the presence of others, and 2) vagal flexibility reflects the ability to calibrate physiological activity to the behavioral demands of the present environment.

These two propositions lead to two concrete predictions regarding the role of vagal tone and vagal flexibility in social connection. First, if vagal tone indeed down-regulates physiological activity in the presence of others, it should also allow us to better understand others' facial expressions. This is because high levels of sympathetic nervous system and HPA axis activity can narrow attentional focus, increase reliance on stereotypes, and impair cognitive processing (Bacon, 1974; Bodenhausen, 2014; Gable & Harmon-Jones, 2010; Heuer & Reisberg, 1992; Mather & Sutherland, 2011). I test the prediction that individual differences in vagal tone predict understanding of facial expressions in Study 1. Second, in order to connect with others, we don't just need to down-regulate our physiological activity when we meet them, we also need to dynamically up- or down-regulate our physiological activity in a way that allows us to meet the ongoing behavioral demands of the situation (Bortoletto et al., 2011; Carver & Scheier, 1982; Leary, 2010). Thus, individual differences in context-dependent modulation of physiological activity, as reflected by vagal flexibility, should relate to increased social engagement behavior (e.g., attending social group meetings) and feelings of social connectedness. I test the hypothesis that vagal flexibility predicts behaviors and feelings that promote social connection in Study 2.

In the next section, I review theoretical and empirical evidence to support each of the predictions outlined above, and show that both abilities involved in social connection have distinct implications for how we connect with others, be it through understanding others' facial expressions or through preparation of contextually-appropriate behavioral responses.

Vagal tone and flexibility relate to social connection through distinct processes

Vagal tone. For many primates, violence and aggression are the rule not the exception (Gómez, Verdú, González-Megías, & Méndez, 2016; Rilling et al., 2012; Wrangham & Glowacki, 2012). High levels of conflict are due, at least in part, to the fact that the close proximity of others and the resultant eye contact can often trigger strong physiological stress responses (Donovan & Leavitt, 1980; Helminen, Kaasinen, & Hietanen, 2011; Nichols & Champness, 1971; Senju & Johnson, 2009; see also, Cole, Balcetis, & Dunning, 2012). However, compared to many of our closest non-human primate relatives, humans are a relatively non-violent species (Gómez et al., 2016; Rilling et al., 2012; Sueur et al., 2011). Human tolerance of social contact is likely a product of our ability to quickly down-regulate physiological activity in the presence of others, and this ability may have deep roots in evolutionary history (Rilling, 2014; Rilling et al., 2007, 2012; Rilling & Insel, 1998). As human ancestors' social environments became increasingly complex, evolutionary pressures likely shaped both branches of the autonomic nervous system to meet the demands of increased social interaction (Porges, 1995, 2001, 2003; Porges & Furman, 2011). In particular, the parasympathetic branch of the autonomic nervous system may have evolved its present day structure and function in order to support non-agonistic engagement with the social environment by down-regulating the sympathetic nervous system and HPA axis responses to the close proximity of others (Porges, 1995, 2001, 2003, 2007).

In his Polyvagal Theory, Porges argues that the mammalian autonomic nervous system progressed through three global evolutionary stages, retaining vestiges of each earlier stage in evolutionary development (Porges, 1995, 2001, 2003, 2007)[2]. The first phylogenetic stage of mammalian autonomic nervous system development was characterized by dominance of slow-to-respond, unmyelinated cardiac vagal control (Porges, 2001). The second stage, spurred by growing socio-ecological demands, resulted in the development of direct sympathetic cardiac innervation (Porges, 2001). On top of the structures developed in the first two stages, in the uniquely mammalian third stage of phylogenetic development, mammals further evolved a quicker myelinated vagal pathway for visceral innervation (Porges, 2001). Because the myelinated vagal pathway responds more rapidly than the unmyelinated pathway developed in the first stage, the myelinated vagal pathway adds more possibilities for rapid down-regulation of physiological activity in the presence of others. By quickly engendering a calm physiological state, myelinated vagal activity is thought to lead to a constellation of behaviors that allow us to connect with others such as social communication, exploration of the social environment, and acknowledgment of social contact (Porges, 2001).

Beyond direct verbal communication, humans communicate a substantial amount of information through nonverbal channels, especially the face (Burgoon, 2011; Knapp, Hall, & Horgan, 2014). By transmitting information about the social environment as well as behavioral

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[2] Although this position has received considerable critiques (see, for example, Grossman & Taylor, 2007), it is nonetheless a useful framework for considering the functional development of the mammalian autonomic nervous system. Such phylogenetic evidence is particularly useful in facilitating the derivation of testable hypotheses.

intentions, facial expressions can regulate perceivers' minds, bodies, and behaviors (Fridlund, 2014; Klinnert, Campos, Sorce, Emde, & Svejda, 2013; Sorce, Emde, Campos, & Klinnert, 1985). But, our ability to understand the signals that others send is attenuated by rampant and unchecked sympathetic nervous system and HPA axis activity. This is because a high levels of sympathetic nervous system and HPA axis activity narrow attentional focus, increase reliance on stereotypes, and impair cognitive processing (Bacon, 1974; Bodenhausen, 2014; Gable & Harmon-Jones, 2010; Heuer & Reisberg, 1992; Mather & Sutherland, 2011). Since successful social connection requires an accurate understanding of others' social signals, down-regulation of physiological activity upon initially encountering someone should allow us to connect with them by facilitating our ability to understand their social signals. In line with others (Porges, 1995, 2003; Quintana, Guastella, Outhred, Hickie, & Kemp, 2012), I argue that inter-individual differences in vagal tone reflect the ability to down-regulate sympathetic nervous system and HPA axis responses that the presence of others engenders, in the service of better understanding the social signals they communicate.

Although being able to recognize and understand others' facial expressions is part and parcel to successful social connection, people vary in their ability to understand facial expressions (Hampson, van Anders, & Mullin, 2006; M. L. Smith, Cottrell, Gosselin, & Schyns, 2005; Wood, Rychlowska, & Niedenthal, 2016). A growing body of research links vagal tone both with the ability to down-regulate physiological activation as well as the ability to recognize others' facial expressions (Lischke, Lemke, Neubert, Hamm, & Lotze, 2017; Quintana et al., 2012; Smeets, 2010). For example, eye contact is a ubiquitous social signal that reliably elicits sympathetic nervous system responses (Akechi, Senju, Uibo, Kikuchi, & Hasegawa, 2013; T. Chen, Peltola, Dunn, Pajunen, & Hietanen, 2017; Emery, 2000; Garner, Mogg, & Bradley, 2006;

Hoffman, Gothard, Schmid, & Logothetis, 2007; Richeson, Todd, Trawalter, & Baird, 2008). Preliminary evidence suggests that individuals with greater vagal tone are better able to down-regulate sympathetic arousal in response to direct eye contact, as evidenced by lesser electrodermal activity when viewing stimuli with direct (versus averted) gaze (Harrod, Martin, Korb, & Niedenthal, *in prep*). Further evidence suggests that Black individuals, who face chronic discrimination and the correspondent necessity of more frequent down-regulation of physiological activation, tend to have higher vagal tone than do White individuals (Hill et al., 2015). Taken together, this and other evidence suggests that individual differences in vagal tone reflect the ability to down-regulate physiological responses to social challenge (Appelhans & Luecken, 2006; Elliot, Payen, Brisswalter, Cury, & Thayer, 2011; Mather & Thayer, 2018; Shahrestani, Stewart, Quintana, Hickie, & Guastella, 2015; Smeets, 2010).

Vagal down-regulation of the prepotent sympathetic nervous system and HPA axis response to the presence of others likely leaves the body in a state that better allows it to thoroughly and accurately process the social signals communicated by others (Bacon, 1974; Bodenhausen, 2014; Gable & Harmon-Jones, 2010; Heuer & Reisberg, 1992; Mather & Sutherland, 2011). Recent empirical evidence suggests that individuals with higher vagal tone are better able to recognize the emotions communicated via subtle differences in facial expressions (Lischke et al., 2017; Quintana et al., 2012). In a separate study, participants who received experimental manipulation to increase their vagal tone (compared to control participants) showed relatively better performance on a facial expression recognition task (Sellaro, de Gelder, Finisguerra, & Colzato, 2017). The association between vagal tone and increased understanding of social signals may be partly explained by findings that suggest, when the body is in a calm state, increased vagal tone relates to quicker and more efficient modulation of attention to task relevant information (Park & Thayer, 2014). Together, the theoretical and empirical evidence reviewed above provide support for the present proposition that individual differences in vagal tone reflect the ability to down-regulate physiological activation (sympathetic nervous system and HPA axis activity) in the service of better recognition of social signals.

Vagal flexibility. In order to connect with others, we need to not only be able to understand their social signals, but also be able to enact appropriate behavioral responses to those signals. As I previously noted, this is because others are more likely to develop feelings of rapport and a motivation to affiliate with us to the extent that we are predictable, socially-aware, and efficacious interaction partners (Baumeister & Leary, 1995; Bernhard et al., 2006; Carver & Scheier, 1982; Leary, 2010; Rofé, 1984). In order for our bodies to appropriately respond to others' social signals, our brains must translate the behavioral relevance of others' social signals into a pattern of physiological activity that facilitates an appropriate behavioral response (Bortoletto et al., 2011; Coombes et al., 2009; Hajcak et al., 2007; Sherwood et al., 1988). In light of the fact that the vagus nerve quickly carries information from the brain to much of the viscera that controls metabolic output required for behavior (e.g., the heart), the vagus nerve is uniquely situated to rapidly modulate the availability of the biological resources required for behavior (Porges, 2001; Vanderah & Gould, 2016). In line with this reasoning, dynamic calibration of vagal activity to meet the behavioral demands of the environment may help us connect with others by preparing our bodies to enact socially-appropriate behaviors.

But how does the brain translate the meaning of others' social signals into physiological responses that adequately prepare the body for situationally-appropriate behavior? In their Neurovisceral Integration Model, Thayer and Lane argue that the vagus nerve serves as a critical nexus, reciprocally connecting the brain and body (R. Smith et al., 2017; Thayer & Lane, 2000). According to this perspective, levels of vagal activation are the output of a distributed network of cortical and subcortical structures that translate the behavioral relevance of a given stimulus into a physiologically adaptive response. Specifically, higher order control systems (e.g., the medial prefrontal cortex) interact with lower order subcortical systems to modulate activity in both branches of the autonomic nervous system in the service of adaptive behavioral responding (Beissner, Meissner, Bar, & Napadow, 2013; Benarroch, 1993; Critchley, 2005; Napadow et al., 2008). Top-down regulation of autonomic states allows the cortical systems that represent the social meaning and behavioral relevance of environmental stimuli to be reflected in levels of vagal activation appropriate to respond to the demands of the present internal or external environment (R. Smith et al., 2017; Thayer, Åhs, Fredrikson, Sollers, & Wager, 2012).

Successful social interactions require a finely-tuned understanding of the appropriate behavior to enact at any given time (Bernhard et al., 2006; Carver & Scheier, 1982). On the one hand, the interpersonal payoffs for aligning our behaviors to conform to our interaction partners' expectations include greater feelings of social closeness and rapport (Behrens, Hunt, & Rushworth, 2009; Klucharev, Hytönen, Rijpkema, Smidts, & Fernández, 2009; Leary, 2010; Seyfarth & Cheney, 2013). On the other hand, the interpersonal costs of failing to produce appropriate behaviors in social encounters include feelings of embarrassment and potential social punishment (Baumgartner, Götte, Gügler, & Fehr, 2012; Bernhard et al., 2006; Berthoz, Armony, Blair, & Dolan, 2002). In light of the significant costs and benefits of successful behavioral regulation in social encounters, we must be able to calibrate our physiological activity to prepare our bodies for situationally-appropriate action (Carver & Scheier, 1982). I argue that inter-individual differences in vagal flexibility reflect the ability to calibrate our physiological activity to the demands of the present situation in the service of preparing a situationally-appropriate behavioral response.

Extant findings support the conclusion that vagal flexibility reflects ongoing efforts at behavior regulation. In one study, participants completed two tasks: refrain from eating a cookie (a difficult task), or refrain from eating a carrot (an easier task). Participants exhibited greater changes in vagal activation (i.e., greater vagal flexibility) in response to the more difficult task compared to when participants were engaged in the easier task (Segerstrom & Nes, 2007). Similarly, regulating emotional behavior during social interaction induces greater vagal activity than not regulating it (Butler, Wilhelm, & Gross, 2006). These and other findings suggest that the vagus nerve is involved in behavior regulation (Holzman & Bridgett, 2017; Reynard, Gevirtz, Berlow, Brown, & Boutelle, 2011; Spangler, Gamble, McGinley, Thayer, & Brooks, 2018), providing evidence for the notion that vagal flexibility is related to the production of contextually-appropriate behaviors. Given that efforts at behavioral regulation are related to greater vagal flexibility (Butler et al., 2006; Segerstrom & Nes, 2007), it stands to reason that individuals who exhibit greater vagal flexibility, in general, are better able to align their behaviors with the demands of the social environment.

If inter-individual differences in vagal flexibility are indeed related to the ability to enact situationally-appropriate behaviors, then individuals with greater vagal flexibility should also be able to enact positive interpersonal behaviors that support social connection when warranted by the situation. Empirical research, though limited, supports the conclusion that individual differences in vagal flexibility are associated with behaviors that support social connection. In one study, adolescents who exhibited greater vagal flexibility were also more likely to display behavioral warmth to their parents, with these effects persisting even at a multi-year follow-up

(Diamond & Cribbet, 2013). In a second study, children with greater vagal flexibility were more likely to show prosocial behaviors at school, although this pattern changed direction for children who experienced high-adversity at home (Obradović, Bush, Stamperdahl, Adler, & Boyce, 2010). In a third study, children with social phobia tended to exhibit *less* vagal flexibility than did their non-social-phobic peers, suggesting that restricted vagal flexibility is related to the tendency to avoid social contact (Schmitz, Krämer, Tuschen-Caffier, Heinrichs, & Blechert, 2011). Taken together, extant empirical findings support the conclusion that individuals with greater vagal flexibility show more frequent behaviors that support social connection.

The health and well-being implications of vagal tone and vagal flexibility

Being able to down-regulate physiological activity in response to others (i.e., vagal tone) and calibrate physiological activity in preparation for situationally-appropriate behavior (i.e., vagal flexibility) are individual differences that are not just useful for connecting with others. These two abilities may also have long-reaching implications for health and well-being. The Neurovisceral Integration Model directly outlines the role of vagal activity in the mechanistic relationships between psychological processes, physiological activity, and disease etiology (Thayer & Lane, 2000). From this perspective, a healthy individual is one who possesses a vagus nerve that dynamically fluctuates its level of activation in response to signals carried to and from the brain. Conversely, individuals who possess a vagus nerve that is not able to flexibly modulate its activity to carry information back and forth from the brain to the viscera are more likely to exhibit poor mental and physical health. In this way, the Neurovisceral Integration Model describes how a dynamic and flexible mind-body connection is indicative of a healthy individual (Thayer & Lane, 2000).

However, little to no extant theoretical work speaks to how interpersonal factors, such as social connection, are tied into the mechanistic relationship between health and well-being, psychological processes, and the vagus nerve (for two possible exceptions, see: Del Giudice, Ellis, & Shirtcliff, 2011; Kok & Fredrickson, 2010). Two theoretical accounts of how the social environment influences the body are particularly germane to the goal of understanding the psychological and interpersonal processes through which vagal activity impacts health and well-being. The first account, Social Baseline Theory (Coan & Sbarra, 2015) explains how the social environment "gets under the skin", connecting socio-environmental factors with health and well-being (see also: Sbarra & Coan, 2018). The second approach, the Biopsychosocial Model (Blascovich, Mendes, Hunter, & Salomon, 1999; Seery, 2013; Tomaka, Blascovich, Kelsey, & Leitten, 1993; Tomaka, Kibler, Blascovich, & Ernst, 1997) explains how situational appraisals influence physiological responses in such a way that chronic threat appraisals can lead to unhealthy physiological responses over time. By integrating these two theoretical perspectives, I derive testable hypotheses regarding how social connection and vagal activity relate to health and well-being.

Social Baseline Theory describes how the social environment influences health and well-being, with a particular focus on social cognition and perception (Coan & Sbarra, 2015). From this perspective, the human brain is wired to expect and seek out social relationships because access to better social partners lowers the risks and efforts involved in meeting critical self-maintenance goals. On the one hand, greater access to quality relational partners increases perceptions of social closeness insofar as relationship partners are mentally represented as an extension of the self. On the other hand, decreased access to quality relational partners decreases perceptions of interpersonal closeness, leading to greater physiological and psychological burden

(Eisenberger, Taylor, Gable, Hilmert, & Lieberman, 2007; Holt-Lunstad et al., 2010; Slavich, O'Donovan, Epel, & Kemeny, 2010). As a result, individuals with lower-quality relational networks experience more of the detrimental health effects of social isolation (Cacioppo et al., 2015; Hawkley, Burleson, Berntson, & Cacioppo, 2003; Steptoe, Shankar, Demakakos, & Wardle, 2013). These claims from Social Baseline Theory suggest that high quality relational partners help buffer against morbidity and mortality by helping us regulate or bodies and minds.

The Biopsychosocial Model adds further nuance to a mechanistic account of how social factors influence biological activity. Specifically, the Biopsychosocial Model describes how psychological factors (in the form of situational appraisals) influence activity in the two key stress axes of the body: the sympathetic-adrenal-medullary axis (epinephrine/nor-epinephrine), and the hypothalamic-pituitary-adrenal axis (cortisol) (Blascovich et al., 1999; Seery, 2011, 2013). When an individual perceives that her resources meet or exceed the demands of her present environment (i.e., a *challenge* appraisal), her body responds with healthy and adaptive physiological activity, including greater and more efficient blood pumped from the heart (Tomaka et al., 1993). A challenge appraisal is conceptually and physiologically similar to perceiving the environment as safe, socially-supportive, and under one's control (Coan, Schaefer, & Davidson, 2006). When an individual perceives that her resources do *not* meet the demands of her present environment (i.e., a *threat* appraisal), her body responds with a different biological profile, including increased vascular resistance and greater cortisol output (Tomaka et al., 1993). In the short run, threat-related biological activity is adaptive, helping the individual meet the demands of the present situation. However, in the long run, if an individual chronically perceives situations as unsafe or threatening (Cisler, Bacon, & Williams, 2009; Maresh, Beckes, & Coan, 2013), the consequent biological activity can lead to negative health consequences, particularly cardiovascular pathologies (Charles, Piazza, Mogle, Sliwinski, & Almeida, 2013; S Cohen, Janicki-Deverts, & Miller, 2007; Gianaros, Jennings, Sheu, Derbyshire, & Matthews, 2007; Hostinar, Ross, Chan, Chen, & Miller, 2017; Kamarck et al., 2005; Kamarck, Shiffman, Sutton-Tyrrell, Muldoon, & Tepper, 2012; K. A. Matthews, 2005; Piazza, Charles, Sliwinski, Mogle, & Almeida, 2013; Richardson et al., 2012; Sawyer, Major, Casad, Townsend, & Mendes, 2012).

Social Baseline Theory suggests that limited access to quality relationship patterns may lead to negative health outcomes (Coan & Sbarra, 2015); the Biopsychosocial Model suggests that chronic threat appraisals can lead to negative health outcomes (Blascovich et al., 1999; Seery, 2011, 2013). An integration of these two models leads to the conclusion that quality social connection can potentially buffer the body against negative health outcomes. This is because the social network can be viewed as a resource from which an individual can draw, and the greater the resource the lesser the likelihood that an individual will make a threat appraisal that, when chronically active, can lead to poor health outcomes (Cohen et al., 2000; DeVries, Glasper, & Detillion, 2003; Lepore, Allen, & Evans, 1993; Sbarra & Coan, 2018).

Integration of Social Baseline Theory and The Biopsychosocial Model leads to testable hypotheses when merged with my propositions about how vagal tone and vagal flexibility function to promote social connection. On the one hand, in conjunction with my proposition that individual differences in vagal tone reflect the ability to down-regulate physiological activation, vagal tone should influence health and well-being directly through regulation of the deleterious effects of chronic sympathetic nervous system and HPA axis activation (Hjemdahl, 2002; Kamarck et al., 2012; Lupien, McEwen, Gunnar, & Heim, 2009; Tsigos & Chrousos, 2002). On the other hand, in conjunction with my proposition that vagal flexibility prepares the body for situationally-appropriate behavioral responses that lead to feelings of social connection and rapport, vagal flexibility should influence health and well-being indirectly through social connection, in the form of feelings of social support and social engagement behaviors (Cohen et al., 2000; Holt-Lunstad et al., 2010; Sbarra & Coan, 2018). The prediction that vagal tone and vagal flexibility each influence health and well-being through distinct pathways is tested in Study 3.

Teasing apart the many metrics of vagal activity: an overview of the present work

Researchers continue to debate whether and how metrics of vagal activity are associated with social connection and related outcomes (Heathers, Brown, Coyne, & Friedman, 2015)[3]. To date, there have been two barriers to progress toward reaching a definitive conclusion regarding how vagal tone and vagal flexibility relate to social connection. First, psychophysiologists often quantify either – but rarely both – vagal tone or vagal flexibility. Because vagal tone and vagal flexibility are correlated (for example, see Muhtadie et al., 2014), it is likely that at least some of the reported findings linking one of these measures with social connection instead would be better indexed by the other measure. Second, theories of the social functioning of the vagus nerve have failed to fully explicate how individual differences in vagal tone and vagal flexibility distinctly relate to social connection (Porges, 2001, 2007; R. Smith et al., 2017; Thayer & Lane, 2000). As such, the question of how vagal tone and vagal flexibility are associated with social connection and related outcomes (e.g., health and well-being) has been obscured both by

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[3] It should also be noted that there is still significant debate about the extent to which non-invasive indicators (such as high-frequency heart rate variability) are even appropriate operationalizations of parasympathetic activity, which can only be directly measured with invasive procedures. Despite considerable decades of considerable debate amongst psychophysiologists, the consensus seems to be that non-invasive indicators can be used as proxies for vagal activity so long as a handful of methodological confounds are also considered, such as respiration, whether or not the participant is talking, and if the task itself is physically demanding (Berntson et al., 2007; Electrophysiology, 1996; Laborde et al., 2017).

divergent approaches to the quantification of vagal activation and lack of sufficient theoretical clarity for derivation and testing of hypotheses.

As I have argued throughout this introduction, I propose that vagal tone and vagal flexibility reflect two separable but related psychological constructs involved in successfully connecting with others. According to my line of reasoning, whereas vagal tone reflects the overall ability to down-regulate physiological activity in the presence of others, vagal flexibility reflects the ability to calibrate physiological activity to the behavioral demands of the present environment. These two propositions, when coupled with previous empirical research, lead to concrete predictions regarding the role of vagal tone and vagal flexibility in social connection that I test in the three studies presented in this dissertation. First, if vagal tone down-regulates physiological activity in the presence of others, then individuals with greater vagal tone should be better at understanding facial expressions, a hypothesis I test in Study 1. Second, if vagal flexibility reflects dynamic up- or down-regulation of physiological activity in a way that allows us to meet the behavioral demands of the situation, then individuals with greater vagal flexibility should show more social engagement behaviors (e.g., attending social group meetings) and feelings of social connectedness, a hypotheses I test in Study 2. Third, if vagal flexibility prepares the body for situationally-appropriate behavioral responses that lead to feelings of social connection and rapport, then individuals with greater vagal flexibility should exhibit better health and well-being, as indirectly influenced through social connection. Vagal tone should also influence health and well-being, but is expected to have a direct rather than mediated effect. I test these hypotheses in Study 3.

A schematic representation of the working model for this dissertation is presented in **Figure 2.** Vagal tone is expected to promote social connection by relating to individual differences in the ability to recognize facial expressions, as evidenced by greater differentiation in physiological responses to facial expressions within a meaningful social context: public speaking. A laboratory-based study (Study 1) tests this prediction. Individuals prepared and delivered a simple speech in front of a confederate and received social signals relevant to their task performance via the facial expressions of their interaction partner. Study 1 tests whether individuals with greater vagal tone are better able to understand the facial expressions of their partner as indicated by greater differentiation of physiological responses to different kinds of facial expressions. That is, if more physiological differentiation between different kinds of facial expressions is taken as an indirect indicator of facial expression understanding, since physiological differentiation would not have occurred had the expressions not been perceived to be different in social meaning.

Studies 2 and 3 test the extent to which both metrics of vagal activity, but particularly vagal flexibility, are associated with social connection and related health and well-being outcomes. Study 2 tests for a relationship between both metrics of vagal activity and social connection. Specifically, greater vagal flexibility is expected to positively predict feelings and behaviors indicative of social connection from both initial and 10-year follow-up social connection assessments. Vagal tone is expected to be either more weakly associated with social connection or show no association.

Study 3 tests the extent to which both metrics of vagal activity predict health and well-being, and the extent to which social connection mediates this relationship. Specifically, both vagal tone and vagal flexibility are expected to be associated with better long-term subjective well-being and physical health (i.e., morbidity and mortality). Whereas vagal tone is expected to have a direct relationship with health and well-being, the relationship between vagal flexibility and health and well-being is expected to be mediated by levels of social connection.

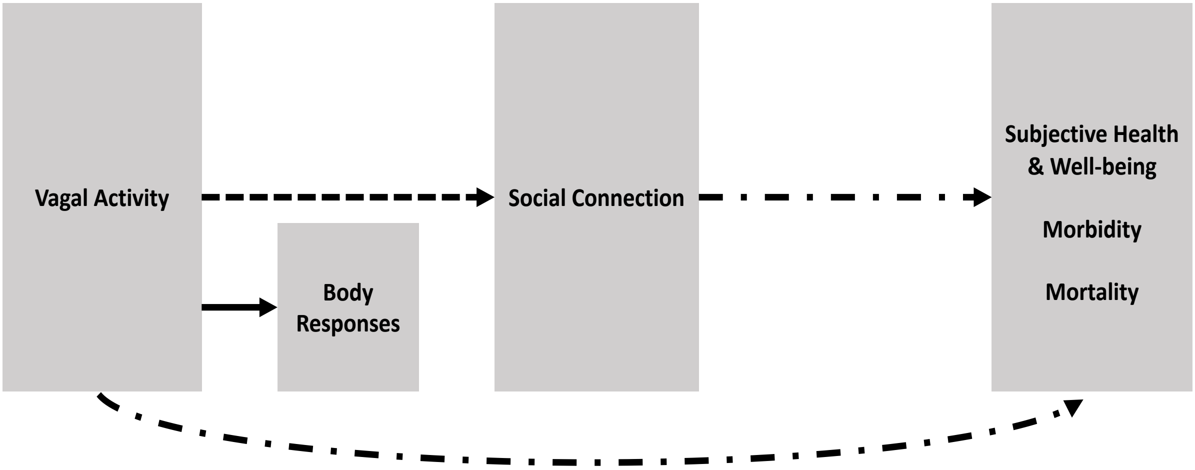

Figure 2: ***Schematic representation of dissertation analyses.*** The schematic representation of studies in this dissertation shows how both metrics of vagal activity (vagal tone and vagal flexibility) are used to predict social connection and related outcomes. Study 1 uses vagal tone to predict body responses and is represented by a solid line in this figure. Study 2 predicts feelings and behaviors indicative of social connection from vagal tone and vagal flexibility, and is represented by a dashed line in this figure. Study 3 predicts health and well-being outcomes from vagal tone and vagal flexibility both directly, as well as mediated through social connection, represented by the dash-dotted lines in this figure.

Study 1: Vagal activity and physiological differentiation of social signals

Sweaty palms, a racing heart, a faltering voice. Most people find the evaluative context of public speaking unpleasant. Indeed, the mere anticipation of social evaluation increases activity across almost all body systems related to stress, with particularly robust activation in the hypothalamic-pituitary-adrenal (HPA) axis (Blackhart, Eckel, & Tice, 2007; Bosch, Geus, Carroll, Annebet, & Edwards, 2009; Dickerson, Gruenewald, & Kemeny, 2004; Dickerson, Mycek, & Zaldivar, 2008). However, scientific inquiry has largely been limited to investigations of the manner in which the body responds to verbal evaluative feedback, of the type "that was/wasn't good." (Eisenberger, Inagaki, Muscatell, Haltom, & Leary, 2011; Fallon, Careaga, Sbarra, & Connor, 2016) Does the HPA axis respond to purely nonverbal feedback, such as facial expression? I investigate this question and demonstrate that evaluators' smiles are sufficient to augment or dampen HPA axis activity – depending upon the distinct meaning of the smile in the social-evaluative context. Furthermore, I find that physiological responses to smile meaning are most differentiated in individuals with higher vagal tone, which is associated with facial expression recognition accuracy (Lischke et al., 2017; Quintana et al., 2012; Sellaro et al., 2017).

Nonverbal feedback in social-evaluative contexts should be at least as impactful as verbal feedback, since nonverbal signals are experienced by perceivers to be spontaneous reactions (Burgoon, Guerrero, & Manusov, 2011) and thus, honest reflections of internal evaluations. In the few studies that have investigated the nonverbal communication of evaluative feedback, participants whose audience displayed smiles and other nonverbal cues to positive evaluation showed lower physiological activity than participants met with frowns and similar cues to negative evaluation (Akinola & Mendes, 2008; Kassam, Koslov, & Mendes, 2009; Taylor et al., 2010). Recent theory and empirical evidence suggests, however, that smiles do not all communicate identical, uniformly positive messages (Martin, Wood, Rychlowska, & Niedenthal, 2017; Niedenthal, Maringer, & Hess, 2010; Rychlowska et al., 2017). Instead, evidence supports the existence of at least three morphologically distinct types of smiles, each of which serves a different social function involved in successful group living: “reward” smiles reinforce behavior, “affiliation” smiles signal lack of threat and facilitate or maintain social bonds, and “dominance” smiles assert claims to higher status in social hierarchies (Martin et al., 2017; Niedenthal, Maringer, et al., 2010). In light of their evolved functions, each of these three smiles should carry distinct meanings when displayed by evaluators. The first aim of the present study is to test the hypothesis that reward, affiliation, and dominance smiles, delivered as evaluative feedback, influence perceivers’ HPA axis activity in a manner congruent with their distinct social meaning. I expected reward smiles to decrease, and dominance smiles to increase, HPA axis activity. In theory, whereas reward smiles show approval of and dominance smiles show disdain for performance, affiliation smiles reassure without being indicative of a specific evaluation and so were expected to buffer HPA axis activity to a lesser degree than reward smiles.

The second aim of the present research is to account for variability in participants’ capacity to understand the evaluative meanings of each smile. Reward smiles are more unambiguous in meaning across contexts than either affiliation or dominance smiles (Rychlowska et al., 2017), which are relevant in more limited contexts. That is, reward smiles can reinforce widely varying behaviors in most any social situation, whereas affiliation smiles serve to smooth existing or potential social bonds and dominance smiles serve to challenge them. Individuals who are more accurate at recognizing facial expressions should exhibit more differentiated physiological activity in response to affiliation and dominance smiles, indicating greater sensitivity to their social-evaluative meanings. Recent empirical evidence suggests that vagal tone is positively associated with facial expression recognition accuracy (Lischke et al., 2017; Quintana et al., 2012; Sellaro et al., 2017). I thus tested the hypothesis that individuals with higher vagal tone exhibit more differentiated physiological activity in response to smiles presented as evaluative feedback, particularly in response to smiles that are more ambiguous in context (i.e., affiliation and dominance smiles).

In an adaptation of the classic Trier Social Stress Test (Clemens Kirschbaum, Karl-Martin, & Hellhammer, 1993), male participants (*N* = 90) extemporaneously addressed three topics about themselves in front of a same-sex evaluator who watched them over a web camera. The evaluator was, in fact, one of two confederates working for the research team – 47 and 43 participants per confederate. To increase believability, the evaluator briefly appeared live on the computer screen, then turned off his web camera for the remainder of the session. After responding to each of the three topics, participants saw videos of their evaluator's facial expressions which they believed represented spontaneous reactions to their performance that had been extracted by facial recognition software. The videos were, in fact, pre-recorded. Participants were assigned to one of three smile conditions such that they saw either one reward, affiliation, or dominance smile after each of their responses to the three topics. Along with one smile video, participants also saw a control video that showed the evaluator making a neutral response such as face scratching or eye blinks. Thus, each participant was exposed to six videos of their evaluator in total (three different instances of one type of smile, three neutral videos) with one smile and one neutral video presented after each of the three responses. Smile videos were constructed to meet *a priori* specifications of morphological activity associated with each of the three smile types (for further details, see "Smile Stimuli Creation and Validation" below)

(Rychlowska et al., 2017). Thus, smile type was the only feature of the evaluative feedback that varied between conditions. Physiological activity, in both the HPA axis and cardiovascular system, was assessed throughout the study; salivary cortisol was measured at seven time points, and a continuous electrocardiograph was collected before, during, and after the speech task.

Methods

Smile Stimuli Creation and Validation

The smile stimuli from the two confederates were created with the social evaluation task in mind, and I therefore ensured that the stimuli reflected the social situation (i.e., listening to a speech over Skype) to the extent possible. To enhance believability, the confederates were filmed in the same room in which they would eventually meet the participants during the experiment, and from the same angle and distance as the web camera through which they would briefly appear on Skype. Confederates wore the same clothing during every session. Results from a separate study validating that each of the three smile types communicates the desired social-functional meaning are reported below.

Participants. 166 participants (M_{age} = 36.5, 60% male) were recruited from Amazon's Mechanical Turk web service. As a requirement for eligibility, all participants currently reside in the United States.

Facial Expression Videos. Informed by models of the three functional smiles derived from a data-driven approach (Rychlowska et al., 2017), I created a set of facial expression videos. Two individuals, who were to serve as confederates in the social evaluation task, were coached to imagine themselves in contexts in which the three smiles (reward, dominance, affiliation) might be encountered and to make a smile that would be displayed in that context. Only in the event that the confederates did not achieve a facial expression resembling the models of Rychlowska and colleagues (Rychlowska et al., 2017) were they given instructions to involve certain facial muscles in the expressions. In addition, the facial expressions of sadness, disgust, anger, positive surprise, and neutrality were also recorded.

I selected three videos of each smile type (nine total), three neutral expressions, and one each of expressions of sadness, positive surprise, anger, and disgust from the two confederates. This resulted in a total of 32 videos for use in the present study. In order to ensure that the smiles were morphologically adequate representations of the smile animations used in previous studies (Rychlowska et al., 2017), I visually examined the stimuli with a computer-assisted facial expression coding platform (Littlewort et al., 2010). Rychlowska and colleagues document that Action Units 1-2 are related to reward smiles, AU 14 to affiliation smiles, and asymmetrical activation of AU12 to dominance smiles (Rychlowska et al., 2017). Visual inspection of the data shows that each smile type is morphologically distinct in physical features outlined by previous research (Rychlowska et al., 2017).

Procedure. The on-line survey involved three tasks, which were always presented in a single order: Smile Categorization, Signal Rating, and Message Choice.

Smile Categorization Task. Facial expression videos were each presented once, for a total of 32 trials. On every trial, participants indicated whether the facial expression was a smile or not, by selecting the label "yes" or "no" with the mouse. The order of video presentation was randomly determined for each participant.

Signal Rating Task. Upon completion of the smile categorization task, participants were randomly assigned to one of three between-subjects rating conditions (happy/good: $N = 54$; approachable/cooperative: $N = 56$; superior/dominant: $N = 56$). According to condition assignment, participants rated all 18 smile stimuli on a single meaning dimension from 1 “not at all” to 7 “very much”: "The expression means the person is feeling good/happy" (reward); "The expression means the person is feeling approachable/cooperative " (affiliation); “The expression means the person is feeling dominant/superior" (dominance). The 18 smile videos were presented in random order.

Message Choice Task. In the final task, participants again saw all 18 smile videos. They were asked to imagine that they had just given a speech in front of the person in the video. Their task was to select the message that best matched the meaning of the facial expression in the video. Participants chose from 7 response options. Three options were evaluative, and related to the functional smiles as follows: reward—“Your speech was good”, affiliation—“Your speech was okay”, dominance—“Your speech was bad.” Three options were written to approximate the functional message communicated by the smile types in a speech context: reward—“Hey, I liked what you said,” affiliation— “Good try, I know it's hard,” dominance—“I could have done better.” Participants were also given the option to choose “None of the above.” The 18 smile videos were presented in random order.

Statistical Analysis and Results*: *Smile Categorization Task. All analyses were conducted in the R statistical environment (R Core Team, 2014). First, I collapsed smile/not smile categorizations across both confederates and all instances of each stimulus type. The left-hand portion of **Figure 3** depicts percentage categorization for each of the eight stimulus categories. In order to analyze whether participants were more likely to categorize instances of smile stimuli as smiles versus not smiles, I fit a logistic regression model with a dummy-coded stimulus factor representing the eight stimulus categories. In this model, a significant intercept value indicates that mean categorization rates were significantly different from chance (50%) for the “reference group” dummy-coded stimulus category. Re-referencing the stimulus factor on each of the eight expressions reveals that all three smile expressions were more likely to be seen as smiles than not (reward: b = 4.59, CI95% = [4.02, 5.28], z = 14.44, p < .0001; affiliation: b = 3.37, CI95% = [3.04, 3.74], z = 19.05, p < .0001; dominance: b = 1.31, CI95% = [1.06, 1.46], z = 16.89, p < .0001). Conversely, all five other expressions were more likely to be categorized as not smiles than as smiles (Neutral: b = -3.83, CI95% = [-4.3, -3.43], z = -17.4, p < .0001; surprise: b = -1.83, CI95% = [-2.01, -1.65], z = -19.93, p < .0001; anger: b = -1.84, CI95% = [-2.02, -1.66], z = -19.96, p < .0001; sadness: b = -1.81, CI95% = [-2.0, -1.64], z = -19.86, p < .0001; disgust: b = -4.05, CI95% = [-4.57, -3.61], z = -16.57, p < .0001). Results remain significant when accounting for multiple ratings from participants via multi-level logistic regression analyses (Bates, Mächler, Bolker, & Walker, 2015). Furthermore, analyses including participant sex as a factor in both the original analysis as well as in a multi-level logistic regression model did not reveal sex as a significant predictor in any categorization (all ps > .9).

Statistical Analysis and Results*: *Signal Rating Task. Three between-subjects groups rated all smile stimuli on one of three dimensions (happy/good: N = 54; approachable/cooperative: N = 56; superior/dominant: N = 56). I analyzed ratings separately by stimulus type. As expected, reward smiles received higher “happy/good” ratings (M=6.39, SD=0.62) than they did “approachable/cooperative” ratings (M=6.29, SD=0.76) or “dominant/superior” ratings (M=3.1, SD=1.54). Using orthogonal contrasts, I compared “happy/good” ratings to “approachable/cooperative” and “dominant/superior” (contrast: 1, -.5, -.5), also including the further comparison “approachable/cooperative” to “dominant/superior” (contrast: 0, .5, -.5) in order to account for residual variance. Results indicated that reward smiles received significantly higher “happy/good” ratings compared to other ratings (b = 2.26, t (163) = 9.68, p < .0001, CI(95%) =[1.8, 2.72], Δr^2 = .18) and were viewed as more “approachable/cooperative” than “dominant/superior” ($b = 3.19$, $t\ (163) = 15.0$, $p < .0001$, $CI(95\%) =[2.8, 3.58]$, $\Delta r^2 = .50$).

As expected, affiliation smiles received higher “approachable/cooperative” ratings (M=5.13, SD=0.93) than “happy/good” (M=5.0, SD=0.97) or “dominant/superior” ratings (M=3.95, SD=1.15). Using orthogonal contrasts, I compared “approachable/cooperative” ratings to “happy/good” and “dominant/superior” (contrast: 1, -.5, -.5) also including the further comparison “happy/good” to “dominant/superior” (contrast: 0, .5, -.5). Results indicated that affiliation smiles received significantly higher “approachable/cooperative” ratings compared to the other ratings ($b = 0.88$, $t\ (163) = 4.24$, $p < .0001$, $CI(95\%) =[0.47, 1.29]$, $\Delta r^2 = .08$) and were viewed as more “happy/good” than “dominant/superior” ($b = 1.05$, $t\ (163) = 5.82$, $p < .0001$, $CI(95\%) =[0.69, 1.41]$, $\Delta r^2 = .16$). Dominance smiles received higher “superior/dominant” ratings (M=5.44, SD=0.97) than “happy/good” (M=4.50, SD=0.89) or “approachable/cooperative” ratings (M=4.11, SD=1.15). Using orthogonal contrasts, I compared “superior/dominant” ratings to “happy/good” and “approachable/cooperative” ratings (contrast: 1, -.5, -.5), again including the further comparison “happy/good” to “approachable/cooperative” (contrast: 0, .5, -.5) in order to account for residual variance. Results indicated that dominance smiles received significantly higher “superior/dominant” ratings compared to the other ratings ($b = 1.51$, $t\ (163) = 6.82$, $p < .0001$, $CI(95\%) =[1.07, 1.95]$, $\Delta r^2 = .22$) and were viewed as more “happy/good” than “approachable/cooperative” ($b = 0.34$, $t\ (163) = 2.05$, $p = 0.42$, $CI(95\%) =[0.02, 0.78]$, $\Delta r^2 = .02$).

Statistical Analysis and Results*: *Message Choice Task. I first collapsed categorizations across both the evaluative and functional messages (i.e., dominance: “I could have done better” or “Your speech was bad”) as well as all instances of each stimulus type for both confederates.

The right-hand confusion matrix in **Figure 3** depicts percentage of response choice for the three stimulus types. Comparison of stimulus category to perceivers' message choice using Cohen's κ, a measure of inter-rater reliability, revealed κ = .45, *CI*95%[.42, .48], which is considered "moderate" by traditional cut-off values (Landis & Koch, 1977).

In order to analyze whether participants were more likely to choose a message label corresponding to one of the two matching messages versus a non-matching message, I employed a similar analysis strategy as in the smile categorization task. I used the "VGAM" package (Yee & Wild, C. J. & Yee, T.W., & Wild, 1996) in R to fit a multinomial logistic regression model (outcomes: "None of the above", "reward message", "dominance message", "affiliation message") with a dummy-coded stimulus factor representing the three smile categories. Re-referencing the stimulus factor on each of the three expressions allows for a comparison of matching message choice to the three alternative choices. Results indicate that participants were more likely to choose the matching message than any other response, for all smile types: reward (reward message vs. affiliation message: $b = -1.7$, *CI*95% = [-1.87, -1.52], $z = -19.04$, $p < .0001$; reward vs. dominance: $b = -3.44$, *CI*95% = [-3.83, -3.05], $z = -17.28$, $p < .0001$; reward vs. "none of the above": $b = -6.01$, *CI*95% = [-7.4, -4.62], $z = -8.49$, $p < .0001$), affiliation (affiliation message vs. reward message: $b = -0.48$, *CI*95% = [-0.63, -0.34], $z = -6.56$, $p < .0001$; affiliation vs. dominance: $b = -0.91$, *CI*95% = [-1.07, -0.74], $z = -10.69$, $p < .0001$; affiliation vs. "none of the above": $b = -3.54$, *CI*95% = [-4.07, -3.01], $z = -13.06$, $p < .0001$), dominance (dominance message vs. reward message: $b = -1.88$, *CI*95% = [-2.11, -1.65], $z = -16.25$, $p < .0001$; dominance vs. affiliation: $b = -0.56$, *CI*95% = [-0.7, -0.42], $z = -8.03$, $p < .0001$; dominance vs. "none of the above": $b = -3.44$, *CI*95% = [-3.91, -2.98], $z = -14.4$, $p < .0001$).

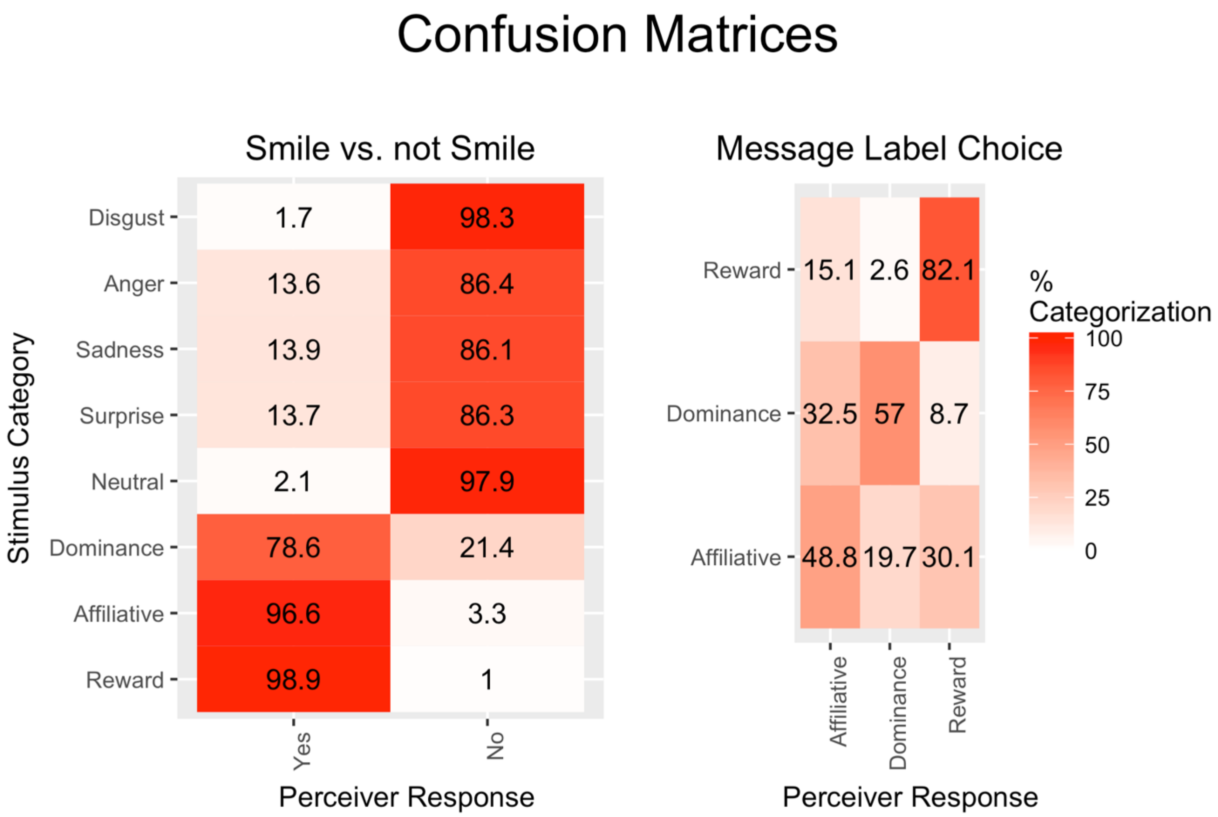

Figure 3: ***Confusion matrices for stimulus creation*****.** Confusion matrices depict the outcomes of Smile Categorization Task (left) and Message Choice Task (right). For the right-hand confusion matrix, note that "None of the above" was factored into the percentages but omitted from the figure.

Laboratory-based Experimental Study of Physiological Responses to Smiles

Participants. Ninety-two male undergraduates at a large university in the Midwest participated in exchange for credit in an introductory Psychology course. Participants provided written consent, indicating full understanding of the requirements for participation. The research protocol was reviewed and approved under the University of Wisconsin – Madison Institutional Review Board. All research was conducted in accordance with institutional guidelines and regulations.

Due to the robust sex differences in cortisol responses to laboratory stressors (Kirschbaum, Wüst, & Hellhammer, 1992) and the variability in cortisol responses introduced by oral contraceptive use (Rohleder, Wolf, Piel, & Kirschbaum, 2003), only males were invited to participate in this study. Since females generally outperform males in the accurate recognition of positive facial expressions (Donges, U. S., Kersting, A., & Suslow, 2012), the expectation was that the present study would underestimate the effects of smiles on physiological responses. Pre-inclusion criteria limited participation to U.S.-born, English-speaking males without a diagnosed heart condition and not currently taking medications that alter hormone levels. Participants were instructed to refrain from exercise on the day of the study and to avoid alcohol and caffeine consumption within twenty-four hours of their participation. Due to a network failure, data collection from one participant was terminated before experimental manipulation. Furthermore, data from a second participant were excluded from analysis due to the presence of an abnormal heart rhythm resembling premature beats (Goldberger Goldberger, Z., & Shvilkin, A., 2013) which made it difficult to score the data and conflicted with the pre-inclusion criterion of cardiac health. The exclusion of all data from these two participants left a final sample of ninety participants (dominance: N = 27; affiliation: N = 36; reward N = 27).

Data collection was limited to the number of participants that could be involved during one academic semester, not to exceed 120 participants (40 per condition). Participants were randomly assigned to one of three between-subjects smile experimental conditions as well as one of two confederates. Given that some participants did not show up for their assigned slots, a certain amount of imbalance between the number of participants in each condition and assigned to each confederate is to be expected.

At the conclusion of the study, participants underwent a funneled debriefing. First, they were asked if they thought they knew what the study was about. In this general interview, no participants brought up suspicions about deception. Participants were then asked if they found anything strange about the study or were suspicious of anything. In a logistic regression model with experimental condition and confederate as predictors of a dichotomous ("yes"/ "no") suspicion outcome, no significant differences were detected by experimental condition (all *p*s > .2) or by confederate (*p* = .93). Participants who thought the study was slightly strange indicated that they were unsure how the filler video was related to the study, were unaccustomed to providing saliva samples, or were uncomfortable giving speeches.

Procedure. In order to reduce variation due to diurnal changes in cortisol levels, experimental sessions took place in the afternoon. Upon arriving at the experimental laboratory, the participant encountered another male "participant" who was actually a confederate—one of the two whose stimuli were validated the preliminary study (see "Smile Stimuli Creation and Validation"). The experimenter then entered from a nearby room and told the two men that he had randomly assigned them to different tasks in the study: the participant was always assigned to "give the speech" and the confederate was always assigned to "judge the speech." After the participant and confederate had provided informed consent, the participant supplied the first of seven saliva samples (collection method described below) and completed an on-line questionnaire assessing his compliance with pre-restriction criteria (alcohol and caffeine use) as well as other medical information (prescription and recreational drug use). The men were told that only the person giving the speech (always the participant and never the confederate) had to answer the online questionnaires and provide the saliva samples because it directly pertained to giving the speech; the confederate waited with the participant and the experimenter while the participant responded to the surveys and provided the saliva sample.

The experimenter then demonstrated a facial expression recognition software, the Computer Emotion Recognition Toolbox (Littlewort et al., 2010). The participant and confederate were informed that the program could extract meaningful facial expressions from live video feed. The experimenter used the computer's built-in web camera and the participant's face as the live feed in a demonstration in order to increase believability in the software's (actual) capabilities.

Next, the participant and confederate were separated. Leaving the confederate behind in the initial room, the experimenter mentioned that a second experimenter would arrive shortly to provide the confederate with further instructions and tasks. The experimenter escorted the participant to a psychophysiology lab in the same building. There, the experimenter attached sensors to the participant's chest and explained that they would be used to measure aspects of his cardiovascular reactivity. The experimenter sat with the participant in the experimental room while a research assistant in an adjacent control room recorded a 3-minute baseline measure of participants' heart activity.

After completion of this baseline recording, the experimenter informed the participant that he would deliver his speech to the "other participant" via Skype. He would not see the evaluator as his web camera would be turned off in order to avoid distraction. The format of the speech involved answering three questions in sequence, with two minutes to respond to each question. The participant was also told that at the conclusion of every two-minute speech period, he would see videos of several of the evaluator's facial expressions. The participant was told that the videos would be "randomly extracted by the facial expression software" while the evaluator watched the participant’s speech. This led the participant to believe that the videos conveyed authentic evaluative responses by the confederate. The facial expressions displayed in these videos constituted the experimental manipulation.

When the participant indicated that he had understood the speech task, the experimenter gave him a sheet of paper with the three questions he was required to answer, and then sat with the participant for three minutes while the participant prepared his speech. A continuous cardiovascular recording was taken during this three-minute “anticipation” period. After the time was over, the second saliva sample was taken.

Next, the experimenter launched Skype. In order to enhance believability, the confederate appeared live on the participant’s screen and waved “hello”. The experimenter asked the evaluator to turn off his camera “so as not to distract” the participant during the speech. With the participant no longer able to see the evaluator, the experimenter asked the participant to begin his speech. Participants responded to each question in order, with two minutes for each question: 1) What makes you happy?, 2) What do you like most and least to eat?, and 3) What is your favorite part of living in Madison, Wisconsin? These questions were designed to be personal and to contain enough positive material to make the smiles sent by the evaluator appear plausible.

At the conclusion of each two-minute speech period, the experimenter stopped the participant and showed him two videos of the evaluator that were “randomly extracted” when he was listening to the participant’s speech. From the other room, the confederate dropped each video into a network-based folder in order to simulate the facial expression recognition program extracting and sending the videos in real time. Each participant saw 6 videos in total, 2 after each question. 3 of the 6 total videos were smiles and the other 3 were a set of different neutral videos—evaluators faced the camera with a neutral expression and occasional small, nonevaluative movements such as face scratching. The smile videos were three different short video clips of the same confederate making only one smile type (dominance, reward, or affiliation). Participants were thus exposed to three different examples of the same type of smile. In sum, smile type was manipulated between-subjects with the 3 neutral videos retained across participants. At the conclusion of the speech task, the third saliva sample was taken. The speech task lasted between 7 – 8 minutes, during which a continuous cardiovascular recording was taken.

Immediately upon concluding his final speech, the participant was directed to reflect on his performance, focusing on how he felt and what his evaluator thought. A continuous cardiovascular recording was taken during this five-minute reflection period. After the reflection/recovery period, the participant was detached from the sensors and led to the final room by a second experimenter who was blind to the participant's video feedback condition.

In the last room, the participant watched a filler video available on YouTube from the series "The Life of Birds"[4] which provided a neutral experience during which cortisol recovery was assessed. The video was the same for all participants. The remaining four saliva samples were taken at 10-minute intervals from the cessation of the speech task. At the conclusion of the filler video, and after completing verbal questions assessing deception suspicion, the participant was debriefed and dismissed.

Collection and Analysis of Physiological Measures: Cortisol. Saliva samples were obtained with cotton salivettes (Fisher Scientific Company, LLC). Participants were instructed to let the cotton salivette touch all parts of their mouth (under their tongue, between their teeth and their cheeks) without chewing on it. Saliva collection was strictly timed for two minutes, after

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[4] Available at https://www.youtube.com/playlist?list=PLB1F251E81DE15E9B

which the sample was returned to its plastic casing. Samples were frozen after collection and stored at -20 C. At the conclusion of the study, samples were express shipped to Dresden, Germany where they were single-assayed at the lab of Dr. Clemens Kirschbaum (T.U. Dresden). Samples were assayed using the chemi-luminescence assay, which has a high sensitivity of .16 ng/mL (IBL-International, Hamburg, Germany) and intra and interassay CVs of < 10%. In total, saliva samples were collected at seven time points during the study and assayed for unbound cortisol. Due to skewness, all cortisol values were first log-transformed. Salivary alpha amylase was assayed but is not reported in these analyses.

In order to test my hypotheses with regard to the HPA axis, Area Under the Curve with respect to increase (AUC*i*: Pruessner, Kirschbaum, Meinlschmid, & Hellhammer, 2003) values were calculated for the cortisol response of each participant. AUC*i* scores index total cortisol response over a given period of time, referenced to each individual's baseline cortisol level. I averaged the two cortisol values collected before experimental manipulation (receipt of smile feedback) as a pre-speech baseline.

Collection and Analysis of Physiological Measures: EKG. EKG data were first scored offline using OpenANSLAB (Wilhelm, F. H., & Peyk, 2005), manually inspected for artifacts, and the resultant inter-beat-interval series were extracted and saved. CMETx software[5] was then used on the extracted inter-beat-interval to quantify metrics of vagal activity (Allen et al., 2007; Hibbert, Weinberg, & Klonsky, 2012).

Continuous EKG recordings were sampled at 1000 Hz via one of the bipolar inputs available on the SynAmps2 Headbox (Compumedics Neuroscan Ltd., U.S.A). Ag/AgCl spot electrodes were placed in a thoracic-modified lead-II configuration to maximize detection of R-

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[5] Available at http://apsychoserver.psych.arizona.edu

spikes while minimizing movement artifacts. I calculated mean heart rate values separately for the baseline period, the "anticipation" period, the speech period, and the post-speech period.

Vagal activity can be non-invasively approximated by the beat-to-beat variability in heart rate within the frequency range of spontaneous respiration, termed *high-frequency heart rate variability* or "HF-HRV" (Malik, 2004; Malik & Camm, 1993). A number of pharmacological blockade studies support the association between HF-HRV and level of vagal activation (Cacioppo et al., 1994; Eckberg, 2004). Insofar as HF-HRV tracks vagal activity, I employ resting HF-HRV as an indicator of vagal tone and the difference between HF-HRV at resting baseline (i.e., vagal tone) and HF-HRV at the beginning of the speech task as an indicator of vagal flexibility. Vagal flexibility values were multiplied by -1 such that greater values indicate greater vagal withdrawal from baseline.

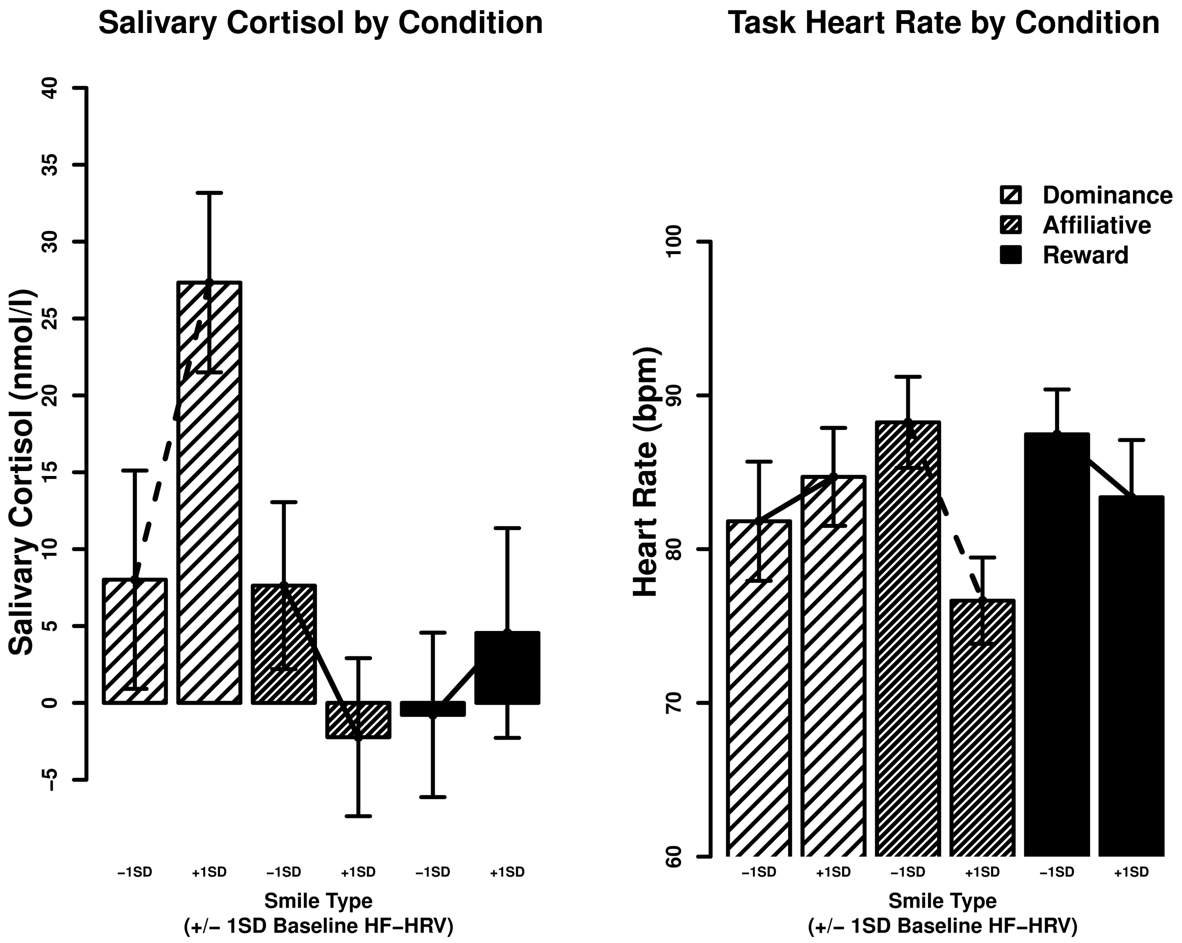
Results

Raw means for total salivary cortisol level by smile condition were consistent with the prediction that reward, affiliation, and dominance smiles influence perceivers' physiological activity in distinctive ways, such that the receipt of dominance smiles is associated with higher HPA axis activity relative to receipt of reward smiles. (AUC*i* – nmol/l: dominance: $M = 19.4$, $SD = 24.74$; affiliation: $M = 2.43$, $SD = 22.3$; reward: $M = 1.21$, $SD = 21.54$). I used dummy-coded condition contrasts to directly compare total salivary cortisol responses between smile types ("*AUCi*", see Methods). Compared to reward smiles, dominance smiles induced a greater overall salivary cortisol response ($b = 18.18$, $t\ (86) = 2.93$, $p = .004$, $CI(95\%) = [5.83, 30.54]$, $\Delta r^2 = .087$). Similarly, even though affiliation smiles do not signal a clear social evaluation in this context, compared to such smiles, dominance smiles induced a greater overall salivary cortisol response ($b = 16.97$, $t\ (86) = 2.92$, $p = .004$, $CI(95\%) = [5.41, 28.53]$, $\Delta r^2 = .086$).

Further corroborating the finding that dominance smiles induce greater HPA axis activity, participants receiving reward or affiliation smiles returned to their individual cortisol baseline by 30-minutes post-speech, whereas those who received dominance smiles continued to have significantly higher cortisol levels than their individual baseline. In this ancillary analysis, cortisol values at 20 and 30-minutes post-speech were predicted from dummy-coded condition contrasts and average baseline cortisol level. Intercepts for each smile condition at both 20 minutes post speech (reward, b = .23, t (86) = 1.49, p = .14, CI(95%) = [-0.08, 0.53]; affiliation, b = 0.25, t (86) = 1.79, p = .08, CI(95%) = [-0.03, 0.53]; dominance, b = .57, t (86) = 4.47, p < .0001, CI(95%) = [0.31, 0.82]) as well as 30 minutes post speech (reward, b = -0.02, t (86) = -0.13, p = .9, CI(95%) = [-0.32, 0.28]; affiliation, b = 0.03, t (86) = 0.2, p = .84, CI(95%) = [-0.25, 0.31]; dominance, b = .36, t (86) = 2.82, p = .006, CI(95%) = [0.11, 0.61]) show that mean salivary cortisol values for the dominance group continued to be significantly greater than zero up to thirty minutes post speech, which was not the case for the other groups. This shows that individuals receiving dominance smiles take significantly longer to return to their individual cortisol baseline, thus corroborating findings from the AUC*i* analysis.

I next tested the extent to which vagal tone moderated the cortisol findings, particularly in response to affiliation and dominance smiles. I again created dummy codes for smile feedback condition in order to compare the effect of smile feedback between conditions. I entered these dummy codes along with a continuous measure of vagal tone and the dummy-code by vagal tone interaction terms into a linear regression model. Results from this analysis generally support the conclusion that individuals with greater vagal tone show more physiological differentiation between smile types. With those who received dominance smiles as the dummy-coded reference group, vagal tone was positively correlated with salivary cortisol responses (b = 9.72, t (84)

=2.02, $p = .046$, $CI(95\%) = [0.14, 19.29]$, $\Delta r^2 = .04$). Comparing the linear association between vagal tone and salivary cortisol responses between individuals who received dominance versus affiliation smiles, the comparison of simple slopes was significant ($b = 14.63$, $t\,(84) = 2.40$, $p = .018$, $CI(95\%) = [2.54, 26.83]$, $\Delta r^2 = .057$), indicating that the relationship between vagal tone and salivary cortisol is more positive for those receiving dominance compared to affiliation smiles as evaluative feedback (**Figure 4**).



Salivary Cortisol by Condition

Task Heart Rate by Condition

Figure 4. ***Physiological response to smiles as evaluative feedback depends on baseline high frequency heart rate variability.*** Salivary Cortisol: Total salivary cortisol (nmol/l: dominance: M = 19.4, sd = 24.74, n = 27; affiliation: M= 2.43, sd = 22.3, n = 36; reward: M = 1.21, sd = 21.54, m = 27) in response to social evaluation was greater for those receiving dominance smiles as evaluative feedback relative to the two other types of smiles. The difference in total salivary cortisol response between the affiliation and dominance groups increased as HF-HRV increased.

Heart Rate: Heart rate assessed during the speech task (bpm: dominance: M = 83.51, sd = 9.84, n = 27; affiliation: M= 82.13, sd = 14.43, n = 36; reward: M = 85.93, sd = 12.65, m = 27) was not significantly different between conditions. The difference in heart rate between the dominance and affiliation groups increased as HF-HRV increased. Dotted lines between the +/- 1SD bars indicate a statistically significant simple slope for baseline HF-HRV in that feedback condition; solid lines are not significant below the .05 level.

Convergent evidence that vagal tone is positively associated with greater differentiation of physiological responses to affiliation and dominance smiles comes from cardiovascular data. Again, I created dummy-coded condition contrasts and entered them into a linear regression model along with vagal tone and the vagal tone by smile feedback dummy-code interaction terms. With the dummy-coded condition contrasts referenced on participants who received affiliation smiles, vagal tone was negatively associated with heart rate during the speech task (*b* = -5.84, *t* (84) =-2.85, *p* = .006, *CI*(95%) =[-9.91, -1.76], Δr^2 = .086). A comparison of the linear association between vagal tone and heart rate between individuals who received affiliation versus dominance smiles reveals that the relationship between vagal tone and heart rate was more negative for those exposed to affiliation compared to dominance smiles as evaluative feedback (*b* = -7.28, *t* (84) = 2.19, *p* = .032, *CI*(95%) =[-13.92, -0.66], Δr^2 = .051).

I next tested the extent to which vagal flexibility moderated the association between smile type with cortisol and heart rate. I entered vagal flexibility into a model similar to the one employed in the vagal tone analyses, entering dummy-coded condition contrasts along with vagal flexibility and the condition by vagal flexibility interactions. Results of this analysis indicate that vagal flexibility was positively associated with physiological responses to social evaluation, regardless of the type of smile feedback a participant received (i.e., vagal flexibility *did not interact* with experimental condition: see **Table 1**). These findings suggest that vagal flexibility might sensitize perceivers to all social signals, regardless of the meaning of the signal. **Table 1** reports these findings.

		b (s.e.)	vs. Affiliation	vs. Dominance
Reward				
	Cortisol (AUC*i*)	7.04 (4.39)	0.95 (5.60)	1.30 (5.83)
	Heart Rate	6.44** (2.31)	-0.32 (2.94)	-1.97 (3.06)
Affiliation				
	Cortisol (AUC*i*)	7.99* (3.46)	--	0.36 (5.16)
	Heart Rate	6.12** (1.82)	--	-1.65 (2.71)
Dominance				
	Cortisol (AUC*i*)	8.35* (00.0)		--
	Heart Rate	4.47* (2.01)		--

Table 1: ***Associations between HF-HRV reactivity (baseline – task) and physiological responses to social evaluation.*** Unstandardized regression coefficients quantifying the association between HF-HRV reactivity (baseline – task) and physiological responses are reported in the left-hand column, for each group. Differences between groups are reported in the middle and right-hand columns. *p<0.05; **p<0.01; ***p<0.001

Analyses were conducted in the R statistical environment (R Core Team, 2014). All results reported in the present work remain significant when adding a dichotomous predictor to account for which of the two confederates a participant interacted with, as well as when statistically accounting for factors known to influence levels of physiological activity (caffeine use, depression severity).

Discussion

In the present study, I tested the extent to which two metrics of vagal activity—vagal tone and vagal flexibility—predict differentiated physiological responses to smiles. I expected vagal tone to moderate the effect of smile type on physiological activity. The results of my analyses confirmed this hypothesis. Specifically, whereas vagal tone was negatively related to participants' physiological activity when they received affiliation smiles and positively related to their physiological activity when they received dominance smiles (i.e., moderation), vagal flexibility was related to greater cortisol and heart rate response to all smiles, regardless of their social meaning (i.e., no moderation).

The observed pattern of results suggests that vagal tone, but not vagal flexibility, is a useful predictor of physiological differentiation of the social meaning conveyed by facial expressions. These findings do not support recent evidence linking vagal flexibility with facial expression recognition (Muhtadie et al., 2014), and there are a handful of potential explanations for this. First, vagal flexibility is highly context-dependent (Berntson, Cacioppo, & Fieldstone, 1996). In fact, recent research suggests that vagal flexibility should be assessed in a context that is as purely "cognitive" as possible (Muhtadie et al., 2014). That is, to the extent that the task itself is stressful, changes in vagal activity are likely confounded with sympathetic nervous system effects and do not necessarily represent purely parasympathetic modulation of cardiac activity. Theory corroborates this position, arguing that the autonomic nervous system is hierarchically organized such that only in socially "safe" scenarios can the parasympathetic nervous system exert its effects on the body (Porges, 2001). Second, respiratory rate is a known confound of vagal activity. In this study, respiratory rate was not assessed, so the two indicators of vagal activity could not be adjusted for respiratory rate. Both of these factors (a more "cognitive" task and assessment of respiratory activity) are addressed in the next set of studies: Study 2 and Study 3. In light of these concerns, the indicator of vagal flexibility in this study is likely a poor one, and corresponding care should be taken when drawing conclusions with regard to vagal flexibility results in this study.

The observed relationship between vagal tone and physiological responsiveness to specific smile meaning is consistent with the proposition set forth in the introduction to this dissertation that individual differences in vagal tone relate to social connection insofar as individual differences in vagal tone predict facial expression recognition. The present finding implies that individuals with particularly low vagal activity may be at risk of poor socio-emotional outcomes due to deficits in understanding the social signals of others. Furthermore, a number of pathological and pre-disease body states are related to lower vagal activity, including heightened inflammation and obesity (Cooper et al., 2015; Laborde, Mosley, & Thayer, 2017). As such, these body states may fundamentally change an individuals' ability to respond physiologically to the social world, and in light of the present findings, may be associated with deficits in understanding the expressions of others. A compelling avenue for future research therefore is to investigate how individuals with relatively low vagal activity recognize and respond to the expressions of others.

Future research should also consider how affective disorders associated with lower vagal activity, such as anxiety (Chalmers, Quintana, Abbott, & Kemp, 2014) and depression (Carnevali, Thayer, Brosschot, & Ottaviani, 2017), relate to cognitive and physiological responses to social stimuli. Given the social stress procedure implemented in the present work, an especially fruitful avenue for future research on the social functions of smiles lies in the relationship between smile processing and social anxiety. Social anxiety disorder involves the fear of embarrassing oneself in front of others in performance or evaluative situations (Morrison & Heimberg, 2013). Although research consistently documents that individuals with social anxiety disorder exhibit heightened negative affect both in anticipation of and in response to social evaluation (Rapee & Lim, 1992; Roelofs et al., 2009), findings are mixed regarding how these individuals respond to positive and supportive social signals (Buckner, DeWall, Schmidt, & Maner, 2010; Maner, DeWall, Baumeister, & Schaller, 2007). Social anxiety was not accounted for in the present study. Although randomization into condition likely mitigated any effect of social anxiety on the present findings, future work is needed to investigate how individuals with social anxiety respond to facial expressions as evaluative feedback. A crucial comparison in this work will be to assess differences in affective and physiological responses between the relatively unambiguous reward smiles and the less clear affiliation smiles.

The present research also contributes to a growing body of literature on the social functions of smiles (Martin et al., 2017). I observed that smiles with different social functions (Niedenthal, Mermillod, et al., 2010), when delivered as evaluative feedback in a stressful social context, exert distinct influences on perceivers' physiological activity. Dominance smiles (compared to reward or affiliation smiles) were associated with increases in heart rate and salivary cortisol that mirror the influences of negative verbal feedback (Kudielka & Wüst, 2010). In contrast, reward and affiliation smiles exerted influences similar to the effects of displays of friendliness (Wiemers, Schoofs, & Wolf, 2013) and positive social evaluation (Akinola & Mendes, 2008), such that, compared to dominance smiles, they buffered physiological activity. The findings thus provide further evidence for the view that smiles do not constitute a homogenous category of “positive” nonverbal feedback. The findings also contribute to a literature that proposes a role for cortisol in adaptive responding to the social environment (Kemeny, Gruenewald, & Dickerson, 2004). In particular, cortisol appears to support the detection of social threat and coordinate biological activity needed to adequately respond to the threat.

One limitation of the present research is that the experimental design contained no “neutral” feedback condition. It would be hard to create such an experience, since neutral feedback is interpreted in highly varied ways across individuals. However, methods to create such a control condition could be imagined for future research. Along similar lines, future research could also directly compare the effects of receiving dominance smiles with the effects of receiving more overt signals of negative evaluation such as disgust, contempt, and anger. By employing the present paradigm to test the physiological effects of facial expressions beyond the smiles tested here, researchers could not only more clearly describe the unique effects of receiving social functional smiles but also understand the effects of facial expressions on perceivers’ physiological activity more generally.

The present work includes other limitations that warrant comment, two of which concern the participant sample. First, the sample size in this study may have been relatively small given the size of the effects detected. Since, to my knowledge, no work has explored the effect of receiving social functional smiles as social evaluative feedback, *a priori* power analyses were difficult to conduct. I estimated required sample size from extant studies with methods and aims as similar to the present research as possible (Akinola & Mendes, 2008; Kassam et al., 2009). Following these guidelines, 90-100 participants is typical for a study of this nature involving three between-subjects conditions. Post-hoc power analyses using G*Power (Faul, Erdfelder, Buchner, & Lang, 2009) indicate that achieved power was modest for the critical comparisons within the HPA axis (dominance vs. affiliation: $\beta = .72$; dominance vs. reward: $\beta = .81$). In light of the achieved power, I recommend that future studies of this sort rely on no fewer than 35-40 participants per between-subjects condition to ensure adequate power.

Second, the present sample was restricted to men. Although I limited the sample to males for reasons that were established and justified before the research was conducted (see Methods, above), generalizations from my findings are necessarily limited. Since sex effects are observed in research on the perception of facial expression of emotion (Hampson et al., 2006; Vassallo, Suzane, Cooper & Douglas, 2009), future work should determine what portion (if any) of the currently documented effects are contingent upon the sex of the smiler or perceiver. Some work suggests that men respond more to threats of physical aggression whereas women respond more to condescending behaviors and social aggression (Bettencourt & Miller, 1996). Thus, men and women may respond to the same type of smile in different ways and may also use each of the smile types with varying degrees of frequency (Fischer & LaFrance, 2014).

The present research demonstrates that functionally different smiles are sufficient to augment or dampen HPA axis activity in accordance with the social functional meaning associated with each smile. Furthermore, physiological responses to each functionally distinct smile are most differentiated in individuals with higher vagal tone, suggesting that vagal tone is a useful individual difference moderator of the ability to connect with others via understanding their facial expressions. The present findings suggest that smiles coordinate the physiological activity that supports interpersonal encounters to a previously undocumented degree, and that facial expressions help regulate the social world, in part, through their impact on the physiological activity of perceivers.

Studies 2 & 3: Analysis of publicly-available data

Study 1 was driven by the reasoning that individual differences in vagal tone support social connection by down-regulating physiological activity in the presence of others in order to better understand their social signals. This theorizing led to the hypothesis that individuals with greater vagal tone exhibit better facial expression recognition as evidenced by increased physiological differentiation between different kinds of smiles, with heart rate and cortisol responses mapping onto the social meaning of the different smiles. Findings from Study 1 support this hypothesis, but present a number of limitations as well as leaving open questions about the role of vagal flexibility in social connection and the potentially separable contributions of vagal tone and vagal flexibility to our ability to connect with others.

Studies 2 and 3 expand upon the methods and questions from Study 1. In Studies 2 and 3, indicators of vagal flexibility were assessed in a more purely cognitive context than in Study 1, better mapping onto previous methods for assessing vagal flexibility (Muhtadie et al., 2014). Furthermore, respiratory data were collected during the assessment of vagal activity in order to appropriately adjust indicators of vagal activity for respiratory rate. Although these factors have little bearing on the finding from Study 1 that vagal tone was related to physiological differentiation of facial expressions, both of these factors make Studies 2 and 3 a stronger test of any association between vagal flexibility and social connection.

All data for Studies 2 and 3 have been collected and made publicly available as part of the nationally-representative Midlife in the United States (MIDUS) study. The MIDUS study is a longitudinal study sponsored by the U.S. National Institute on Aging. The project investigates factors related to physical and mental well-being from young adulthood to senescence. Three waves of data have been collected. In the initial wave, begun in 1994 (MIDUS 1), participants aged 25 to 74 responded via phone interviews and mailed questionnaires. In the second wave, begun in 2004 (MIDUS 2), participants again responded to phone interviews and mailed questionnaires. Some of these participants also contributed data to sub-projects that assessed distinct aspects of psychological and physical functioning. The third wave (MIDUS 3) began in 2013 and continued data collection from the same set of participants via phone interviews, mailed questionnaires, and further sub-projects. A schematic of the data collection timeline for the data analyzed in this dissertation is presented in **Figure 5.**

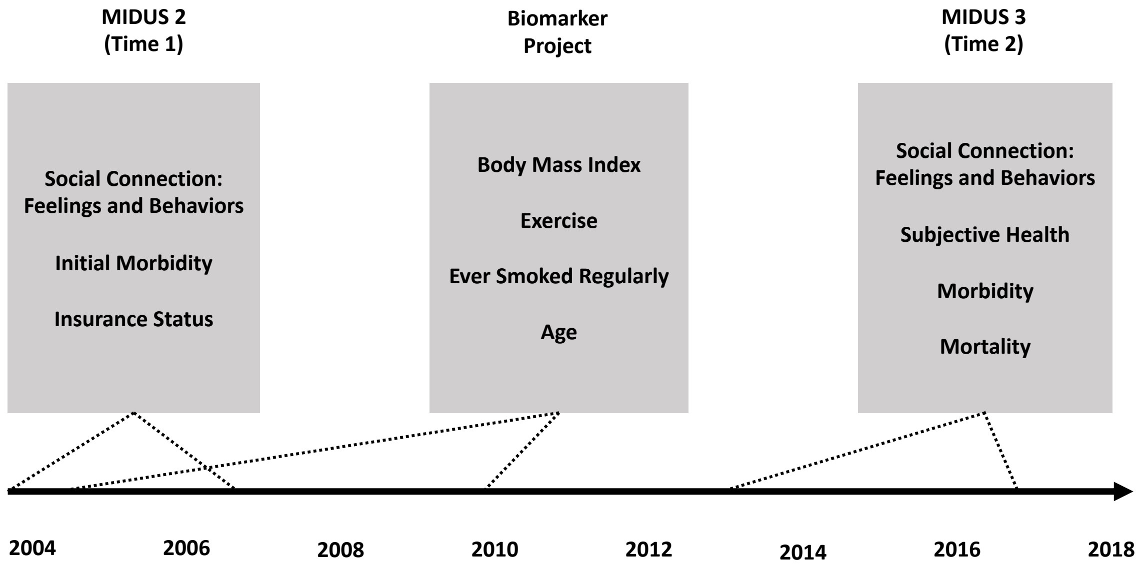


Figure 5: ***MIDUS data collection schedule.*** This figure is a visual representation of the data collection schedule for the MIDUS data analyzed in this dissertation. Subjective and objective measures of social connection were assessed at two time points (referred to as Time 1 and Time 2). Initial disease morbidity status was assessed at Time 1, with new occurrence of these diseases coded at Time 2. Mortality status was assessed at Time 2. All physiological data, including vagal tone and vagal flexibility, was assessed during the Biomarker Project which occurred between Time 1 and Time 2.

All physiological data for both Study 2 as well as Study 3 come from the Biomarker sub-project of MIDUS 2, to which 1255 participants contributed data. In order to be eligible for the

Biomarker project, participants must first have completed the at-home MIDUS 2 survey assessment. Initial indicators (i.e., subjective and objective social connection, disease morbidity, insurance status) were assessed *before* physiological indicators were collected. Follow-up indicators of all initial measures as well as mortality status were assessed 10 years after MIDUS 2 began. All participants had completed physiological assessment *before* providing follow-up data. Thus, assessment of physiological indicators was book-ended by initial and follow-up survey assessments, which occurred after (MIDUS 2) and before (MIDUS 3) assessment of psychological and other self-report variables for all participants.

As outlined in the introduction to this dissertation, Studies 2 and 3 aim to test the extent to which both indicators of vagal activity predict social connection and related health and well-being outcomes. Results are generally expected to confirm the hypothesis that individuals with higher vagal flexibility are more socially connected, and this social connection positively impacts health and well-being. In Study 2, I test whether individual differences in vagal tone and vagal flexibility predict levels of social connection, with the expectation that individual differences in vagal flexibility are positively associated with a greater degree of social connection. In Study 3, I test the extent to individual differences in vagal tone and vagal flexibility predict long term health and well-being as mediated by feelings of social connection, with the expectation that individual differences in vagal tone and vagal flexibility both are related to health and well-being, but that whereas the relationship between vagal tone and health and well-being is direct, the relationship between vagal flexibility and health and well-being is indirect, as mediated by social connection.

Study 2: Vagal activity and social connection

Study 2 aims to test the extent to which individual differences in indicators of vagal activity, particularly vagal flexibility, are positively associated with feelings and behaviors reflecting social connection. As stated in the introduction to this dissertation and summarized above, greater vagal flexibility is expected to be positively associated with feelings and behaviors related to social connection at both initial and 10-year follow-up assessments. Vagal tone is expected to be either more weakly associated with social connection or to show no association.

Methods

Data for Study 2 were drawn from the self-administered questionnaires in MIDUS 2 and MIDUS 3 (i.e., 10-year follow-up) as well as the physiological data acquired during MIDUS 2, Project 4: Biomarker, to which 1255 participants contributed data. During collection of Biomarker data, participants spent two days, including an overnight visit, at one of three clinical research center sites: University of Wisconsin – Madison, University of California, Los Angeles, or Georgetown University. Aside from answering a set of questionnaires concerning medical history, participants underwent a physical exam in the afternoon/evening of their first day at their regional clinical research center. Before breakfast on the second day of their visit, participants underwent fasting blood draws. After breakfast on the second day of visiting their regional clinical research center, participants engaged in laboratory-based cognitive and physical tasks while their physiological activity was assessed. During the laboratory protocol, participants' cardiovascular and respiratory activity were measured at rest (11 minutes), followed by two cognitive tasks (mental arithmetic and color-word Stroop, 6 minutes each) in counterbalanced order. Following each cognitive task, participants also had a 6-minute period for recovery. Resting, task, and recovery all occurred in a sitting position.

The mental arithmetic task was either the Paced Auditory Serial Addition Test “PASAT” (Diehr, Heaton, Miller, & Grant, 1998) or the Morgan and Turner-Hewitt “MATH” (Turner, Sims, Carroll, Morgan, & Hewitt, 1987). The mental arithmetic task was changed from the PASAT to the MATH task three months after data collection began. Since only a small number of participants engaged in the PASAT and the task took twice as long to complete, data from these participants will be excluded. The MATH task is a computer-assisted mental arithmetic task ranging in difficulty from operations on a pair of one-, two-, or three-digit numbers. Participants are asked to add or subtract the numbers shown on the screen and then a potential answer is displayed. Using a set of buttons, participants then respond with whether or not the displayed answer is correct. Participants begin the task at a moderate difficulty, and the task progresses in difficulty when participants respond correctly. The 6-minute MATH task was followed by a 6-minute recovery period during which physiological activity was continuously measured.

All participants also engaged in a modified color-word Stroop task. In this task, one of a set of four color names (red, blue, yellow, green) was presented on a computer screen. The font color of each word was either congruent or incongruent with the color name presented on the screen. Using a keypad with four buttons, participants were required to respond to the color of the font, not to the word color name. In order to standardize the difficulty of the task across participants, the rate of trial presentation increased with the number of correct responses. Average accuracy was 67%. Following the 6-minute, modified color-word Stroop task, participants had 6 minutes to rest and recover.

Physiological data acquisition and analysis

Electrodes were attached to the left and right shoulder. Beat-to-beat analog signals were collected and digitized at 500 Hz using a 16-bit National Instruments analog-to-digital board. Research staff at Columbia University Medical Center in the laboratory of Dr. Richard Sloan visually inspected ECG waveforms in accordance with published procedures (Berntson, Quigley, Jang, & Boysen, 1990), after using proprietary software to identify R spikes in the ECG waveform. The extracted RR series was then used to calculate HF-HRV, an indicator of vagal activation. HF-HRV was calculated in the .15-.50 Hz range using a method similar to that employed by DeBoer and colleagues (Deboer, Karemaker, & Strackee, 1984). First, the mean from the RR series was subtracted from each value in the series and the resultant series was filtered via a Hanning window. After applying a fast-Fourier transform, power in the high-frequency (.15-.50 Hz) band was summed and adjusted for attenuation due to this procedure (Harris, 1978). HF-HRV was calculated on a minute-by-minute basis for the resting, task, and recovery periods. All HF-HRV data were then natural log transformed.

Participants underwent continuous respiratory monitoring via inductive plethysmography using the Portable Inductotrace system (Bio-logic Systems Corporation, Mundelein, Illinois). Analog signals were sampled at 20 Hz, digitized, and then visually inspected and corrected. Because respiration is known to influence HF-HRV, confounding its correlation with vagal activity, HF-HRV was adjusted for respiratory rate on a minute-by-minute, person-by-person basis (Cyranowski, 2011; Sloan et al., 2001). In order to make this adjustment, respiratory rate for each one-minute interval was regressed on HF-HRV for that epoch, controlling for whether the epoch was during resting, task, or recovery on a subject by subject basis. Resultant, unstandardized residual HF-HRV scores were saved. These natural log transformed, respiratory-rate adjusted HF-HRV scores will be used for all analyses.

Vagal tone was calculated as the average natural log-transformed, respiration-rate adjusted HF-HRV for the last six minutes of the resting baseline period. Vagal flexibility was calculated as the maximum difference in HF-HRV from baseline to task. Values were natural log-transformed and respiration-rate adjusted and multiplied by -1 so that greater vagal flexibility values indicate larger decreases from baseline.

Social connection measures

Initial self-reports of feelings and behaviors reflecting social connection were collected between 0 and 2 years before collection of physiological data as part of the main MIDUS study survey protocol. Although much of the self-report data for individuals who participated in the Biomarker sub-project are readily available to the research community, a subset of these data were collected from an over-sample of African American individuals in Milwaukee, Wisconsin. Due to the restricted geographic area of this oversample, researchers are required to complete a certification of confidentiality before accessing Milwaukee data. Researchers must contact the National Archive of Computerized Data on Aging (NACDA), at the University of Michigan ICPSR for access. All analyses in this dissertation include data from all participants in the Biomarker project, including both the main survey sample and the Milwaukee over-sample.

For indicators of feelings of social connection, in line with previous research (Geisler et al., 2013), I use the social integration and social acceptance measures from the Social Well-being Scale (Keyes, 1998). Furthermore, I also employ self reports of loneliness, and social closeness as additional indicators of feelings of social connection. All items assessing feelings related to social connection, including means and standard deviations, are available in **Appendix I.**

With regard to behavioral measures of social connection, I use self-reports of the frequency of social contact (neighbors, friends, and family) as well as the frequency of participation in community groups (professional groups, social groups, other). All survey items related to behaviors of social connection, including means and standard deviations, are available in **Appendix II.**

Participants provided follow-up data on the same social connection items after no fewer than four years (*M* = 6.75, *SD* = 1.25, min-max = 4.16-9.16). Means and standard deviations for these survey items at follow-up assessment are available in **Appendices I** & **II**. Follow-up data are included in a second set of analyses in order to test whether relationships between vagal activity and social connection are stable over time. A brief description of the survey items with representative questions are provided below.

Indicators of Social Connection: Feelings

- ***Social well-being: social integration.*** This scale measures the extent to which an individual feels that he or she belongs to a community. Participants responded to three items on a 1-7 scale ranging from “Strongly Agree” to “Strongly Disagree”. Higher values on this scale represent a greater sense of being integrated with society. Prompts were of the type: “I don’t feel I belong to anything I’d call a community.”
- ***Social well-being: acceptance of others.*** This scale measures the extent to which an individual accepts the presence of others. Participants responded to three items on a 1-7 scale ranging from “Strongly Agree” to “Strongly Disagree”. Greater values on this scale represent a greater acceptance of others. Prompts were of the type: “People do not care about other people’s problems.”
- ***Loneliness.*** This item assesses the extent to which an individual felt lonely over the last thirty days, responding to the question: “Over the last 30 days, how often did you feel

lonely?" Participants responded on a 1-5 scale ranging from "All of the time" to "None of the time."

- ***Felt close to others.*** This item assesses the extent to which an individual felt close to others, responding to the question: "During the past 30 days, how much of the time did you feel close to others?" Participants responded on a 1-5 scale ranging from "All of the time" to "None of the time."
- ***Few close friends.*** This item assesses the extent to which an individual felt that they had few close friends with whom to share their concerns, responding to the question: "I often feel lonely because I have few close friends with whom to share my concerns." Participants responded on a 1-7 scale ranging from "Agree strongly" to "Disagree strongly."

Indicators of Social Connection: Behaviors

- ***Contact with neighbors.*** Participants reported how often they had more sustained conversations with their neighbors, including "get-togethers", during a typical month. Participants responded on a scale from 1-6 with 1 being "almost every day" and 6 being "never or hardly ever." On this item, higher scores reflect *less* frequency of contact with neighbors.
- ***Contact with family.*** Participants reported how often, during a typical month, they were in contact with members of their family (brothers, sisters, parents, and children) who did not live with them. Contact could be in any of a number of forms including visits, phone calls, letters, and email. Participants responded on a scale from 1-8 with 1 being "several times a day" and 8 being "never or hardly ever." On this item, higher scores reflect *less* frequent contact with family.

- ***Contact with friends.*** Participants reported how often, during a typical month, they were in contact with friends. Contact could be in any of a number of forms including visits, phone calls, letters, and email. Participants responded on a scale from 1-8 with 1 being "several times a day" and 8 being "never or hardly ever." On this item, higher scores reflect *less* frequent contact with friends.
- ***Professional group attendance.*** Participants reported how often they attended union meetings or other professional groups during a typical month. Responses ranged from 0 to 30 times per month.
- ***Social group attendance.*** Participants reported how often they attended social group meetings, including sports, during a typical month. Responses ranged from 0 to 75 times per month.
- ***Other group attendance.*** Participants reported how often they attended other group meetings during a typical month, not including those required by their job. Responses ranged from 0 to 20.

In light of the fact that vagal activity is correlated with a number of behavioral and demographic factors that could confound the statistical relationship between vagal activity and social connection, I included a host of covariates in the present analyses (Laborde et al., 2017). The covariates included are age, sex, body mass index, time lag between self-report and collection of psychophysiological data, smoking status, exercise frequency, and health history (heart disease, stroke, Parkinson's, and other neurological disorders).

Results and Discussion

Descriptive statistics

Of the full 1255 participants who contributed data to the MIDUS Biomarker project, 1076 participants (462 male) had physiological data of sufficient quality to calculate both vagal tone as well as vagal flexibility metrics. This sample of participants was of late middle age (M = 56.69, SD = 11.21), and tended to be somewhat overweight (Mean BMI = 29.82, SD = 6.57). As is typical in studies of assessing both vagal tone and vagal flexibility (for example, see Muhtadie et al., 2014), vagal tone (M = 5.81, SD = 1.79) and vagal flexibility (M = 1.38, SD = 1.29) were correlated in this sample (r = .52). A visualization of these demographics is shown in **Figure 6.**

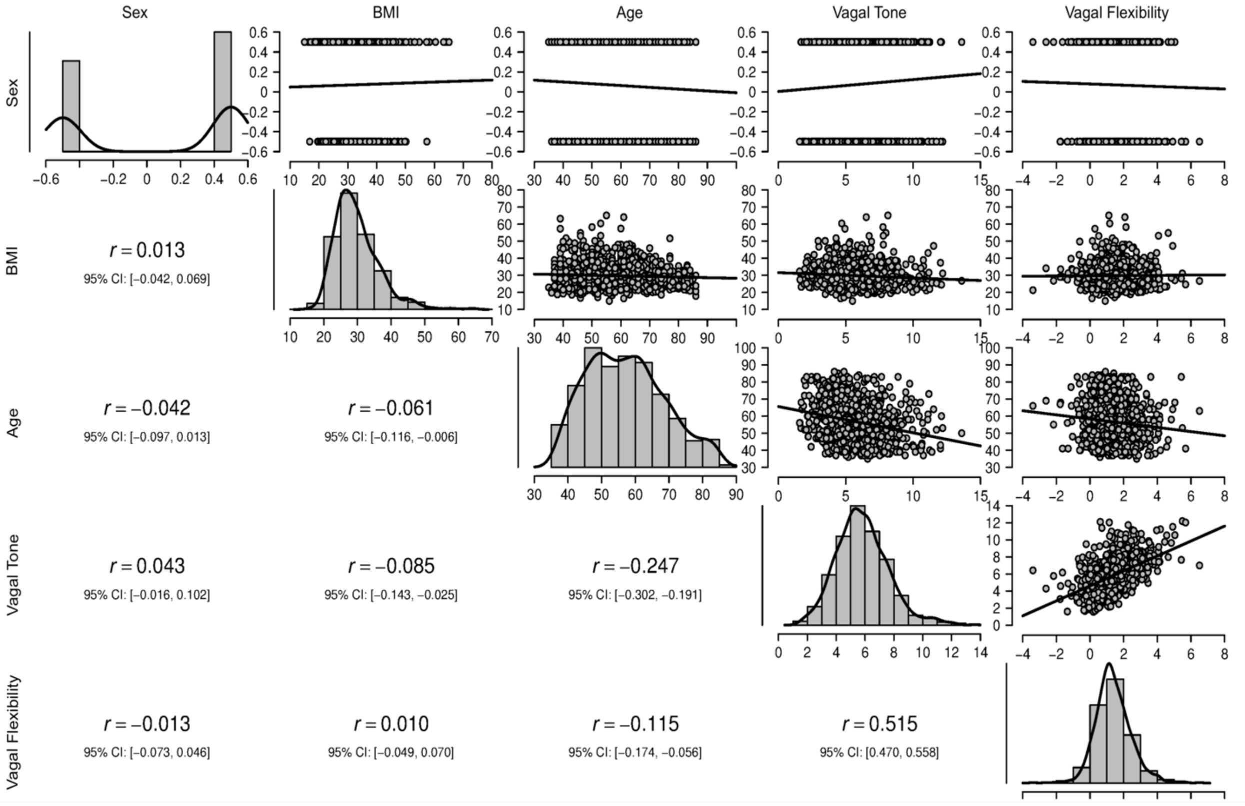


Figure 6: ***MIDUS Biomarker demographics.*** Demographic characteristics of the 1076 participants from the Biomarker project with physiological data of sufficient quality. The main diagonal of this figure displays histograms of variable distributions; the upper right triangle displays scatterplots with best fitting lines for each of the 2-way associations between variables; the bottom left triangle reports the correlation coefficients with 95% confidence intervals.

Indicators of social connection: feelings and behaviors at initial assessment

The five indicators of feelings of social connection at initial assessment were all strongly correlated with each other, as shown below in **Figure 7.** In light of the strong correlations, I created one summary score for feelings of social connection at initial assessment by first standardizing responses within each of the five responses and then averaging across them. Standardized alpha for the single summary indicator of feelings of social connection at initial assessment was .73.

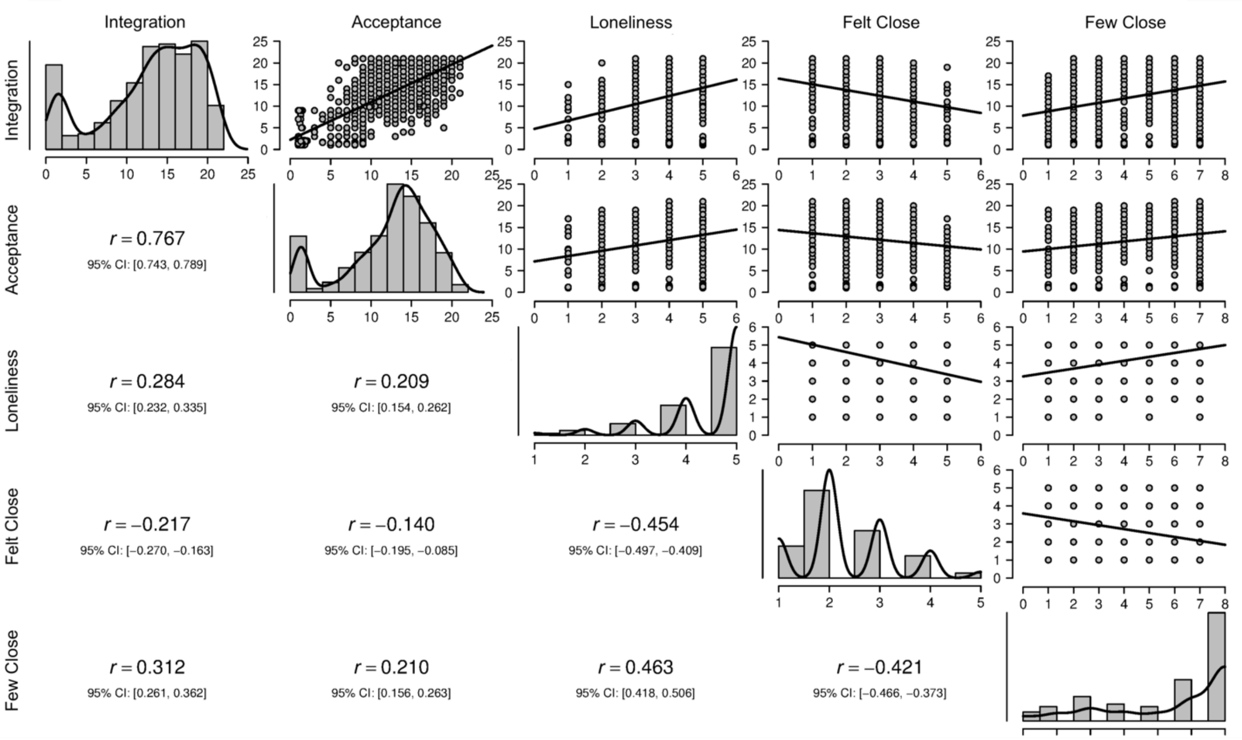


Figure 7: ***Correlations among feelings indicating social connection at initial assessment.*** The main diagonal of this figure displays histograms of variable distributions; the upper right triangle displays scatterplots with best fitting lines for each of the 2-way associations between variables; the bottom left triangle reports the correlation coefficients with 95% confidence intervals.

The six indicators of behaviors of social connection at initial assessment were only modestly correlated (see **Figure 8**). As with the indicators of feelings of social connection, I created one summary score for behaviors of social connection at initial assessment by first standardizing responses within each of the six responses and then averaging across them.

Standardized alpha for single summary indicator of behaviors of social connection at initial assessment was poor (alpha = .4).

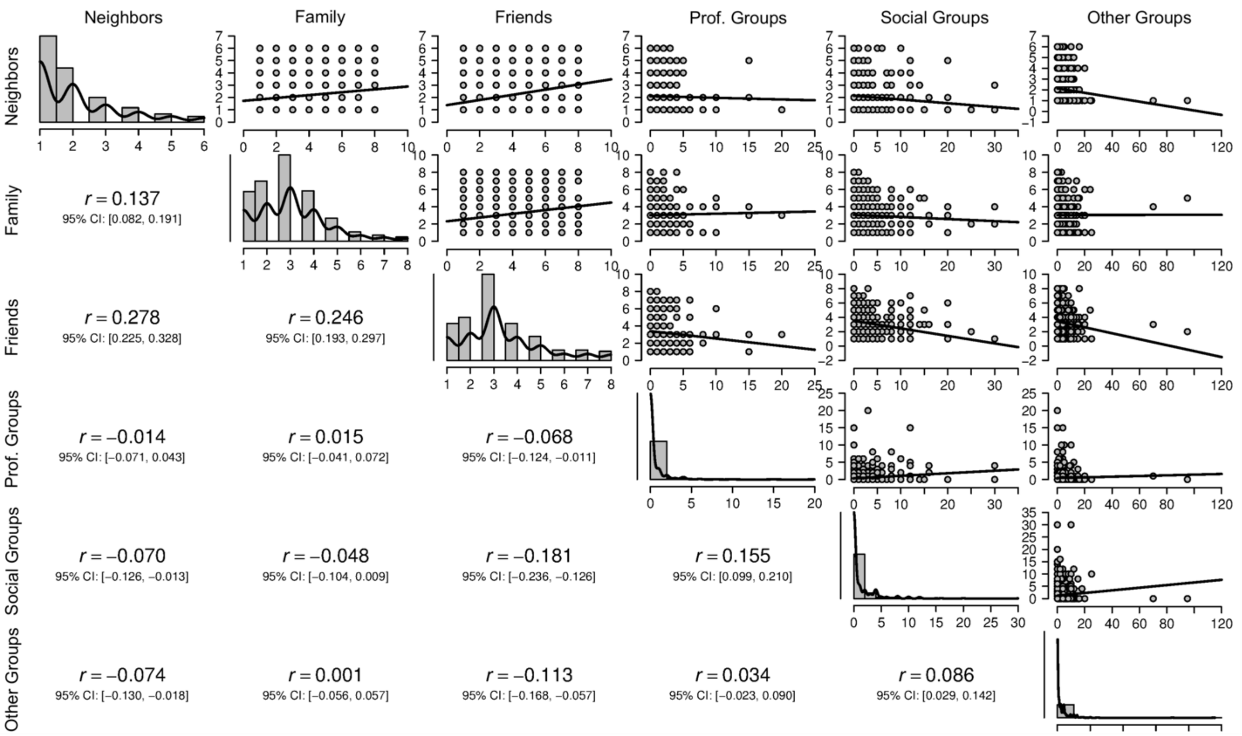


Figure 8: ***Correlations among behaviors indicating social connection at initial assessment.*** The main diagonal of this figure displays histograms of variable distributions; the upper right triangle displays scatterplots with best fitting lines for each of the 2-way associations between variables; the bottom left triangle reports the correlation coefficients with 95% confidence intervals.

Results: initial assessment

In order to test the hypothesis that vagal flexibility, above and beyond vagal tone, is associated with greater social connection, I ran two linear regression models. In the first, I regressed the feelings summary score for social connection at initial assessment on vagal tone, vagal flexibility, age, sex, and body mass index. In the second, I regressed the summary score for behaviors indicating social connection on the same predictors. Vagal flexibility was positively associated with feelings (b = 0.08, 95%CI [.03, .12], t (1044) = 3.41, p < .0001), but not behaviors (*b* = 0.005, 95%CI [-.03, .04], *t* (1029) = 0.28, *p* = .78), indicating social connection. On the other hand, vagal tone was not related to either summary indicator (*p*s > .25). These results are displayed in **Figure 9.**

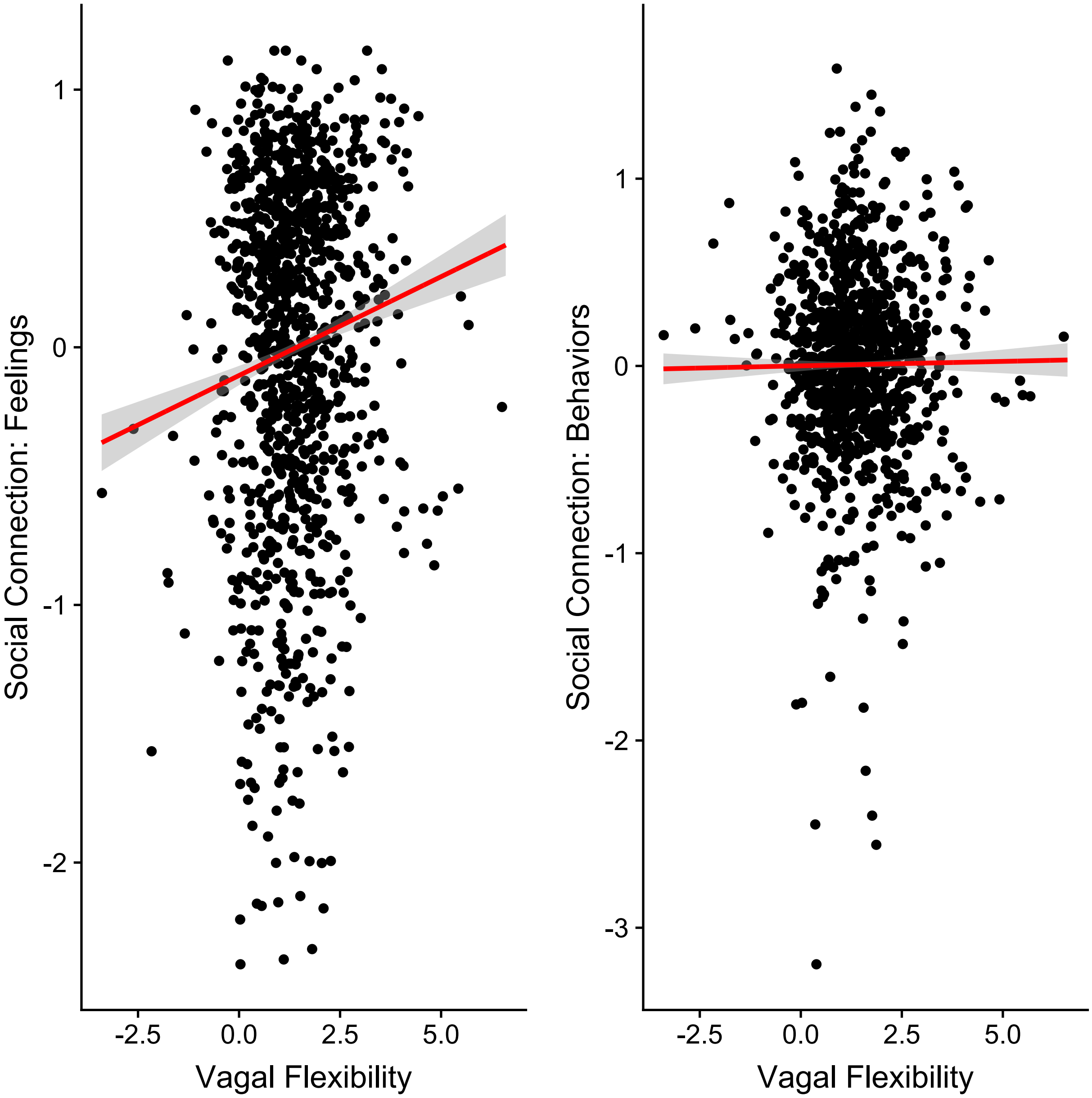


Figure 9: ***Feelings, but not behaviors, indicating social connection are associated with vagal flexibility at initial assessment.*** Model estimates are displayed by red lines, surrounded by a 95% confidence envelope. Model estimates for the regression slope are displayed at the mean level of all other regressors in the model (i.e., vagal tone, age, sex, BMI). Data points are raw data.

To test the robustness of these findings, I then ran two follow-up analyses. In the first follow-up analysis, I added further covariates to the linear model regressing the summary feelings score on vagal tone, vagal flexibility, age, sex, and BMI. To this base model, I further included regressors for: level of exercise, smoking status, number of months lag between self-report and physiology assessment, whether or not the participant had history of a heart condition, history of stroke, history of Parkinson's, or history of another neurological disorder. Vagal flexibility continued to be a significant predictor of summary scores of feelings of social connection in this extended model (p = .002).

A component of the MIDUS dataset includes a twin sample. I conducted a second follow-up analysis in order to account for the correlated errors between family members. In order to do this, I ran the same extended linear regression model with additional covariates (as detailed in the previous paragraph) in a mixed-effects model framework, with a by-family random intercept. In this model, vagal flexibility was no longer a significant predictor of the summary indicator of social connection at initial assessment (p = .11). Taken together, findings generally support the hypothesis that vagal flexibility, to a greater extent than vagal tone, predicts indicators of social connection, specifically those related to feeling social connectedness.

Indicators of social connection: feelings and behaviors at follow-up assessment

In order to strengthen the initial finding that vagal flexibility but not tone, is associated with feelings but not behaviors indicating social connection, I conducted an identical set of analyses as reported above, with data collected at follow-up assessment in place of initial assessment. By using the same measures and approach as before, this analysis of follow-up indicators of social connection provides a test of the over-time stability of the effect preliminarily detected at initial assessment.

I again created summary scores of feelings and behaviors indicating social connection by standardizing within items and then averaging across. **Figures 10** and **11** report correlations between items for feelings (**Figure 10**) and behaviors (**Figure 11**) respectively. Summary score reliability remained acceptable for the feelings indicator (standardized alpha = .63), but was again low for the behaviors summary indicator (standardized alpha = .39).

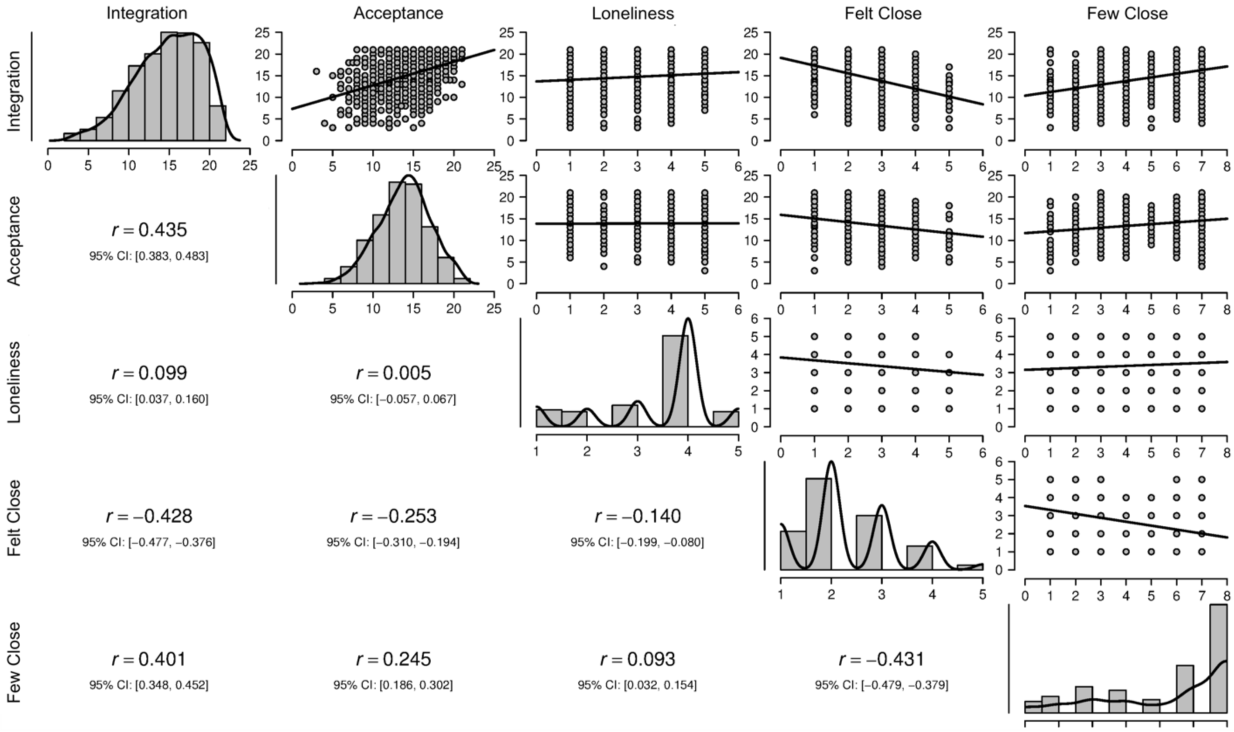


Figure 10: ***Correlations among feelings indicating social connection at follow-up assessment.*** The main diagonal of this figure displays histograms of variable distributions; the upper right triangle displays scatterplots with best fitting lines for each of the 2-way associations between variables; the bottom left triangle reports the correlation coefficients with 95% confidence intervals.

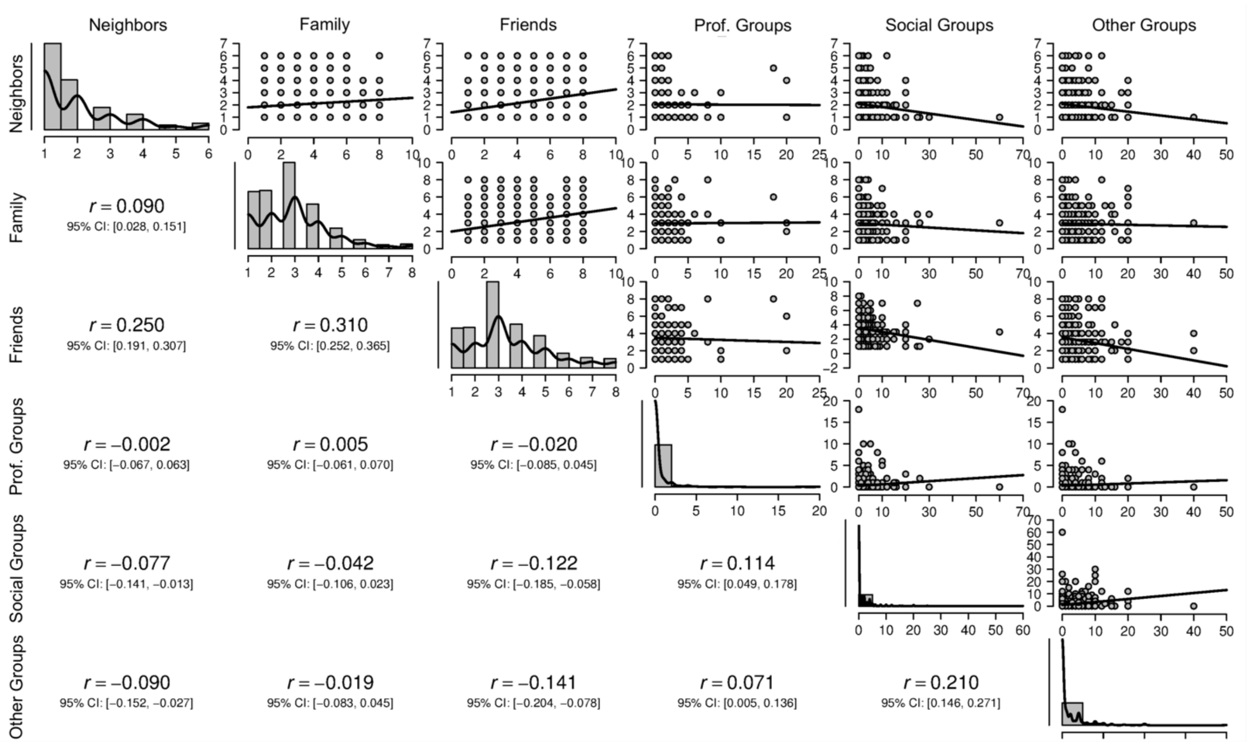


Figure 11: ***Correlations among behaviors indicating social connection at follow-up assessment.*** The main diagonal of this figure displays histograms of variable distributions; the upper right triangle displays scatterplots with best fitting lines for each of the 2-way associations between variables; the bottom left triangle reports the correlation coefficients with 95% confidence intervals.

Results: follow-up assessment

Identical to the analysis at initial assessment, I again regressed both the summary score for feeling as well as the summary score for behaviors on vagal tone, vagal flexibility, age, sex, and BMI. As was the case at initial assessment, vagal flexibility continued to be a significant predictor of feelings (b = 0.07, 95%CI [.02, .11], t (878) = 2.88, p = .004), but not behaviors (b = -0.02, 95%CI [-.06, .02], t (791) = -1.13, p = .25) indicating social connection. As before, this was not the case for vagal tone (ps > .4). These results are displayed in **Figure 12**.

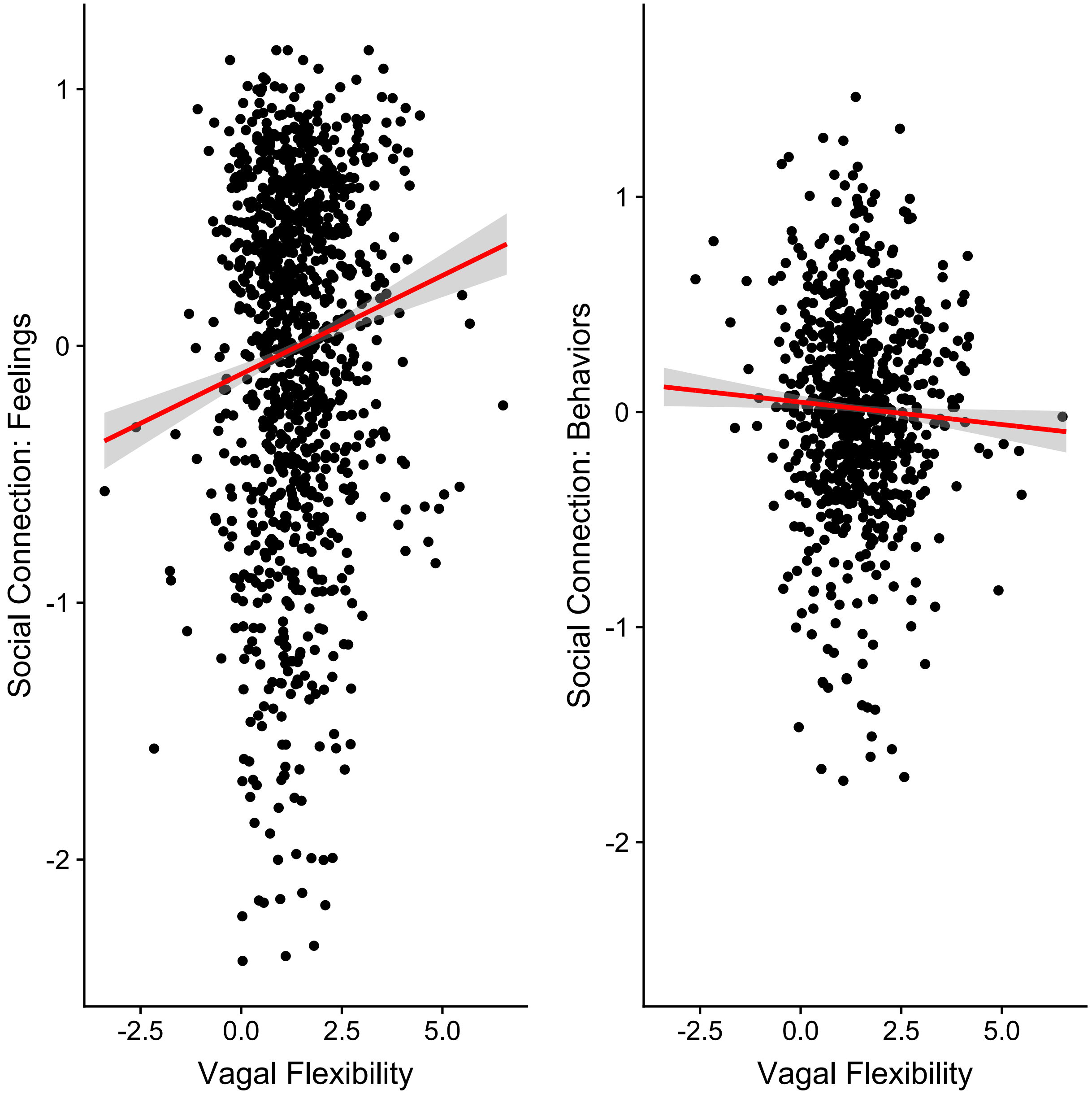


Figure 12: ***Feelings, but not behaviors, indicating social connection are associated with vagal flexibility at follow-up assessment.*** Model estimates are displayed by red lines, surrounded by a 95% confidence envelope. Model estimates for the regression slope are displayed at the mean level of all other regressors in the model (i.e., vagal tone, age, sex, BMI). Data points are raw data.

As before, I tested the robustness of the relationship between vagal flexibility and feelings of social connection in two follow-up models: the first a linear regression model with additional covariates, the second a mixed-effects model with the same, extended set of covariates as well as a random intercept for family membership. Vagal flexibility continued to be a significant predictor of feelings of social connection in both the linear regression model (*p* = .01) as well as the mixed-effects model (*p* = .047). These findings provide a sort of internal replication of the robustness of the association between vagal flexibility and feelings of social connection. Findings from initial and follow-up assessments, when taken together, provide support for the conclusion that vagal flexibility, to a greater extent than vagal tone, predicts indicators of social connection, particularly those related to feeling connected with others.

Summary of Study 2

The goal of Study 2 was to test the hypothesis that individual differences in vagal flexibility, and to a lesser extent vagal tone, positively predict feelings and behaviors indicating social connection. Findings supported hypotheses for feelings, but not behaviors. Importantly, the relationship between vagal flexibility and feelings of social connection were not statistically-attributable to vagal tone and were generally robust to the presence of covariates and mixed-effects modeling for within-family correlations. Findings strongly suggest that vagal flexibility, but not tone, is associated with feeling socially-connected and that this relationship is stable over time.

Contrary to hypotheses, neither vagal tone nor vagal flexibility showed consistent relationships with behaviors indicative of social connectedness. Furthermore, the data present a limitation that warrants further discussion. One component of the MIDUS project involves a twin sample, and data from some of these twins appear in the present analyses. As noted above, in addition to the main analyses, I also conducted a mixed-effects analyses regressing social connection measures on metrics vagal activity while accounting for the presence of twins with by-family random intercepts. Although this mixed-effects approach led to vagal flexibility no longer being a significant predictor of feelings of social connection at initial assessment, the significance of the relationship at follow-up assessment was not affected by a mixed-effects modeling approach. In light of the relative consistency of effects across modeling strategies and time, it is my conclusion that findings from Study 2 provide moderately strong evidence that vagal flexibility, but not tone, predicts feelings of social connection, and that this relationship is relatively stable over time.

Study 3: Vagal activity and long-term health and well-being

Social relationships are good for our bodies and minds (e.g., Holt-Lunstad et al., 2010). To the extent that vagal activity (particularly vagal flexibility) is related to feelings of social connection, one might reasonably predict that vagal activity is also related to health and well-being (Sloan et al., 2017). Building on the finding from Study 2 that vagal activity (particularly vagal flexibility) is related to feelings of social connection, Study 3 tests the extent to which metrics of vagal activity predict subjective well-being (i.e., life satisfaction) and physical health (i.e., morbidity and mortality). As discussed in the introduction to this dissertation, reasonable arguments can be made that both vagal tone and vagal flexibility should predict health and well-being, in related but different ways. On the one hand, vagal tone is strongly related to physical health, showing tight relationships with physical activity and levels of systemic inflammation (Cooper et al., 2015; Laborde et al., 2017). On the other hand, vagal flexibility is related to feelings of social connection, as documented in Study 2. Thus, I generally expect vagal tone to predict health and well-being directly, but vagal flexibility to predict health and well-being indirectly through feelings of social connection. That is, whereas relationships between vagal flexibility and health and well-being are expected to be mediated by feelings of social connection, mediation by social connection is not expected for vagal tone.

Methods

Data were drawn from the full sample of 1255 participants who provided data in the MIDUS 2 Biomarker Project. Subjective well-being (e.g., self-reported health rating) as well as physical health measures of morbidity and mortality are tested here. Measures of health and well-being were collected at 10-year follow-up, no fewer than four years (M = 6.75, SD = 1.25, min-max = 4.16-9.16) after initial collection of vagal tone and flexibility.

Indicators of Subjective Well-being

A set of six indicators of subjective well-being are assessed in this dissertation. A description of the different measures is provided below, with complete documentation of items available in **Appendix III**.

- ***Life satisfaction.*** Participants reported how satisfied they were with their lives in five domains: overall, work, health, relationship with partner/spouse, relationship with children. The two relationship measures (partner/spouse and children) were first averaged, then that averaged relationship score was averaged with the three remaining measures to provide an overall mean score for life satisfaction (Prenda & Lachman, 2001).
- ***Positive affect.*** Participants reported how frequently, over the past thirty days, they experienced each of four positive adjectives from 1 “All of the time” to 5 “none of the time”: enthusiastic, attentive, proud, active (Mroczek & Kolarz, 1998). The mean for the four items was calculated and then the mean was reverse scored so that more positive values reflected greater levels of positive affect.
- ***Negative affect***. Participants reported how frequently, over the past thirty days, they experienced each of five negative adjectives from 1 “All of the time” to 5 “none of the time”: afraid, jittery, irritable, ashamed, upset (Mroczek & Kolarz, 1998). The mean for the five items was calculated and then reverse scored so that more positive values reflected greater levels of negative affect.
- ***Current health***. Participants provided a rating of their current health from 0 “the worse possible” to 10 “the best possible.”
- ***Future health.*** Participants provided an estimate of their expected future health by

responding to the following question: "Looking ahead 10 years into the future, what do you expect your health will be like at that time?"

- ***Your health compared with others'.*** Participants provided an estimate of their health compared to other people of their age, from 1 "Excellent" to 5 "Poor."

Physical Health Measures: Morbidity and Mortality

Data on whether or not participants had ever received a diagnosis of a chronic medical condition (i.e., morbidity data) was collected at both initial assessment as well as 10-year follow-up. The over-time nature of the data makes it possible to assess whether participants developed a new health condition between initial and follow-up assessment. I assigned those who developed a new health condition a value of "1" (all others received a "0") for seven specific health conditions related to cardiovascular, psychological, and neurological functioning:

- ***Hypertension***
- ***Neurological***
- ***Stroke***
- ***Heart Disease***
- ***Cancer***
- ***Diabetes***
- ***Mental Health (anxiety and depression)***

I also coded for participant mortality status at 10-year follow-up such that individuals who had died between initial and follow-up assessment received a "1", with all others receiving a "0". As in Study 2, I included a host of covariates in the present analyses (Laborde et al., 2017). The covariates included are age, sex, body mass index, time lag between collection of psychophysiological data and outcome, smoking status, exercise frequency, and insurance status at initial assessment.

Results and Discussion

Results: subjective well-being

The analytic procedure for this study closely follows the procedure documented in Study 2. The six indicators of subjective well-being were all strongly correlated with each other, as shown below in **Figure 13.** I again created one summary score by first standardizing responses within each of the responses and then averaging across them. Standardized alpha for the single summary indicator of subjective well-being at follow-up assessment was good (alpha = .83).

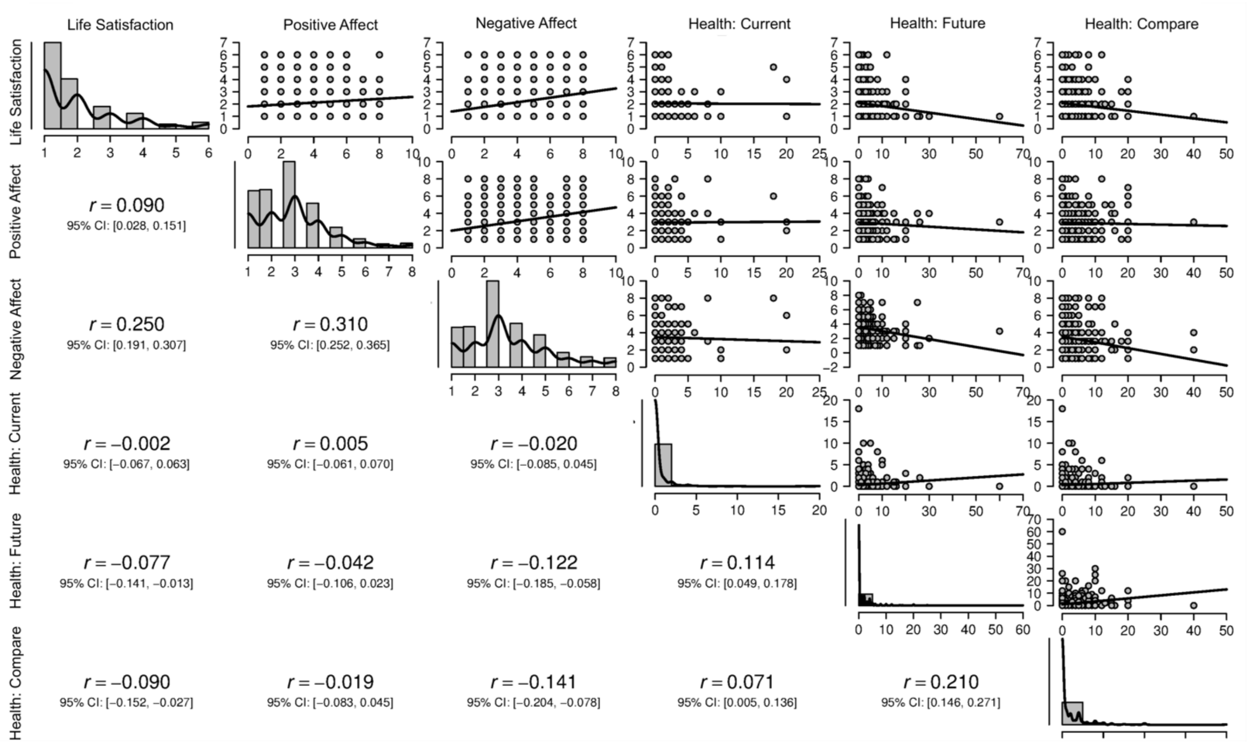


Figure 13: ***Correlations among indicators of subjective well-being at follow-up assessment.*** The main diagonal of this figure displays histograms of variable distributions; the upper right triangle displays scatterplots with best fitting lines for each of the 2-way associations between variables; the bottom left triangle reports the correlation coefficients with 95% confidence intervals.

As in Study 2, I regressed the summary score for subjective well-being on vagal tone, vagal flexibility, age, sex, and BMI. Vagal tone (b = 0.04, 95%CI [.01, .07], t (890) = 2.72, p = .006), but not vagal flexibility (b = 0.03, 95%CI [-.02, .08], t (890) = 1.07, p = .29) was a significant predictor of subjective well-being at follow-up assessment. These results are displayed in **Figure 14**.

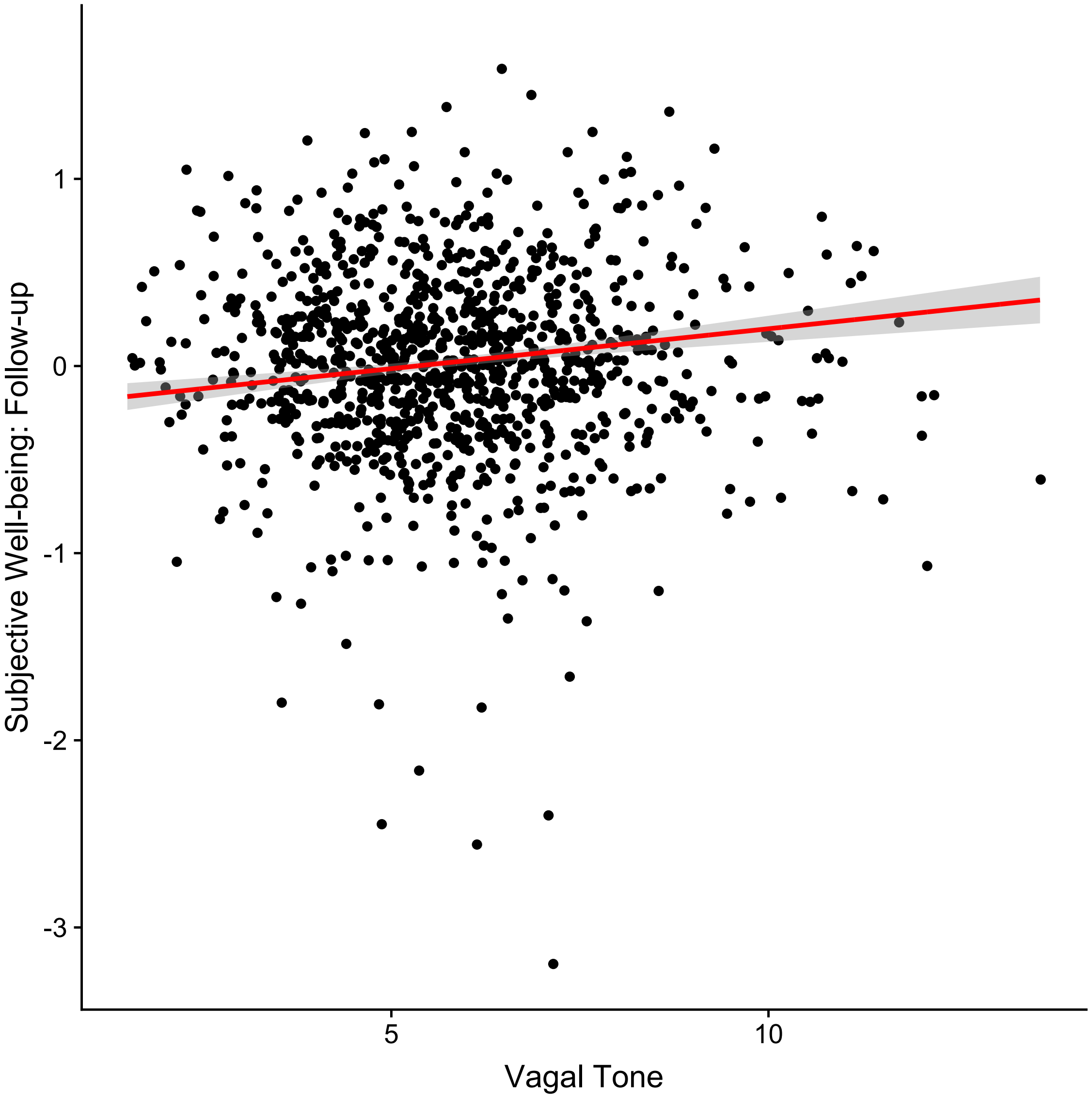


Figure 14: ***Vagal tone, but not vagal flexibility, predicts subjective well-being at follow-up assessment.*** Model estimates are displayed by red lines, surrounded by a 95% confidence envelope. Model estimates for the regression slope are displayed at the mean level of all other regressors in the model (i.e., vagal flexibility, age, sex, BMI). Data points are raw data.

As before, I tested the robustness of this relationship (i.e., vagal tone and subjective well-being) in two follow-up models: the first a linear regression model with additional covariates (exercise, smoking status, number of months lag between physiological assessment and follow-up, health insurance status at MIDUS 2), the second a mixed-effects model with the same, extended set of covariates as well as a random intercept for family membership. Vagal tone continued to be a significant predictor of subjective well-being in both the linear regression model (*p* = .002) as well as the mixed-effects model (*p* = .004).

Results: physical health (morbidity and mortality)

I next considered the relationships between vagal tone and vagal flexibility with indicators of physical health: morbidity and mortality. In order to test these relationships, physical health outcomes (development of a new health condition or mortality status at follow-up) were regressed on vagal tone, vagal flexibility, age, sex, and BMI using logistic regression models. Results from these models are displayed in **Table 2**. Contrary to expectations, neither vagal tone nor vagal flexibility were significant predictors of physical health outcomes at 10-year follow-up.

	Outcome	***b***	***se***	**l95%CI**	**u95%CI**	***t***	***p***
Tone	Hypertension	-0.01	0.01	-0.03	0.02	-0.56	0.57
	Neurological	0.00	0.00	-0.01	0.00	-1.43	0.15
	Stroke	0.00	0.00	0.00	0.01	1.45	0.15
	Heart	0.00	0.01	-0.02	0.01	-0.25	0.80
	Cancer	-0.01	0.01	-0.02	0.00	-1.54	0.12
	Diabetes	-0.01	0.01	-0.02	0.01	-1.03	0.30

	Outcome	*b*	*se*	l95%CI	u95%CI	*t*	*p*
	Mental	0.00	0.01	-0.01	0.02	0.50	0.62
	Mortality	0.00	0.00	-0.01	0.00	-0.97	0.33
Flexibility	Hypertension	-0.01	0.02	-0.04	0.03	-0.39	0.70
	Neurological	0.01	0.01	-0.01	0.02	1.03	0.30
	Stroke	0.00	0.00	-0.01	0.00	-0.78	0.43
	Heart	0.00	0.01	-0.03	0.03	0.00	0.99
	Cancer	-0.01	0.01	-0.03	0.01	-0.87	0.39
	Diabetes	0.00	0.01	-0.02	0.02	0.11	0.91
	Mental	0.00	0.01	-0.02	0.03	0.27	0.79
	Mortality	-0.01	0.01	-0.02	0.00	-1.39	0.16

Table 2: ***Morbidity & Mortality, 10 year follow-up.*** Results from logistic regression models predicting seven indicators of physical health (across morbidity and mortality) from vagal tone, vagal flexibility, age, sex, and BMI. Note that neither vagal tone nor vagal flexibility prospectively predicted physical health outcomes.

Mediation analyses

The results of the analysis of subjective well-being indicated that vagal tone, but not vagal flexibility, prospectively predicted long-term subjective well-being. However, the results from Study 2 connecting vagal flexibility with feelings of social connection in conjunction with research documenting an association between social connection and health and well-being (for example, see Holt-Lunstad et al., 2010), lead to the hypothesis that vagal flexibility indirectly predicts subjective well-being through feelings of social connection. To examine this, I ran mediation analyses with vagal flexibility and vagal tone as focal predictors, feelings of social connection at follow-up assessment as the mediator, and subjective well-being as the outcome. Furthermore, age, sex and BMI were included for each path in the mediation model. Results from this mediation model are presented in **Figure 15.**

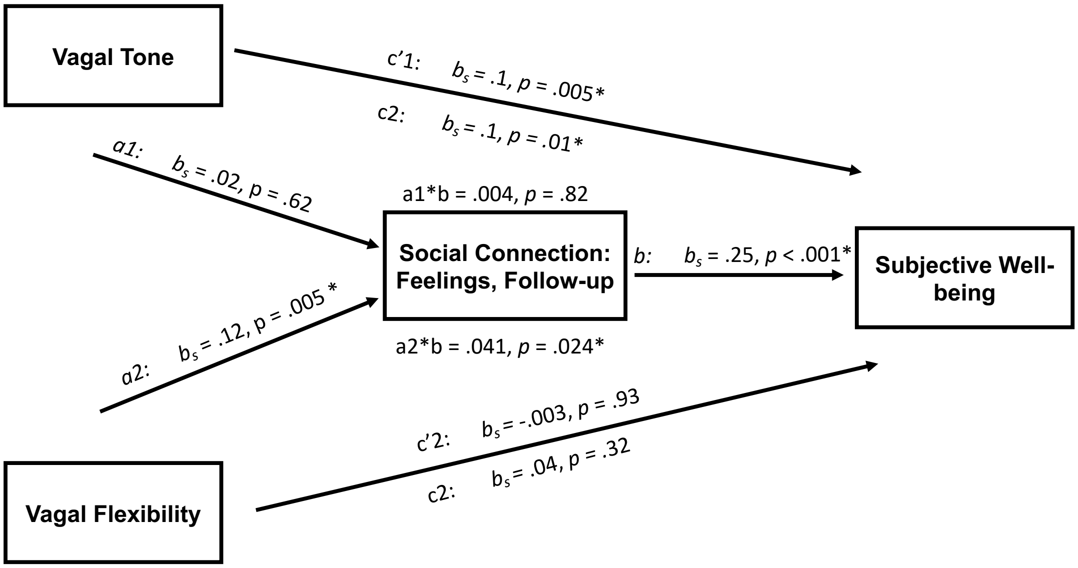


Figure 15: ***Vagal tone and vagal flexibility on subjective well-being through feelings of social connection.*** Mediation model of vagal tone and vagal flexibility on subjective well-being through feelings of social connection. Note: regression coefficients are from the "fully-standardized model." Furthermore, each path in the model was adjusted for age, sex, and BMI.

The mediation analysis shows that both vagal tone and vagal flexibility are related to subjective well-being at 10-year follow-up assessment. In the case of vagal tone, the relationship is direct, with no statistical mediation by feelings of social connection. In the case of vagal flexibility, the relationship is wholly indirect, with the feelings of social connection fully statistically mediating the relationship between vagal flexibility and subjective well-being. Importantly, the detected relationships hold up in the presence of covariates. Furthermore, I conducted a reverse mediation model with subjective well-being as the mediator and feelings of social connection as the outcome. Insofar as the relationship between vagal flexibility and feelings of social connection was not statistically mediated by subjective well-being (a*b = .02, *p* = .32), results were not consistent with a reverse mediation model. Taken together, results from these analyses partially support hypotheses: although neither vagal tone nor vagal flexibility related to physical aspects of health, vagal tone was directly related to subjective well-being, whereas vagal flexibility was indirectly related to subjective well-being through its relationship with feelings of social connection.

Summary of Study 3

Study 3 followed up the findings from Study 2 by considering the downstream predictive utility of vagal tone and vagal flexibility for long-term health and well-being. Although no relationships were detected between either vagal tone or vagal flexibility and physical health indicators (morbidity and mortality), Study 3 revealed a direct relationship between vagal tone and a summary index of subjective well-being. Furthermore, mediation analyses suggest that whereas the relationship between vagal tone and subjective well-being may be direct, vagal flexibility may be indirectly related to subjective well-being through feelings of social connection.

General Discussion

The overarching goal of this dissertation is to clarify the literature on vagal activity and social connection. Throughout this dissertation, I have made the argument that two metrics of vagal activity, vagal tone and vagal flexibility, are predictive of related but separable processes involved in social connection. On the one hand, vagal tone reflects the overall ability to down-regulate physiological activity in the presence of others. On the other hand, vagal flexibility reflects the ability to calibrate physiological activity to the behavioral demands of the present environment. These propositions led to a set of hypotheses that were tested across three studies. Whereas individual differences in vagal tone were expected to predict better facial expression recognition, individual differences in vagal flexibility were expected to predict social connection, with down-stream effects on health and well-being.

The results of Study 1 and the analyses of publicly available data (Studies 2 and 3) offer preliminary evidence for the notion that vagal tone and vagal flexibility predict unique aspects of social connection with differential pathways of influence on health and well-being. In Study 1, vagal tone predicted physiological differentiation of subtle differences in facial expressions. In Study 2, vagal flexibility was a strong predictor of feelings of social connection, both at initial assessment as well as 10-year follow-up. This was not the case for vagal tone, or for the relationships between either metric of vagal activity and behaviors indicating social connection. In Study 3, neither vagal tone nor vagal flexibility predicted physical aspects of health. However, mediation analyses suggest that vagal tone may have a direct relationship with subjective well-being and vagal flexibility may have an indirect relationship with subjective well-being through feelings of social connection. Taken together, these findings suggest that vagal tone and vagal flexibility are individual difference markers that relate to social connection in related but separable ways.

General support was found across all three studies for hypotheses. In Study 1, I expected vagal tone to be related to better facial expression recognition. Findings from this study supported this hypothesis indirectly, insofar as differentiated physiological activity can be seen as reflective of more nuanced processing of facial expressions. Nonetheless, using HPA axis activity and heart rate as indicators of facial expression understanding is only an indirect test of this hypothesis, a limitation I discuss further below.

In the second study, I expected vagal flexibility to relate to both feelings as well as behaviors indicative of social connection. Results supporting only the feelings aspect of this hypothesis. That is, contrary to expectations, behaviors related to social connection were not predicted by vagal flexibility. Failure to detect the hypothesized effect could be for any number of reasons. For example, the behavioral items had poor reliability, so they may not have been good measures. Furthermore, it's possible that behavioral adjustment to context (what I have argued vagal flexibility helps us do) must be assessed at a finer-grained time scale than over the span of months, as was the case in Study 2. Regardless, future work is necessary to definitely determine the extent to which vagal flexibility predicts behavioral aspects of social connection, a possibility I discuss at length below. In the event that it does not, the distinction I have advanced between the social functions of vagal tone and vagal flexibility would need to be revised such that vagal flexibility allows for socio-emotional accommodation to context rather than behavioral.

In the third study, I tested the hypothesis that vagal tone and vagal flexibility were related to long term health and well-being with the expectation that each metric of vagal activity influenced health and well-being differently, either directly (in the case of vagal tone) or indirectly through feelings of social connection (in the case of vagal flexibility). Findings from Study 3 offered partial support for these hypotheses. Although vagal tone and vagal flexibility were not related to physical aspects of health, they were related to subjective well-being, directly and indirectly as hypothesized. The lack of behavioral findings in Study 2 and lack of physical health findings in Study 3 suggest that perhaps indicators of vagal activity are better predictive at the level of the mind, rather than at the level of behavior or physical health. Future research will be required to determine the level, and time-scale specificity of the utility of vagal tone and vagal flexibility as they relate to indicators of social connection.

A number of questions and avenues for future research arise from the findings of these studies. The first question is perhaps most general: what insight, if any, does vagal activity provide with respect to an individual's psychological state? That is, is there a systematic mapping between measurable body states, and psychological states or cognitive processes? Ultimately, these questions are challenging what vagal activity even *means*. Psychologists have long been interested in the bidirectional relationship between the mind and body (for example, see Garfinkel & Critchley, 2013). Although the literature on vagal activity has not come to a definitive conclusion about what vagal activity represents in terms of psychological states, one potential response is that vagal activity represents the output of a domain-general brain system that processes the social-relevance of a given stimulus and prepares the body to meet the opportunities afforded by that stimulus. This conclusion is in line with predominant accounts of the brain-body connection function sub-served by the vagus nerve (Thayer & Lane, 2000) as well as empirical findings that individuals with greater social-contextual sensitivity show higher vagal flexibility (Muhtadie et al., 2014). No doubt, future research is required to dig deeper into the psychological states and processes that drive changes in vagal activity so as to better understand the mental processes that connect vagal activity with social connection.

Another question that arises from this research is to what extent are vagal tone and vagal flexibility separable, or inter-related? That is, do vagal tone and vagal flexibility exert independent, orthogonal influences on physiological activity and behaviors or rather are their effects interactive? It would be reasonable to hypothesize that individuals with high vagal tone are also those with high vagal flexibility, and in fact, extant evidence supports this conclusion (Muhtadie et al., 2014). Thus, it may be the unique combination of high vagal tone with high vagal flexibility that best allows an individual to connect with others. Although researchers have implied such an interactive hypothesis (Thayer & Lane, 2000), to date, the interactive hypothesis has been sufficiently tested. As statistical techniques continue to advance, particularly in the analysis of over-time data, researchers investigating the relationship between vagal activity and socio-emotional outcomes will have further opportunities to explore the interactive and other related hypotheses, such as the potential for non-linear effects, or context-dependent effects (Kogan et al., 2014; Kogan, Gruber, Shallcross, Ford, & Mauss, 2013).

A further question raised by the research presented in this dissertation is why vagal flexibility is related to feelings, but not behaviors, indicating social connection. As discussed above, there are a number of possible explanations for this finding, with the most obvious being that the objective indicators of social connection were poor indicators. Assuming that this is not the case, the present findings suggest that what vagal flexibility tracks isn't an individual's *actual* connection with the social environment, but rather his perceptions of connection with others. This line of reasoning is consistent with the intuitive idea that an individual can have many social ties, but still feel isolated from others. A solid body of research suggests that what really matters for physiological outcomes is how close we *feel* to others rather than how close we actually are in terms of number or frequency of connections (Cacioppo et al., 2015; Sbarra & Coan, 2018).

The present research has implications across domains in psychology. I will briefly discuss implications for two specific research areas: 1) affective science and 2) health and well-being.

Implications for research in affective science

The notion that investigating the temporal patterning of physiological activity will tell us more about the nature and function of emotion is known as the *affective chronometry* approach to emotion (Davidson, 2015). Findings from this dissertation are consistent with this approach, showing that the temporal dynamics of vagal activity (i.e., separating vagal activity into vagal tone and vagal flexibility) are informative above and beyond simply assessing vagal activity at rest. In fact, assessment of patterns of vagal responses over time allows for the researcher to start to make sense of inconsistent findings in the literature on vagal activity and social connection. Specifically, a more temporally-sensitive analysis, such as those that are presented in this dissertation, suggests that vagal tone and vagal flexibility may influence subjective well-being through different mechanisms. Without the temporal approach to analysis, the present finding would have likely been overlooked.

Both the affective chronometry perspective as well as the present findings suggest that researchers in emotion who are attempting to tackle questions that have currently inconclusive or mixed evidence might benefit from adopting an over-time approach to the analysis of their data. Especially in light of quick progress in methods for computation and data analysis, the present findings suggest that researchers should continue to move forward with a temporally-sensitive analysis to all relevant research problems, particularly those that have been stuck at an evidentiary impasse.

Within the context of research on the relationship between vagal activity and interpersonal processes, the present findings suggest that at least two further avenues for temporally-sensitive research would be informative. First, researchers should continue to refine measures of vagal activity over time, such as with moving window analyses (for example, see Gates, Gatzke-Kopp, Sandsten, & Blandon, 2015). A fine-grained, temporally-sensitive approach to vagal activity will open the door for multiple research questions, from individual differences in patterns of vagal responding over time to questions of physiological linkage within dyads (for example, see Waters, West, & Mendes, 2014) or even larger social groups. Second, with the advent and increasing deployment of mobile sensing technologies, researchers should continue to invest time and energy into assessing physiological activity in real-world contexts. Especially given that vagal activity is highly sensitive to modulation by social and other contextual factors (for example, see Berntson et al., 1996), it is logical that findings regarding the social functioning of the vagus nerve might not generalize outside of the lab. A temporally-sensitive approach to the question of how vagal activation relates to social connection (and other similar questions) would undoubtedly yield fruit.

Implications for research on health and well-being

The present findings also have potential implications for applied research on health and well-being. Some have argued that the world is facing a public health crisis, particularly in the domain of non-communicable conditions, such as obesity and mental health disorders (Beaglehole et al., 2011; Marrero, Bloom, & Adashi, 2012). Indeed, non-communicable diseases are the leading causes of death globally, more than all other sources combined (World Health

Organisation, 2010). In order to stem the tide of death and disease, the World Health Organization has called for increased public health monitoring, particularly among individuals from low-resource settings (i.e., rural populations and the poor; World Health Organisation., 2010). With recent technological advances allowing for broad dissemination of wearable health technology, new avenues have opened for the basic as well as the applied researcher to meet this call. Specifically, leveraging wearable health technology would allow basic researchers to better understand the biological indicators (such as, potentially, vagal tone and vagal flexibility) of health and well-being and may help applied researchers to better design public health interventions.

By adding further clarity regarding how vagal tone and vagal flexibility relate to social connection, this dissertation contributes to growing efforts at developing impactful public health interventions by providing a route for personalized health feedback (DiClemente, Marinilli, Singh, & Bellino, 2001; Resnick, 2003). Researchers could potentially provide nuanced individual feedback to assist people in modifying their health behaviors by first collecting potentially-useful information about individual’s parasympathetic nervous system activity.

Avenues for scalable public health interventions with wearable technology are undoubtedly exciting, yet they may have hidden costs insofar as their effectiveness may not generalize across all sectors of the population. For example, at particular risk for developing noncommunicable diseases are people who occupy lower social positions: members of racial and ethnic minority groups, and individuals from low socio-economic-status backgrounds (Banks, Marmot, Oldfield, & Smith, 2006; Chen & Miller, 2013; Major, Mendes, & Dovidio, 2013; Matthews & Gallo, 2010; Mcewen & Gianaros, 2010; Wendy Berry Mendes, Gray, Mendoza-Denton, Major, & Epel, 2007; World Health Organisation., 2010). Furthermore, previous research has identified racial and ethnic differences in vagal activity, suggesting that the parasympathetic nervous system may index race or ethnicity-dependent aspects of socio-emotional functioning (Hill et al., 2015). As such, before instituting a broad public health campaign targeted at increasing vagal tone or vagal flexibility, researchers must first determine *for whom* and *how* vagal tone and vagal flexibility influence health and well-being. An ideal indicator would have high predictive validity irrespective of race or ethnicity, and be associated with a psychological mechanism known to influence health and well-being, such as feelings of social connection.

Limitations

There are a handful limitations for the studies in this dissertation that are worth noting. In Study 1, by using activity in the HPA axis as an outcome measure reflective of the extent to which an individual processed the social meaning of smiles, Study 1 only indirectly tested the hypothesis that vagal tone is related to better understanding of facial expressions. Potentially even more troublesome: how does the increased HPA axis activity for individuals with high vagal tone fit into my argument that vagal tone helps us *decrease* physiological responses to the presence of others? Admittedly, Study 1 was not initially designed to test this theorizing, but rather to test how perceivers respond to different kinds of smiles. Nonetheless, findings from Study 1 are not inconsistent with my theoretical argument. This is because down-regulating physiological activity upon meeting someone is not the same thing as increasing HPA axis activity later when that person evaluates you negatively. One immediately apparent difference is the time course. In the first instance, vagal tone helps keep us calm when meeting others. In the second instance, vagal tone could indicate a perceiver who is ready to respond to the meaning of social signals. Regardless, better theoretical clarity is required for future tests of the thinking I outlined in the introduction.

A further significant limitation generally restricts the interpretation of findings from the present dissertation. This limitation specifically concerns the sympathetic branch of the autonomic nervous system. Although classically conceived as being in diametric opposition, activity in the sympathetic and parasympathetic branches of the autonomic nervous system can occur in any combination (i.e., reciprocal activation, co-activation, etc., as discussed in Berntson et al., 1991). Without a measure of sympathetic nervous system activity in these studies, conclusions about the causal role of vagal tone and vagal flexibility in facilitating social connection are somewhat tenuous. Future work should assess the contribution of sympathetic cardiac control (i.e., pre-ejection period, see Mendes, 2009) alongside cardiac vagal control (i.e., HF-HRV) in predicting social connection.

Conclusion

The overarching motivation of this dissertation is to better understand the physiological systems that predict social connection. Overall, findings from this dissertation provide preliminary evidence for the argument that individual differences in vagal tone and vagal flexibility relate to social connection through two distinct abilities: vagal tone reflects the general ability to down-regulate physiological activity in the presence of others, and vagal flexibility reflects the ability to calibrate physiological activity to the behavioral demands of the present environment.

Findings from Study 1 suggest that individuals with greater vagal tone exhibit more differentiated physiological responses to subtle social stimuli, likely enabling a greater degree of social connection. Findings from Studies 2 and 3 show that individuals with greater vagal flexibility, but not individuals with greater vagal tone, feel more strongly integrated in the social worlds. Furthermore, individuals with greater vagal tone and vagal flexibility reported more long-term subjective well-being, with the relationship being direct for vagal tone but fully mediated by feelings of social connection for vagal flexibility. These findings suggest that vagal tone and flexibility are related to social connection in separable ways, and may predict the extent to which we lead healthy and satisfying lives.

The present findings contribute to a comprehensive understanding of how individual differences in activity of physiological systems relate to social connection, and the health and well-being consequences of that social connection. By attempting to disentangle the metrics of vagal activity that predict social connection and have far-reaching implications for health and well-being, findings from studies presented in this dissertation could ultimately have the potential to inform interventions aimed at helping us live happier, healthier, and more socially-connected lives.

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Appendix I: Indicators of Social Connection, Feelings

Social Integration[6]:

"I don't feel I belong to anything I'd call a community."
"I feel close to other people in my community." (R)
"My community is a source of comfort." (R)

MIDUS 2, Main Sample, valid responses (N = 4000, M = 14.72, SD = 3.99)[7]
MIDUS 2, Milwaukee Sample, valid responses (N = 410, M = 13.93, SD = 4.09)
MIDUS 3, Main Sample, valid responses (N = 2859, M = 14.74, SD = 4.06)
MIDUS 3, Milwaukee Sample, valid responses (N = 321, M = 13.58, SD = 3.69)

Acceptance of Others[6]:

"People who do a favor expect nothing in return."(R)
"People do not care about other people's problems."
"I believe that people are kind." (R)

MIDUS 2, Main Sample, valid responses (N = 4001, M = 14.04, SD = 3.30)
MIDUS 2, Milwaukee Sample, valid responses (N = 410, M = 11.97, SD = 3.42)
MIDUS 3, Main Sample, valid responses (N = 2859, M = 13.99, SD = 3.20)
MIDUS 3, Milwaukee Sample, valid responses (N = 320, M = 12.38, SD = 3.29)

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[6] Coding: 1 Strongly agree; 2 Somewhat agree; 3 A little agree; 4 Neither agree or disagree; 5 A little disagree; 6 Somewhat disagree; 7 Strongly disagree.
Scaling: Scales are constructed by calculating the sum of the values of the items. All items marked with (R) were reverse-coded so that high scores reflect higher standing in each scale. For an item with a missing value, the mean value of completed items is imputed.

[7] Alphas could not be calculated because raw scores for each item are not publicly available.

Loneliness:

“During the past 30 days... how much of the time did you feel LONELY?”

MIDUS 2, Main Sample (percent of valid responses, N = 3985):
All of the time: 0.83%
Most of the time: 2.61%
Some of the time: 9.41%
A little of the time: 22.38%
None of the time: 64.77%

MIDUS 2, Milwaukee Sample (percent of valid responses, N = 592):
All of the time: 3.89%
Most of the time: 6.25%
Some of the time: 13.34%
A little of the time: 18.58%
None of the time: 57.94%

MIDUS 3, Main Sample (percent of valid responses, N = 2865):
All of the time: 1.12%
Most of the time: 2.16%
Some of the time: 10.82%
A little of the time: 19.55%
None of the time: 66.35%

MIDUS 3, Milwaukee Sample (percent of valid responses, N = 388):
All of the time: 3.35%
Most of the time: 4.90%
Some of the time: 13.92%
A little of the time: 14.95%
None of the time: 62.89%

Felt close to others:

“During the past 30 days... how much of the time did you feel CLOSE TO OTHERS?”

MIDUS 2, Main Sample (percent of valid responses, N = 3997):
All of the time: 14.84%
Most of the time: 46.13%
Some of the time: 25.57%
A little of the time: 11.53%
None of the time: 1.93%

MIDUS 2, Milwaukee Sample (percent of valid responses, N = 590):
All of the time: 25.59%
Most of the time: 42.54%
Some of the time: 18.31%
A little of the time: 9.66%
None of the time: 3.90%

MIDUS 3, Main Sample (percent of valid responses, N = 2889):
All of the time: 14.99%
Most of the time: 46.59%
Some of the time: 24.82%
A little of the time: 11.08%
None of the time: 2.53%

MIDUS 3, Milwaukee Sample (percent of valid responses, N = 387):
All of the time: 25.58%
Most of the time: 35.92%
Some of the time: 22.74%
A little of the time: 12.92%
None of the time: 2.84%

Few close others:

“Please indicate how strongly you agree or disagree with each of the following statements - I OFTEN FEEL LONELY BECAUSE I HAVE FEW CLOSE FRIENDS WITH WHOM TO SHARE MY CONCERNS.”

MIDUS 2, Main Sample (percent of valid responses, N = 4016):
Agree strongly: 3.24%
Agree somewhat: 6.32%
Agree a little: 10.88%
Neither agree nor disagree: 8.89%
Disagree a little: 6.77%
Disagree somewhat: 18.92%
Disagree strongly: 44.97%

MIDUS 2, Milwaukee Sample (percent of valid responses, N = 409):
Agree strongly: 8.07%
Agree somewhat: 10.02%
Agree a little: 10.27%
Neither agree nor disagree: 11.98%
Disagree a little: 5.13%
Disagree somewhat: 10.27%
Disagree strongly: 44.25%

MIDUS 3, Main Sample (percent of valid responses, N = 2908):
Agree strongly: 3.85 %
Agree somewhat: 6.64%
Agree a little: 10.56%
Neither agree nor disagree: 10.25%
Disagree a little: 7.12%
Disagree somewhat: 19.29%
Disagree strongly: 42.30%

MIDUS 3, Milwaukee Sample (percent of valid responses, N = 323):
Agree strongly: 7.12%
Agree somewhat: 8.05%
Agree a little: 13.93 %
Neither agree nor disagree: 10.84%
Disagree a little: 7.74%
Disagree somewhat: 10.84%
Disagree strongly: 41.49%

Appendix II: Indicators of Social Connection, Behaviors

Contact with neighbors:

"How often do you have any contact, even something as simple as saying 'hello', with any of your neighbors?"

MIDUS 2, Main Sample (percent of valid responses, N = 3989):
Almost every day: 45.48%
Several times a week: 28.80%
About once a week: 12.51%
1-3 times a month: 6.69%
Less than once a month: 4.04%
Never or hardly ever: 2.48%

MIDUS 2, Milwaukee Sample (percent of valid responses, N = 591):
Almost every day: 51.78%
Several times a week: 19.46%
About once a week: 8.29%
1-3 times a month: 6.26%
Less than once a month: 3.72%
Never or hardly ever: 10.49%

MIDUS 3, Main Sample (percent of valid responses, N = 2873):
Almost every day: 43.96%
Several times a week: 29.13%
About once a week: 13.19%
1-3 times a month: 7.45%
Less than once a month: 3.31%
Never or hardly ever: 2.96%

MIDUS 3, Milwaukee Sample (percent of valid responses, N = 388):
Almost every day: 47.68%
Several times a week: 23.71%
About once a week: 9.28%
1-3 times a month: 6.44%
Less than once a month: 3.611%
Never or hardly ever: 9.28%

Contact with family:

“How often are you in contact with any members of your family, that is, any of your brothers, sisters, parents, or children who do not live with you, including visits, phone calls, letters, or electronic mail messages?”

MIDUS 2, Main Sample (percent of valid responses, N = 4009):
Several times a day: 15.84%
About once a day: 22.62%
Several times a week: 30.81%
About once a week: 16.36%
2 or 3 times a month: 7.96%
About once a month: 3.12%
Less than once a month: 2.07%
Never or hardly ever: 1.22%

MIDUS 2, Milwaukee Sample (percent of valid responses, N = 590):
Several times a day: 22.37%
About once a day: 21.36%
Several times a week: 20.85%
About once a week: 15.42%
2 or 3 times a month: 8.64%
About once a month: 5.25%
Less than once a month: 2.71%
Never or hardly ever: 3.39%

MIDUS 3, Main Sample (percent of valid responses, N = 2879):
Several times a day: 19.87%
About once a day: 21.74%
Several times a week: 31.40%
About once a week: 13.89%
2 or 3 times a month: 6.74%
About once a month: 2.64%
Less than once a month: 2.01%
Never or hardly ever: 1.70%

MIDUS 3, Milwaukee Sample (percent of valid responses, N = 315):
Several times a day: 27.30%
About once a day: 18.73%
Several times a week: 23.81%
About once a week: 10.79%
2 or 3 times a month: 9.52%
About once a month: 2.86%

Less than once a month: 2.54%
Never or hardly ever: 4.44%

Contact with friends:

“How often are you in contact with any of your friends, including visits, phone calls, letters, or electronic mail messages?”

MIDUS 2, Main Sample (percent of valid responses, N = 3999):
Several times a day: 12.58%
About once a day: 17.33%
Several times a week: 32.71%
About once a week: 15.50%
2 or 3 times a month: 10.25%
About once a month: 4.48%
Less than once a month: 4.03%
Never or hardly ever: 3.13%

MIDUS 2, Milwaukee Sample (percent of valid responses, N = 589):
Several times a day: 13.92%
About once a day: 16.30%
Several times a week: 25.64%
About once a week: 15.45%
2 or 3 times a month: 9.68%
About once a month: 5.77%
Less than once a month: 3.23%
Never or hardly ever: 10.02%

MIDUS 3, Main Sample (percent of valid responses, N = 2873):
Several times a day: 12.08%
About once a day: 16.71%
Several times a week: 30.14%
About once a week: 15.04%
2 or 3 times a month: 12.08%
About once a month: 5.78%
Less than once a month: 4.91%
Never or hardly ever: 3.27%

MIDUS 3, Milwaukee Sample (percent of valid responses, N = 314):
Several times a day: 20.06%
About once a day: 10.51%
Several times a week: 26.43%
About once a week: 14.65%
2 or 3 times a month: 11.78%
About once a month: 4.78%

Less than once a month: 4.78%
Never or hardly ever: 7.01%

Group attendance: Professional group

"In a typical month, about how many times do you attend the following? (If none, enter "0".) – MEETINGS OF UNIONS OR OTHER PROFESSIONAL GROUPS"

MIDUS 2, Main Sample, valid responses (N = 3758, M = 0.36, SD = 1.26)
MIDUS 2, Milwaukee Sample, valid responses (N = 589, M = 0.48, SD = 1.52)
MIDUS 3, Main Sample, valid responses (N = 2511, M = 0.27, SD = 1.36)
MIDUS 3, Milwaukee Sample, valid responses (N = 389, M = 0.59, SD = 2.4)

Group attendance: Social group

"In a typical month, about how many times do you attend the following? (If none, enter "0".) – MEETINGS OF SPORTS OR OTHER SOCIAL GROUPS"

MIDUS 2, Main Sample, valid responses (N = 3739, M = 1.37, SD = 2.95)
MIDUS 2, Milwaukee Sample, valid responses (N = 587, M = 0.84, SD = 3.6)
MIDUS 3, Main Sample, valid responses (N = 2578, M = 1.32, SD = 3.48)
MIDUS 3, Milwaukee Sample, valid responses (N = 389, M = 0.97, SD = 3.16)

Group attendance: Other groups

"In a typical month, about how many times do you attend the following? (If none, enter "0".) – MEETINGS OF ANY OTHER GROUPS (NOT INCLUDING ANY REQUIRED BY YOUR JOB"

MIDUS 2, Main Sample, valid responses (N = 3807, M = 1.73, SD = 3.64)
MIDUS 2, Milwaukee Sample, valid responses (N = 587, M = 1.18, SD = 4.84)
MIDUS 3, Main Sample, valid responses (N = 2613, M = 1.66, SD = 3.8)
MIDUS 3, Milwaukee Sample, valid responses (N = 389, M = 0.95, SD = 2.52)

Appendix III: Indicators of Subjective Well-being

Life Satisfaction (5 items)[8]:

Respondents were asked to rate their life satisfaction in five areas: overall, work, health, relationship with spouse/partner, and relationship with children.

MIDUS 3, Main Sample, valid responses (N = 2923, M = 7.78, SD = 1.33)
MIDUS 3, Milwaukee Sample, valid responses (N = 384, M = 7.56, SD = 1.16)

Positive Affect (PANAS)[9]:

"During the past 30 days, how much of the time did you feel..."
enthusiastic?
attentive?
proud?
active?

MIDUS 3, Main Sample, valid responses (N = 2899, M = 3.55, SD = 0.77)
MIDUS 3, Milwaukee Sample, valid responses (N = 388, M = 3.69, SD = 0.87)

Negative Affect Adjectives (PANAS)[9] :

"During the past 30 days, how much of the time did you feel..."
afraid?
jittery?
irritable?
ashamed
upset?

MIDUS 3, Main Sample, valid responses (N = 2878, M = 1.49, SD = 0.54)
MIDUS 3, Milwaukee Sample, valid responses (N = 388, M = 1.67, SD = 0.72)

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[8] Coding: Each item was coded from 0 (the worst possible) to 10 (the best possible).
Scaling: [C1SSATIS] and [C1SSATIS2] are constructed by calculating the mean of the items. The scores for relationship with spouse/partner and relationship with children are averaged to create one "item". Then, this score is used along with the remaining three items to calculate an overall mean score. Higher scores reflect higher levels of overall life satisfaction.

[9] Coding: 1 All of the time; 2 Most of the time; 3 Some of the time; 4 A little of the time; 5 None of the time.
Scaling: Scales are constructed by calculating the mean across each set of items. Items were recoded so that higher scores reflect higher levels of positive/negative affect. Missing Values: The scales are computed for cases that have valid values for at least one item on the particular scale. Scale scores are not calculated for cases with no valid item on the scales, and coded as "8" for "NOT CALCULATED (Due to missing data)".

Health Rating: Current

"Using a scale from 0 to 10 where 0 means 'the worst possible health' and 10 means 'the best possible health,' how would you rate your health these days?"

MIDUS 3, Main Sample, valid responses (N = 2912)
MIDUS 3, Milwaukee Sample, valid responses (N = 323, M = 6.65, SD = 1.88)

Health Rating: Future

"Looking ahead ten years into the future, what do you expect your health will be like at that time? Using a scale from 0 to 10 where 0 means 'the worst possible health' and 10 means 'the best possible health'"

MIDUS 3, Main Sample, valid responses (N = 2903)
MIDUS 3, Milwaukee Sample, valid responses (N = 324, M = 6.51, SD = 2.36)

Health Rating: Compare

"Compared to other people your age, how would you rate YOUR OVERALL HEALTH?"

MIDUS 3, Main Sample (percent of valid responses, N = 2903):
Excellent: 18.53%
Good: 47.40 %
Average: 22.08%
Fair: 9.75%
Poor: 2.24%

MIDUS 3, Milwaukee Sample (percent of valid responses, N = 387):
Much better: 14.21%
Somewhat better: 22.74%
About the same: 36.95%
Somewhat worse: 20.93%
Much worse: 5.17%