Title

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Permalink

https://escholarship.org/uc/item/71b3h6tg

Journal

Journal of Personality and Social Psychology, 109(1)

ISSN

0022-3514

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Publication Date

2015-07-01

DOI

10.1037/pspp0000016

Peer reviewed

Journal of Personality and Social Psychology

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Online First Publication, December 29, 2014. http://dx.doi.org/10.1037/pspp0000016

CITATION

Muhtadie, L., Koslov, K., Akinola, M., & Mendes, W. B. (2014, December 29). Vagal Flexibility: A Physiological Predictor of Social Sensitivity. *Journal of Personality and Social Psychology*. Advance online publication. http://dx.doi.org/10.1037/pspp0000016

Journal of Personality and Social Psychology

0022-3514/14/$12.00 http://dx.doi.org/10.1037/pspp0000016

Vagal Flexibility: A Physiological Predictor of Social Sensitivity

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This research explores vagal flexibility—dynamic modulation of cardiac vagal control—as an individual-level physiological index of social sensitivity. In 4 studies, we test the hypothesis that individuals with greater cardiac vagal flexibility, operationalized as higher cardiac vagal tone at rest and greater cardiac vagal withdrawal (indexed by a decrease in respiratory sinus arrhythmia) during cognitive or attentional demand, perceive social-emotional information more accurately and show greater sensitivity to their social context. Study 1 sets the foundation for this investigation by establishing that vagal flexibility can be elicited consistently in the laboratory and reliably over time. Study 2 demonstrates that vagal flexibility has different associations with psychological characteristics than does vagal tone, and that these characteristics are primarily social in nature. Study 3 links individual differences in vagal flexibility with accurate detection of social and emotional cues depicted in still facial images. Study 4 demonstrates that individuals with greater vagal flexibility respond to dynamic social feedback in a more context-sensitive manner than do individuals with less vagal flexibility. Specifically, compared with their less flexible counterparts, individuals with greater vagal flexibility, when assigned to receive negative social feedback, report more shame, show more pronounced blood pressure responses, and display less sociable behavior, but when receiving positive social feedback display more sociable behavior. Taken together, these findings suggest that vagal flexibility is a useful individual difference physiological predictor of social sensitivity, which may have implications for clinical, developmental, and health psychologists.

Keywords: cardiac vagal reactivity, vagal flexibility, social sensitivity

Why do some individuals seem to be exquisitely aware of, and profoundly responsive to, the subtle social-emotional cues in their environment, whereas others appear oblivious to the same information? Are these differences in social-emotional sensitivity undergirded by specific physiological substrates? And if so, can they be reliably measured and used to predict important affective, physiological, and behavioral outcomes in real-life social contexts? If there *are* distinct physiological indicators associated with greater social sensitivity, are they necessarily advantageous, or can they also prove to be taxing under certain conditions? We explore these questions by examining individual differences in physiological reactivity, specifically in cardiac vagal control, which may shed light on individual differences in sensitivity to social cues.

Neurobiological Underpinnings of Social Context Sensitivity

Mammals are social by nature and mammalian neurobiology evolved, at least in part, to enable rapid and flexible responding to the social milieu. Generally speaking, healthy physiological responding involves the interaction of multiple control mechanisms that allow individuals to adapt to unpredictable changes and exigencies in their environment (Lipsitz & Goldberger, 1992). Nonetheless, individuals are also likely to differ in the degree of sensitivity with which their physiology adjusts to the vicissitudes of daily life. Indeed, Belsky and colleagues (Belsky et al., 2009; Belsky & Pluess, 2009) have argued that from a fitness-optimizing standpoint, nature would have likely selected for variation in individuals' plasticity or susceptibility to the influence of their social environment, with some people being less malleable—and more robust—across conditions, and others showing greater vulnerability to adverse conditions on the one hand, and a greater tendency to thrive in supportive or at least benign conditions on the other (Belsky & Pluess, 2009; Pluess & Belsky, 2012).

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We are grateful to our dedicated confederates and research assistants at Harvard and UCSF for their assistance in conducting these experiments, scoring the physiological data, and behavioral coding, especially Amy Lai. The research was supported by NHLBI grant (RO1 HL079383) and the Sarlo-Ekman endowment awarded to the last author and an NIMH T32-MH-20006 to L.M.

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In recent years, there has been a burgeoning interest among developmental, social, and clinical psychologists in identifying neurobiological indices across systems and levels that have the capacity to predict individual differences in context-sensitive responding. At the neural level, for example, there is evidence that individuals with greater trait-level frontal cortical asymmetry (greater activation in the left prefrontal cortex relative to the right) are more buffered against social rejection (Harmon-Jones & Allen, 1998; Koslov, Mendes, Pajtas, & Pizzagalli, 2011). Neuroendocrinology studies of young adults with lower baseline levels of dehydroepiandrosterone-sulfate (DHEAS) show heightened vulnerability to experiencing negative affect in the context of threatening social situations involving social rejection (Akinola & Mendes, 2008). A study of young children found those with high cortisol reactivity to be more prosocial under low adversity conditions, but less prosocial under high adversity conditions compared with children with low cortisol reactivity (Obradović, Bush, Stamperdahl, Adler, & Boyce, 2010). In terms of genes, a preponderance of research has focused on the serotonin-transporter-linked polymorphic region (5-HTTLPR), most commonly comparing the short (s/s, s/L) versus long (l/L) allele variants. Results of some of these studies suggest that short allele carriers experience the worst outcomes under adverse conditions and the best outcomes under supportive or benign conditions (Belsky et al., 2009; Belsky & Pluess, 2009).

In the present article, we examine a physiological index at the level of the autonomic nervous system (ANS) and its association with social cue sensitivity. We use the term “vagal flexibility,”[1] which we operationalize as higher cardiac vagal tone at rest and greater cardiac vagal withdrawal (indexed by a decrease in respiratory sinus arrhythmia [RSA]) during cognitive or attentional demand. Across four studies, we provide evidence to suggest that vagal flexibility: (a) is an individual difference physiological index that can be elicited consistently in the laboratory using a variety of mental challenges and reliably within-individuals over time; (b) provides unique and socially specific information beyond that provided by vagal tone, a more commonly used individual difference index of emotion and well-being; (c) predicts more accurate detection of social-emotional cues in still facial images; and (d) predicts greater awareness of, and more sensitive affective, behavioral, and physiological responding to social cues during a dynamic interpersonal interaction.

Polyvagal Theory and the Biology of the Vagus Nerve

The vagus, or 10th cranial nerve, is a primary component of the parasympathetic branch of the ANS. Both the structure and function of the vagus nerve implicates it as a plausible biomarker of complex social behavior. The term “vagus” is Latin for “wanderer,” and this is a fitting term to describe the vast regulatory control the vagus nerve has on multiple organs from the pharynx to the large intestine. More important, the vagus has pathways that are both afferent (i.e., flowing toward organs) and efferent (i.e., flowing from organs) and facilitate a bidirectional influence of the brain and bodily organs on each other, enabling efficient coregulation and responsiveness to changes in the environment.

Researchers since Darwin have theorized that the vagus nerve is intimately involved in regulating humans’ emotional responses to their social environment. Indeed, in the *Expression of Emotions in Man and Animals*, Darwin wrote:

> . . . the heart, which goes on uninterruptedly beating night and day in so wonderful a manner, is extremely sensitive to external stimulants . . . When the heart is affected it reacts on the brain; and the state of the brain again reacts through the pneumo-gastric [vagus] nerve on the heart; so that under any excitement there will be much mutual action and reaction between these, the two most important organs of the body. (Darwin, 1872, p. 69)

More recently, Porges’ polyvagal theory has posited that the phylogenetically newer “smart” vagus is a central feature of a social communication circuit comprising autonomic and somatomotor components, which serves to facilitate interactions with conspecifics and allow for flexible responding in social situations (Porges, 2001, 2003, 2007, 2009). The autonomic component of this circuit centers on the myelinated branch of the vagus nerve, which originates in the nucleus ambiguus of the medulla and provides efferent control of the heart via its sinoatrial node, or pacemaker. The somatomotor component focuses on neural regulation of the striated muscles of the head and face by way of visceral efferent pathways embedded within five cranial nerves (V, VII, IX, X, and XI). These cranial nerves are involved in producing head gestures (cranial nerve XI) and facial expressions (cranial nerves V and VII); tuning the muscles of the middle ear to the frequency of human speech (cranial nerves V and VII); and modulating vocal production via the larynx (cranial nerves IX and X). The shared origin of both neural regulation of the heart by the myelinated vagus and visceral efferent control of the head and face muscles in the brain stem results in a neurophysiological “face–heart” connection that forms an integrated social engagement system (Porges, 2001, 2003, 2007, 2009). It should be noted, however, that some contemporary evolutionary considerations challenge polyvagal theory’s differentiation between the two source nuclei involved in parasympathetic control of the myelinated, or smart vagus (i.e., the nucleus ambiguus) on the one hand, and the more primitive “vegetative” vagus (i.e., dorsal motor nucleus) on the other.

Vagal Regulation of the Heart and Respiratory Sinus Arrhythmia

The myelinated vagus promotes effective social communication by inhibiting sympathetic influences on the heart and promoting a state of calm. Because of this inhibitory influence of the vagus, the resting heart rate of a healthy adult (60–80 beats per minute [bpm]) is typically much lower than the intrinsic rate of the cardiac pacemaker (~100–150 bpm; Porges, 2003). RSA enables the quantification of myelinated vagal control of the heart by measuring fluctuations in heart rate during spontaneous respiration (Porges, 1995). Respiration acts as a gate through which vagal control of the heart is admitted during exhalation and obstructed during inhalation, leading to a characteristic variation in the heart’s

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[1] The vagus nerve innervates just about every major organ in the body, yet the primary method of assessing vagal nerve activity focuses on vagal nerve influences at the heart. Therefore, the reader should assume that every reference to “vagal tone,” “vagal reactivity,” and “vagal flexibility” has the implied “cardiac” modifier preceding the phrase.

rhythm when an individual is at rest: a slowing of heart rate during exhalation and a speeding during inhalation. This variability in heart rate, which occurs in the frequency band of human respiration (.12 to .40 Hz), is indexed by RSA. Higher RSA reflects greater myelinated vagal control of the heart, which, in turn, suggests greater parasympathetic nervous system influence on the heart. When there is a shift in the environment that places increased metabolic demand on the individual, the vagus nerve *may* withdraw its inhibitory influence to enable the heart to beat more regularly to meet this demand. Assuming respiration rate remains within the 0.12 to 0.4 Hz frequency band, this demand-related withdrawal of the vagus nerve can produce a change from the situation of higher covariance between heart rate and respiration rate observed at rest to one of lower covariance, manifesting as a decrease in RSA.

Because the social world is dynamic and ever changing, it continuously calls upon individuals to calibrate their physiology to best support shifts in attention, energy, and behavior in response to varying social cues. This would seem to suggest that *dynamic* modulation of vagal control of the heart in response to shifts in the environment would be a particularly useful index for assessing the flexibility and context-appropriateness (i.e., sensitivity) of individuals' responses to their social world. Indeed, polyvagal theory explicitly makes this point by highlighting that "successful adaptation of mammals is dependent on the systematic and reliable withdrawal and reengagement of the vagal brake as a mechanism to rapidly regulate metabolic output in response to environmental demands" (Porges, Doussard-Roosevelt, Portales, & Greenspan, 1996, p. 700). Thus, the rapid application and withdrawal of vagal inhibition is viewed as an adaptive substrate for flexible behavioral routines (Friedman, 2007; Rottenberg, Salomon, Gross, & Gotlib, 2005). Given the importance of such dynamic responding, then, it is surprising that the majority of studies examining the association between vagus nerve activity and social cue sensitivity have focused on vagal tone—the basal influence of the vagus nerve on the heart. Although higher vagal tone can indicate a soothed or calm state, which is certainly adaptive at rest, rigid maintenance of either high or low RSA is less adaptive. For example, under conditions that pose greater metabolic demand on the individual (e.g., increased attention and information processing, exercise, coping with negative emotion, and threats to life and limb), vagal withdrawal is more likely to facilitate successful responding.

Contrasting Vagal Tone With Vagal Reactivity

Vagal tone is usually measured as RSA recorded during at least 5 min of rest, and reflects tonic levels of parasympathetic nervous system influence on the heart (Berntson et al., 1997). Past studies have generally found that higher vagal tone (i.e., higher resting RSA) is associated with more positive social-emotional outcomes, including less affective rigidity (Thayer & Lane, 2000a); greater extraversion (Oveis et al., 2009), social competence (Beauchaine, 2001), and empathy (Fabes, Eisenberg, & Eisenbud, 1993; Fabes, Eisenberg, Karbon, Troyer, & Switzer, 1994); and a better ability to discriminate emotionally salient stimuli (Park, Van Bavel, Vasey, Eagan, & Thayer, 2012), though extreme levels of vagal tone in either direction may be maladaptive (Kogan, Gruber, Shallcross, Ford, & Mauss, 2013).

Far fewer studies have examined vagal reactivity, or decreases in RSA in response to challenge, and these have predominantly focused on the associations between vagal reactivity and cognitive as opposed to social-emotional outcomes. What these studies tend to find, however, is that tasks requiring increased cognitive effort or attentional control reliably elicit vagal withdrawal, or decreases in RSA from baseline (Böhm, Rötting, Schwenk, Grebe, & Mansmann, 2001; Porges, 1980; Van Roon, Mulder, Althaus, & Mulder, 2004; van Roon, Mulder, Veldman, & Mulder, 1995; Walter & Porges, 1976). Critically, the magnitude of the RSA decrease in response to tasks posing attentional and cognitive demands is associated with better task performance (Akinola & Mendes, 2014; Duschek, Muckenthaler, Werner, & Reyes del Paso, 2009; Kassam, Koslov, & Mendes, 2009; Mathewson et al., 2010; Morgan, Aikins, Steffian, Coric, & Southwick, 2007).

Only a paucity of studies have examined vagal reactivity in conjunction with social cue sensitivity, but the existing ones provide some early clues that vagal withdrawal during mental challenge is associated with heightened social sensitivity. For example, Obradović and colleagues (2010) showed that children with high RSA reactivity (i.e., greater vagal withdrawal) in response to cognitive, social, emotional, and sensory challenge tasks demonstrate greater prosociality and school engagement under low-adversity conditions, but less prosociality and school engagement under high-adversity conditions than do children with low RSA reactivity (Obradović et al., 2010). Another study found that adolescents who responded with greater RSA decreases during a mental stressor showed greater increases in behavioral warmth toward their parent 2 years later (Diamond & Cribbet, 2013). Moving from developmental psychology to clinical investigations, Schmitz and colleagues showed that children with social phobia, a psychiatric disorder characterized by a persistent and context-insensitive fear of social situations, exhibited restricted RSA reactivity in response to a stressful speech task (Schmitz, Kramer, Tuschen-Caffier, Heinrichs, & Blechert, 2011). In light of this association between RSA rigidity and internalizing psychopathology, greater RSA flexibility may predict better responses to treatment for internalizing disorders. Indeed, Rottenberg and colleagues found that depressed individuals who showed greater RSA reactivity (i.e., withdrawal) in response to a sad film showed better recovery from depression 6 months later than did their counterparts with low RSA reactivity, controlling for medication use and baseline depressive symptoms (Rottenberg et al., 2005).

The present investigation extends prior work by exploring the idea that an adaptive vagal system will demonstrate appropriate flexibility in response to the needs of the situation—that is, higher vagal tone at rest and greater vagal withdrawal (indexed by a decrease in RSA) during cognitive or attentional demand. The difference between vagal activation in these two types of mental states (relaxation vs. challenge) is what we are calling "vagal flexibility." In this study, we sought to examine whether individuals with greater vagal flexibility, compared to those with less flexibility, are more sensitive to social and emotional information in their environment. We hypothesized that individuals with greater vagal flexibility would show more accurate detection of subtle social-emotional cues and respond more sensitively to dynamic social feedback.

In the following four studies, we first establish that vagal flexibility is a reliable physiological individual difference variable that is relatively consistent in individuals across tasks and time (Study 1). In Study 2, we examine the links between vagal flexibility and a series of psychological measures to test whether vagal flexibility provides unique information beyond that provided by the more commonly used measure of vagal tone. In Study 3, we explore whether vagal regulation predicts individuals' ability to accurately perceive subtle social-emotional cues in still facial images. Finally, in Study 4, we examine the influence of vagal flexibility on responses during a social interaction in which participants were randomly assigned to receive positive or negative social feedback. We hypothesized that the type of social feedback provided would moderate the associations between vagal flexibility and affective, physiological, and behavioral responses during the interaction. Specifically, we expected individuals with greater vagal flexibility would show a more adaptive profile of responding when receiving positive social feedback and a more deleterious response profile when receiving negative feedback than would individuals with less vagal flexibility.

Study 1

Method

Setting and participants. We recruited female participants from the community (*N* = 198; 50% European American, 48% African American, and 2% mixed race) between the ages of 18 and 30 to participate in a study on "interpersonal interactions." We prescreened for pregnancy, physician-diagnosed heart disease (e.g., heart murmur, arrhythmia), and use of medications affecting cardiovascular function, such as β-adrenergic blocking agents. The study was conducted in a social psychophysiology laboratory with a sound-attenuated experimental room, where participants completed study procedures while their physiological signals were acquired continuously, and a separate control room that allowed for continuous and surreptitious monitoring of the participant.

Procedure. This study involved three visits to the laboratory, with 1 week on average between the study visits. Each study visit began with a trained research assistant attaching sensors to obtain the electrocardiographic (ECG) and impedance cardiographic (ICG) signals while participants sat upright in a comfortable chair for a 5-min baseline physiological recording. Following this baseline, participants were informed that there was another "participant" in this study with whom they would be interacting in subsequent tasks. This other person was a trained research assistant (i.e., female confederate) who acted friendly toward the participant. The confederate was moved into the participant's room and wore similar (but nonoperating) physiological sensors. During each study visit, the participant and confederate spent 10 min asking and answering scripted questions that we provided.[2] The participant and confederate then completed a series of cooperative cognitive tasks, during which ECG recordings were obtained and used to calculate changes in RSA from baseline (i.e., RSA reactivity).

We used a variety of cognitive tasks across the three visits to ensure novelty and to avoid habituation effects. All tasks posed some degree of mental challenge and were grouped into three sets lasting 5 min each, which were counterbalanced across the three study visits. Set A included a Password task in which the participant and confederate were given a set of cards with target words and took turns providing their partner with one-word clues in an effort to get her to guess the target word. For example, if the target word was "BUTTER," the participant might say "margarine" or "bread." Set B comprised a 3-min Improvisation Task followed by a 2-min Word Context Test with no intervening breaks. In the Improvisation Task, the participant and confederate took turns creating a verbal story from an initial sentence prompt that we provided, by each adding a single sentence following on what their partner had just said. In the Word Context Test, derived from the widely used Delis-Kaplan Executive Function System (D-KEFS; Delis, Kaplan, & Kramer, 2001), participants were read a series of sentences containing a made-up word (e.g., *prifa*) and were required to identify the meaning of the word based on its use in the sentences. Set C included two modified tasks from the D-KEFS battery. The first, 3-min task was the Twenty Questions Test, in which participants had to guess which of 20 pictures the confederate had selected as a target by asking only yes or no questions. The second, 2-min task was the Verbal Fluency Test, Category Switch, in which participants had to generate sets of words in two different categories (e.g., if the categories were "Vegetables and Musical Instruments," the participant could say "Cucumber Violin"). The confederates' clues and answers were scripted on all tasks. After the participant and confederate completed a set of cognitive tasks, the confederate left the room and the experimenter returned to remove the participant's sensors. At the end of their final study visit, participants were debriefed and compensated. Although there was variation in the five tasks completed across three visits, all posed some degree of attentional and/or cognitive demand. Therefore, we expected to see decreases in RSA reactivity on average among participants while they performed the different tasks, which would enable us to examine the stability of RSA changes within individuals across tasks and time.

Measures.

Physiological measures. Cardiac measures were acquired continuously during the 5-min baseline period at the outset of each study visit and throughout the cognitive tasks. Electrocardiography was obtained using a standard Lead II configuration (right arm, left leg) with an ECG module from Biopac (Goleta, CA), and respiration rate was derived from impedance cardiography (HIC-2000). Both signals were collected at a sampling rate of 1,000 Hz with a Biopac MP150 integrative system. All data were scored offline and included visually inspecting the waveform and then averaging the responses into 1-min bins. To calculate RSA we used Mindware software's HRV 2.6 module (Lafayette, OH), which estimates RSA in accordance with the recommendations of the Society for Psychophysiological Research committee on heart rate variability (Berntson et al., 1997). All minutes of the digitized ECG signal were visually inspected by trained research assistants, and artifacts and incorrectly identified R spikes were edited. A 4 Hz time series was applied to interpolate the interbeat interval (IBI) time series (Berntson, Cacioppo, & Quigley, 1993) and a second-order polynomial was applied to minimize nonstationary trends. The residual series was then tapered with a Hanning window and submitted to

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[2] This study manipulated same-race versus cross-race dyads and the level of intimacy of the scripted questions provided (Akinola & Mendes, in preparation). As our question here focuses on individual consistency of vagal flexibility, we ran partial correlations controlling for these condition effects, and effects did not differ.

a Fast Fourier Transform to derive the spectral distribution. RSA was quantified as the integral power within the respiration frequency band (.12 to .4 Hz). Respiration rate was extracted from the dz/dt signal using the impedance scoring module (Mindware) and used as a covariate in all analyses (the presence or absence of respiration rate as a covariate did not significantly alter any of the results, so the more parsimonious models without respiration rate are reported in this manuscript).

Results

For each study visit, we calculated mean baseline RSA, then calculated *RSA reactivity* by subtracting the last minute of the baseline RSA (when participants were most relaxed, as reflected in maximal RSA values on average) from RSA during the first minute of each of the five cognitive tasks. Mean *RSA reactivity* values from each task showed the expected RSA decreases: Password, Improvisation, Word Context, 20 Questions, and Category Switch were: $M = -.49$ ($SD = 1.20$); $M = -.49$ ($SD = 1.13$); $M = -.24$ ($SD = 1.02$); $M = -.56$ ($SD = .98$); $M = -.22$ ($SD = .95$), respectively. For ease of interpretation—because we conceptualize vagal flexibility (i.e., RSA decreases during mental challenge) as a positive, adaptive state—we multiplied RSA reactivity scores by -1 so that greater vagal withdrawal would be reflected by positive vagal flexibility scores.

We first examined reliability in vagal tone across the three visits. Because vagal tone is frequently used as an individual difference variable without much evidence for its reliability across time (cf. Salomon, Matthews, & Allen, 2000), we thought it would be important to compare the relative reliabilities of vagal tone and vagal flexibility. We did expect the reliability of vagal tone to be higher than that of vagal flexibility because vagal tone was calculated during identical resting conditions across the three study visits, whereas vagal flexibility was calculated in response to a range of tasks that posed varying magnitudes of mental challenge. Consistent with this expectation, reliabilities across the three visits for vagal tone was high, $\alpha = .84$.

We then calculated α-coefficients for vagal flexibility for each of the cognitive tasks. Across the five tasks, vagal flexibility showed good reliability, $\alpha = .79$. The scale reliability was largest when all five tasks were included, $\alpha = .79$, and weakest when the Improvisation task was excluded, $\alpha = .71$. We further explored correlations across each of the tasks to determine reliability within a study day versus across study visits (see Table 1).[3] On two of the three study visits, participants completed two tasks, and in both cases, vagal flexibility values for the two tasks were strongly correlated with each other, $r(162) = .62$, $p < .001$; $r(159) = .63$, $p < .001$. We then examined vagal flexibility across study days focusing on the first task completed on each day. Here, vagal flexibility yielded significant, though smaller, correlations relative to those obtained within study day: $r(146) = .42$, $p < .001$; $r(145) = .38$, $p < .001$; $r(146) = .44$, $p < .001$. The overall reliability for first tasks was $\alpha = .68$. Correlations were lowest, but still significant, when one of the tasks was completed second on a study day: *r*s ranged from .27 to .46, all *p*s $< .001$. It is important to note that the tasks varied greatly in their structure and demands and were counterbalanced across study visits to avoid being confounded by initial exposure to the laboratory environment (Blascovich, Mendes, Vanman, & Dickerson, 2011). In view of these constraints, individual differences in vagal flexibility yielded moderate to strong reliabilities across tasks and over time. Finally, vagal tone and vagal flexibility were moderately negatively correlated with each other: Set A, $r = -.28$, $p < .000$; Set B, $r = -.49$, $p < .000$; Set C, $r = -.36$, $p < .000$.

Discussion

Study 1 established that vagal flexibility can be conceptualized as a relatively stable individual difference (trait-like) physiological response that is consistently obtained across a variety of tasks posing mental demand. Each of the five tasks in Study 1 was associated with a mean decrease in RSA, and participants who showed greater decreases in RSA in response to one cognitive task also demonstrated greater decreases to the other tasks. Thus, individual difference in vagal flexibility appear to be of similar magnitude over time (i.e., one month). Because of the added complexities introduced by running opposite-sex pairs, we included only female participants in this first study, which limits the generalizability of our findings; however, we address this limitation in Studies 2 through 4 by including both sexes.

Given this initial evidence for the reliability of vagal flexibility, we next explored whether this trait-like physiological response provides unique information about psychological and social states beyond that provided by the more widely used measure of vagal tone. Specifically, in Study 2 we examined how individual differences in vagal flexibility would relate to various psychosocial variables. We used a visual tracking task to engender attentional demands and calculated vagal flexibility as the difference between vagal activation during the resting state and vagal activation during a visual tracking task. Before completing this task in the lab, participants provided self-report ratings of perceived stress, anxiety, depression, and loneliness. We hypothesized that vagal tone and vagal flexibility would show distinct associations with these psychosocial measures. Specifically, drawing on past findings showing that higher vagal tone is associated with more positive physical and mental health (Brosschot & Thayer, 1998; Thayer, Yamamoto, & Brosschot, 2010), we hypothesized that vagal tone would be negatively associated with self-reported levels of stress, anxiety, and depression, whereas vagal flexibility would be uniquely associated with loneliness—the only measure in our battery that is intimately linked to social functioning.

Study 2

Setting and Participants

We recruited participants from the community ($N = 76$; 52% female) to complete a study on “life span autonomic flexibility.” Participants were between the ages of 20 and 74 ($M = 44.5$, $SD = 20.6$) and racially/ethnically diverse (76.3% European American, 13.2% Asian American, 5.3% Hispanic or Latino, 3.9% mixed

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[3] To examine whether changes in respiration rate could account for the relationships between vagal flexibility scores, we ran regression analyses for each task’s vagal flexibility score, predicting the change in RSA with the change in respiration rate, and saved the residuals. When these residuals were correlated, we found no difference from the zero-order correlations of vagal flexibility.

Table 1
Correlations Between Vagal Flexibility on Different Study Tasks, Across Days

	Set A	Set B		Set C	
	Password	Improv	Word context	20 questions	Category switch
Set A					
Password	—	.42** (n = 148)	.27** (n = 149)	.38** (n = 147)	.46** (n = 146)
Set B					
Improv		—	.62** (n = 164)	.44** (n = 148)	.45** (n = 147)
Word context			—	.39** (n = 149)	.33** (n = 149)
Set C					
20 questions				—	.63** (n = 161)

** $p < .001$.

race, and 1.3% African American). The study was conducted in a social psychophysiology laboratory with a sound-attenuated experimental room, where participants completed study procedures while their physiological signals were acquired continuously, and a separate control room that allowed for continuous and surreptitious monitoring of the participant.

Procedure

Self-reported psychosocial variables. Before their visit to the lab, participants were asked to complete a series of online questionnaires from their homes. These questionnaires asked participants about their current levels of stress (Perceived Stress Scale; Cohen, Kamarck, & Mermelstein, 1983), anxiety (Burns Anxiety Inventory; Burns & Eidelson, 1998), depression (Center for Epidemiological Studies Depression Scale [CESD]; Radloff, 1977), and loneliness (UCLA Loneliness Scale; Russell, 1996). The Perceived Stress Scale (PSS) is a 10-item measure that assesses the degree to which people perceive their lives as stressful. Participants are asked to rate how often their lives have been unpredictable, uncontrollable, and overloaded in the past month on a scale from 1 (*never*) to 5 (*very often*). The Burns Anxiety Inventory (BAI) is a checklist of 33 affective, cognitive, and physiological symptoms related to anxiety. We chose this measure because it circumvents the common problem among anxiety measures of confounding symptoms of anxiety with those of depression (Persons, Roberts, & Zalecki, 2003). Participants are asked to rate how frequently they experience each anxiety symptom on a scale from 0 (*not at all*) to 3 (*a lot*). The 20-item CESD was developed for use in studies of the epidemiology of depressive symptomatology in the general population. Participants are asked to rate how often they experience a series of symptoms, on a scale from 1 (*rarely or none of the time*) to 4 (*most or all of the time*). The UCLA Loneliness Scale assesses subjective feelings of loneliness or social isolation. Participants are asked to read 20 statements and to rate how often they feel the way described on a scale ranging from 1 (*never*) to 4 (*always*), for example, "*How often do you feel that people are around you but not with you?*" and "*How often do you feel that you are *in tune* with the people around you?*" (reverse-scored).

Physiological measures. After arriving at the laboratory and completing informed consent, participants were escorted to a private room where trained research assistants attached physiological sensors to obtain electrocardiographic and impedance cardiographic signals as in Study 1. The two electrocardiographic sensors were placed in a modified Lead II configuration, with one electrode positioned under the right collarbone and the other positioned on the left lateral side between the two lower ribs, to reduce potential movement artifacts during our critical measurement period (i.e., computer-based visual tracking task). For impedance cardiography, a mylar tape electrode system provided basal transthoracic impedance and the first derivative of basal impedance using a HIC-2000 impedance cardiograph. Two pairs of mylar tapes were applied to encircle the participant at the neck and torso (Sherwood et al., 1990). A 4mA AC 100 kHz current passes through the two outer electrodes and measures basal impedance from the two inner electrodes. Respiration rate was again derived from impedance cardiography. Following sensor application, participants completed a 5-min baseline physiological recording.

Attention task. After baseline, participants performed a visual tracking task (Cavanagh & Alvarez, 2005) that is commonly used in visual cognition experiments to measure multiple-object tracking capacity. The choice of this task was based on two rationales. First, we sought to elicit vagal withdrawal (decreases in RSA) using a task that was mentally demanding, but did not pose higher-level executive functioning demands that might be sensitive to differences in participants' IQ and education levels. Second, we sought to refine the vagal manipulation used in Study 1 (namely, the cooperative cognitive tasks) by using a "pure" attentional task that was itself free of social and emotional content to avoid the tautology of predicting social-emotional outcomes using a measure linked to social-emotional skills.

In this task, participants completed a total of 16 trials. Each trial began with 12 black dots presented against a gray background. At the beginning of each trial, a subset of these dots flash yellow for 2 s to designate themselves as the targets to be tracked by the participant. The target dots then return to black, camouflaging with the others, and participants are required to continue tracking these target dots, along with the distractors, for another 12 s as they move around the screen in random fashion. At the end of each trial, the dots stop and participants use the mouse to identify which among the 12 dots on the screen had been preselected as targets (i.e., which subset of dots had flashed yellow at the outset of the trial). Participants completed four blocks each comprising four trials. In the four blocks of trials, participants are required to track 2, 3, 4 and 5 targets, respectively, such that the task becomes increasingly difficult as it progresses. We used RSA reactivity recorded during this attention task to compute vagal flexibility.

Results

RSA flexibility. In line with past research showing that RSA decreases during mental demand, we expected overall mean decreases in RSA from resting levels during the attention task. As before, we are interpreting greater decreases in RSA to indicate vagal flexibility. As expected, mean RSA reactivity was negative, indicating an overall pattern of vagal withdrawal across participants, $M = -.42$ $SD = .75$, but a considerable range of responses was observed: -2.91 to 1.61. A t test revealed that on average participants experienced significant vagal withdrawal from baseline during the attention task, $t(75) = -4.86$, $p < .001$, 95% CI [$-.59$, $-.25$]. We then multiplied participants' reactivity scores by -1 so that greater decreases in RSA—or vagal flexibility—would be reflected by positive values.

Vagal tone, vagal flexibility, and associations with psychosocial variables. Next, we examined the associations of vagal tone with each of the self-reported psychosocial variables, controlling for age, gender, and BMI. Vagal tone was significantly negatively correlated with perceived stress (PSS total score), $pr(72) = -.26$, $p < .03$, and depression (CESD total score), $pr(72) = -.25$, $p < .03$, and marginally correlated with anxiety, $pr(72) = -.22$, $p < .06$ (BAI total score), controlling for age, gender, and BMI; that is, consistent with previous findings, individuals with higher vagal tone reported lower levels of perceived stress, anxiety, and depression. By contrast, vagal tone was not significantly correlated with self-reported loneliness (UCLA-L total score), $p > .13$. We then examined correlations between vagal flexibility and the aforementioned psychosocial variables, controlling for age, gender, BMI, and vagal tone. Only the correlation between vagal flexibility and loneliness was significant, $pr(68) = -.25$, $p = .035$, all other prs $< .13$, ps $> .30$. We then compared the correlation of vagal flexibility and loneliness with vagal flexibility and the other psychosocial variables and observed a minimum statistical difference, $z = 2.30$, $p = .022$. In summary, vagal flexibility was only significantly correlated with loneliness and this correlation was significantly different than the correlations between vagal flexibility and the other psychosocial variables. Finally, consistent with Study 1, vagal tone and vagal flexibility (raw, not reverse-scored) were moderately negatively correlated with each other, $r = -.35$, $p = .002$.

Discussion

Study 2 demonstrated that a mental challenge involving simple attentional demand is capable of eliciting decreases in RSA from baseline. Moreover, individual differences in the magnitude of this withdrawal (i.e., vagal flexibility) provide unique information about psychosocial variables beyond that provided by vagal tone. Whereas vagal tone was associated with perceived stress, anxiety, and depression—all of which describe individuals' intrapsychic experiences—vagal flexibility was uniquely associated with loneliness, the one measure in our battery that captured individuals' interindividual experiences.

In Study 1, we established that vagal flexibility is a trait-like physiological variable that can be elicited consistently through mental challenge and reliably over time. In Study 2, we showed that greater vagal flexibility (but not greater vagal tone) is associated with less loneliness. This latter finding appears to suggest, albeit indirectly, that individuals with greater vagal flexibility might have a greater capacity to "tune in" to their social world and engage with others. In Study 3, we sought to assess the link between vagal flexibility and social attunement in a more direct and rigorous manner. Specifically, we examined the association between individual differences in vagal flexibility and social-emotional perception—the ability to accurately perceive subtle social and emotional cues. To do so, we used the same visual tracking attention task to engender RSA decreases and obtain a measure of vagal flexibility. Participants then completed the Reading the Mind in the Eyes Task (RMET; Baron-Cohen, Wheelwright, Hill, Raste, & Plumb, 2001), which required them to view a series of photos of people's eye area and to choose a response that best describes how the person in each photo is thinking or feeling. We hypothesized that greater vagal flexibility would be associated with greater accuracy of social-emotional perception on the RMET.

Study 3

Method

Participants. We recruited participants from the community ($N = 103$; 51% female) to complete a study on "person perception." Participants were between the ages of 17 and 40 ($M = 23.6$, $SD = 4.8$) and racially/ethnically diverse (55% European American, 14% Asian American, 13% African American, 9% Latino, 7% mixed race, and 2% did not disclose). The study was conducted in a laboratory that had private cubicles outfitted with computer monitors and physiological recording equipment.

Procedure. After completing informed consent, participants were escorted to a private room where trained research assistants attached seven pregelled spot sensors to the participant's torso to obtain electrocardiographic and impedance cardiographic signals. The two electrocardiographic sensors were again placed in a modified Lead II configuration to reduce movement artifacts during our critical measurement periods. Impedance cardiography was assessed using a spot electrode system. The two current-transmitting spot electrodes were placed on the participants' back, one at the base of the neck between vertebrae C3 and C4 and the other just to the left of the participant's spine between vertebrae T8 and T9. The two current-recording sensors were placed at the jugular notch of the sternum and at the xiphoid process of the sternum. Participants were then escorted to a cubicle and seated in a chair and the leads from the sensors were attached to a 16-channel Mindware system that allowed us to monitor and record signals from a computer station separate from the participant. Participants sat alone and uninterrupted for the duration of the experiment and were prompted over the computer monitor and an intercom system on how to proceed.

Participants began the session by providing demographic information and then, via computer, completed one of the verbal subtests of the Wechsler Adult Intelligence Scale, third edition (WAIS-III; Weschler, 1997), which served as a proxy for verbal IQ. During the WAIS-III, participants were given 5 min to supply word definitions to as many words as possible, which were presented one at a time in the same order as the standard paper and pencil version of the test. We conducted this test to control for verbal intelligence on emotional accuracy scores. Following the WAIS-III, participants were instructed to relax for a 5-min recording of their resting physiological responses, which served as a baseline.

After baseline, participants completed the same visual tracking attention task described in Study 2. After this task, participants completed our primary outcome measure, the RMET, which is a test of social-emotional perception accuracy. After completing the RMET, an experimenter removed the sensors and compensated the participants.

Measures.

Physiological measures. We obtained ECG and ICG recordings from the 7-spot sensor configuration using a system from Mindware Technologies (Lafayette, OH). All signals were sampled at 1,000 Hz. We used the ECG data to estimate RSA and the impedance signal to derive respiration rate. Details of RSA scoring are otherwise identical to those reported in Study 1.

Social-emotional perception accuracy test. The RMET was developed to test the accuracy of social-emotional perception. In this test, participants are presented with 36 still images of men and women in which only the eye region of the face is displayed. For each image, participants are required to select from four options the response that best describes what the person in the image is thinking or feeling. Because we recruited a diverse sample of individuals with a broad range of education levels, and because the RMET is anchored in verbal responses, we supplied participants with a "dictionary" that defined the response options on the RMET. This enabled participants to confirm any word definition about which they felt uncertain before making their responses, thereby minimizing the possibility that individual differences in verbal intelligence would eclipse those for vagal flexibility in predicting social-emotional perception accuracy. After each judgment, participants rated how confident they were of their answer on an 11-point scale anchored at 0% and 100%. We created a single emotional accuracy score by summing the number of correct answers ($M = 26.3$; $SD = 4.0$, range 11 to 35).

Results

RSA flexibility. As in Study 2, we calculated vagal flexibility by subtracting the mean RSA obtained during the baseline recording from the mean RSA obtained during the attention task. As expected, mean RSA reactivity for the sample was negative, indicating an overall pattern of vagal withdrawal across participants, $M = -.13$, $SD = .60$, but a considerable range of responses was again observed: -1.64 to 1.94. A t test revealed that on average participants experienced a significant decrease in RSA from baseline during the attention task, $t(102) = -2.32$, $p = .02$. Again, we multiplied participants' RSA reactivity scores by -1 so that greater decreases in RSA from baseline—or vagal flexibility—would be reflected by a positive value.

RSA flexibility as a predictor of emotional accuracy. We predicted that greater *vagal flexibility* would be associated with greater social-emotional perception accuracy. Further, to demonstrate the unique effects of vagal flexibility on social-emotional accuracy, we controlled for intelligence (total scores on the WAIS verbal subtest) as well as attentional capacity on the visual attention task. The latter covariate is important because greater motivation or effort might increase both attentional capacity and social-emotional perception accuracy scores. As with the previous studies, we controlled for factors known to influence vagal responses—namely, age, gender, and BMI.[4]

Our primary regression analysis predicted social-emotional perception accuracy from vagal flexibility, controlling for the aforementioned covariates (see Table 2). In Step 1 of the model, we entered all covariates, and the overall model significantly predicted accuracy on the social-emotional perception task, $F(6, 96) = 6.32$, $p < .001$, $R^2 = .28$, adjusted $R^2 = .24$. Importantly, when vagal flexibility was added in Step 2 of the model, it produced a significant change in R^2, $F(1, 95) = 4.37$, $p = .04$: the greater the vagal flexibility, the greater the accuracy on the RMET. In an effort to control for "good guesses" on the multiple-choice format of the RMET, we also examined a similar model predicting accuracy weighted by participants' confidence ratings (the sum of each correct answer multiplied by its confidence score). Step 1 of the model did not significantly predict accuracy on the social-emotional task, $F(6, 96) = 1.89$, $p = .091$, $R^2 = .11$, adjusted $R^2 = .05$, but when vagal flexibility was added in Step 2, the overall model yielded a similar pattern of significant findings to the nonweighted model, $F(7, 95) = 2.188$, $p = .042$, $\Delta R^2 = .03$.

Discussion

Study 3 demonstrated that individual differences in vagal flexibility are related to social-emotional accuracy beyond verbal intelligence and attentional capacity. These initial data support the idea that individuals with greater vagal flexibility might be especially sensitive to subtle social and emotional cues in their environment, as indicated by their increased accuracy in detecting nonverbal expressions with limited information (i.e., context-free still images of the eye area only). More important, vagal tone (i.e., resting RSA) was unrelated to performance on the RMET, providing evidence that flexibility of vagus nerve activity is more closely linked to social and emotional perception than is resting activation level (cf. Hopp et al., 2013; Park et al., 2012).

Given these findings, we next explored whether individuals with greater vagal flexibility would display more affective, physiological, and behavioral sensitivity to social feedback during dynamic, face-to-face interpersonal interactions. Unlike still images, interpersonal interactions involve multiple communication channels—including the voice, body posture, facial expression, and language—which allow more social information to be communicated and to which we would expect individuals with greater vagal flexibility to show greater sensitivity. Whereas the use of still images in Study 3 provided more rigor and precision for examining the association between vagal flexibility and social sensitivity,

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[4] We included respiration rate as a covariate, but respiration rate was not related to either emotion accuracy or vagal flexibility and was not retained in the model.

Table 2

Study 3: Regression Analysis Predicting Accuracy on Reading the Mind in the Eyes Test

Variable	*B*	*SE* B	β
Step 1			
Age	0.16	0.08	0.20*
BMI	−0.19	0.07	−0.27***
Gender	1.09	0.73	0.14
WAIS score	0.16	0.04	0.36***
Attentional capacity	0.52	0.43	0.11
Vagal tone	0.08	0.29	0.03
Step 2			
Age	0.14	0.08	0.17
BMI	−0.20	0.07	0.29**
Gender	1.11	.72	0.14
WAIS score	0.15	0.04	0.35***
Attentional capacity	0.59	0.42	0.13
Vagal tone	0.17	0.31	−0.06
Vagal flexibility	1.29	0.62	0.19*

Note. $R^2 = .28$ for Step 1; $\Delta R^2 = .03$ for Step 2 ($p = .04$).
* $p < .05$. ** $p < .01$. *** $p < .001$.

examining the link between vagal flexibility and responses during a dynamic interpersonal interaction builds on our investigation by providing a test with more ecological validity and meaning.

In Study 4, participants were randomly assigned to complete an evaluative task in which they received real-time positive or negative social feedback. This evaluative task took the form of a mock job interview in which participants prepared an 8-min speech about their ideal job, delivered this speech to a panel of two evaluators, and then underwent a 5-min question-and-answer period. We predicted that individual differences in vagal flexibility would be associated with differences in sensitivity to this dynamic social interaction. Specifically, we expected that individuals with greater vagal flexibility would respond to positive social feedback with more adaptive physiological and psychological responses, and to negative social feedback with more maladaptive responses. In other words, greater vagal flexibility would be beneficial when the social environment was positive and accepting, but detrimental when the social environment signaled negativity and rejection. In Study 4, we explore these hypotheses using self-reported affective responses, cardiovascular reactivity (i.e., blood pressure changes), and observable social behavior.

Study 4

Participants

We recruited 68 participants (68% female) between the ages of 18 and 30 ($M = 21.8$, $SD = 3.3$) from the community. The study was conducted in a social psychophysiology laboratory with a sound-attenuated experimental room, where participants completed study procedures while their physiological signals were acquired continuously, and a separate control room that allowed for continuous and surreptitious monitoring of the participant.

Procedure

Participants began the session by reading and signing a consent form that described the assessment of physiological responses, but did not give any indication of the upcoming evaluative task. This was done to avoid contaminating baseline measurements with anticipatory stress. Following informed consent procedures, participants completed baseline self-report measures of affect (Positive and Negative Affect Schedule; Watson, Clark, & Tellegen, 1988), followed by the WAIS-III verbal subtest. The experimenter then applied a variety of physiological sensors for monitoring RSA and blood pressure, and participants sat for a 5-min recording of their baseline physiological signals.

Attention task. To avoid an overly lengthy study session, we used a different mental challenge task to induce RSA decreases (and calculate vagal flexibility) in this study—one that was integral to the study protocol. Specifically, we examined RSA changes during the speech preparation phase of the task, which demanded focus and was thus expected to engender decreases in RSA. Vagal flexibility was calculated as the difference between RSA during speech preparation and RSA at baseline.

Social stress task. Following the baseline and attention task, the experimenter reentered the room and informed the participant about the upcoming interview task. Specifically, the participant was asked to prepare and then deliver an 8-min speech about his or her ideal job to a panel of two evaluators. Because participants did not receive informed consent at the beginning of the study, we reminded them that they did not have to continue with the experiment. None of the participants elected to withdraw at this point. After obtaining verbal consent, the experimenter brought the two evaluators—one male, one female—into the room. The evaluators reiterated the task instructions and asked the participant if he or she had any questions. The participant was then left alone in the room for 2 min to silently prepare the speech. During speech preparation, the evaluators learned which condition the participant had been assigned. Specifically, the participant was randomly assigned to receive either positive/accepting or negative/rejecting nonverbal feedback from the evaluators. Once the preparation period was over, the evaluators reentered the room and sat 1 meter in front of where the participant was seated. The evaluators then instructed the participant to begin his or her speech.

Based on random assignment, the evaluators displayed subtle nonverbal feedback during the participant's speech. For participants assigned to the acceptance condition, ~30 s after the participant began to speak, the evaluators began to display positive nonverbal feedback, such as smiling, nodding, and leaning forward. These behaviors began slowly so as to convince participants that the quality of their speech had elicited the evaluators' responses. In contrast, evaluators assigned to participants in the rejection condition slowly began to display negative nonverbal feedback, such as frowning, shaking their head, sighing, and leaning back and crossing their arms.

After 8 min, the evaluators informed the participant that they would ask a series of job interview-type questions, for example, "If you had to hire someone for a job, would you hire someone with experience but no education, or education but no experience?" After 5 min of Q&A, the evaluators informed the participant that the interview was over and left the room. Once alone, participants completed postinterview PANAS items. After this, the experimenter entered the room to remove sensors, debrief, pay, and thank participants.

Measures

Physiological measures. We measured vagal activity using ECG acquired from a standard Lead II configuration with an ECG module from Biopac (Goleta, CA). The ECG data were collected at 1,000 Hz with an MP150 then visually inspected and manually scored offline using the Mindware HRV software module (Lafayette, OH). Additionally, we collected continuous blood pressure responses with a Colin blood pressure monitor (CBM 7000), which uses tonometric technology to obtain a continuous recording from the radial artery that is calibrated periodically with blood pressure measured from the brachial artery. From this signal, we obtained systolic and diastolic blood pressure values, which allowed us to calculate mean arterial pressure (MAP) using the formula $(2^{*}\text{DBP} + \text{SBP})/3$. Data were averaged across 1-min epochs and reactivity values were calculated by subtracting the last minute of baseline values (when participants were most relaxed) from the average of the second half of the interview task—namely, the question-and answer period—at which point the tone of the social feedback (positive vs. negative) was well established but the task was novel (see Ayduk, Gyurak, Akinola, & Mendes, 2013; Koslov et al., 2011; and Mendes & Koslov, 2013, for the same strategy and justification). This timing was decided a priori because feedback begins to come online during the initial speech portion of the task, making precise timing difficult, if not impossible; at the same time, choosing later minutes of the speech would have also been suboptimal because participants would have begun to habituate to the task at that point.

Self-report measures. Participants completed the PANAS (Watson et al., 1988) at the outset of the study and at the end of the social stress task. We hypothesized that vagal reactivity would be related to more sensitive emotional responding, and specifically, to shame—a self-conscious emotion that relates to people's awareness of others' reactions to, and evaluations of, them. Participants also completed a resources and demands questionnaire before and after the speech task to assess their appraisals of the situation (Mendes, Gray, Mendoza-Denton, Major, & Epel, 2007). Items on the resources scale ($\alpha = .81$) included: "I felt I have/had the abilities to perform well in the task," and "I felt that the task challenged me in a positive way." Items on the demands scale ($\alpha = .80$) included: "I exerted a lot of effort during the task" and "I am uncertain about how I performed." As in previous research (Mendes et al., 2007), we created a threat ratio by dividing demands by resources with higher numbers indicating greater threat appraisals.

Behavioral coding. We videotaped the interview task and later coded it for observable behavior.[5] Four female research assistants who were blind to the feedback condition were trained as coders by first watching videos ($n = 10$) together and then coding participants' behaviors and discussing any discrepancies therein. The four coders then all watched a second sample of videos ($n = 10$) and coded these independently; interrater reliability was acceptable, $\alpha = .79$. Finally, each of the trained coders coded a subset of the videos (between 20 and 30 videos each) such that every video was rated by at least two coders. Coders rated participants on three aspects of social behavior that occurred during the social stress task: "smiling and laughing," "gesturing and animated," and "engaged with evaluators." These behaviors were rated on a 6-point scale anchored at *not at all* on one end and *completely* on the other. Together these behavioral codes produced acceptable reliability, $\alpha = .76$, and were averaged to create a single index of sociable behavior for each participant.

Results

Self-reported responses to the social stress task. We first examined whether the different social feedback conditions produced the expected effects. There were no differences between participants in the two feedback conditions in positive or negative emotions at baseline. An ANCOVA (analysis of covariance) controlling for baseline positive emotion revealed a significant effect of social feedback on positive emotions after the speech task: accepting feedback, $M = 3.02$, $SD = .93$; rejecting feedback, $M = 2.44$, $SD = .80$, $F(1, 65) = 5.60$, $p = .03$. The social feedback condition did not have a significant effect on self-reported negative emotions, though there was a trend for participants receiving rejecting feedback to report higher levels of negative emotions, $M = 1.74$, $SD = .80$, than those receiving accepting feedback, $M = 1.47$, $SD = .45$; $F(1, 65) = 2.28$, $p = .14$.

We then examined posttask appraisals and observed that participants in the negative feedback condition perceived the situation as more demanding, $M = 4.58$, $SD = 1.30$, and reported having fewer resources to cope with the situation, $M = 3.83$, $SD = .65$, than did those in the positive feedback condition, $M = 3.97$, $SD = 1.05$; $M = 4.25$, $SD = .69$ and $F(1, 66) = 4.51$, $p = .04$; $F(1, 66) = 6.63$, $p = .01$, respectively. Not surprisingly given these differences, there was a significant difference in the threat ratio (calculated as demands divided by resources) between participants in the two feedback conditions: $F(1, 66) = 9.37$, $p = .01$. Participants who received positive feedback reported smaller threat ratios, $M = 0.96$, $SD = .29$, than did those who received negative feedback, $M = 1.23$, $SD = .41$.

Vagal flexibility. We calculated vagal flexibility by first subtracting RSA obtained during the baseline period from RSA obtained during the first minute of speech preparation. As in the previous studies, there was a significant decrease in RSA such that the mean vagal change was -1.38 ($SD = 1.30$, range -3.56 to 2.94), which was significantly less than zero, $t(60) = -2.29$, $p = .03$. We then multiplied this value by -1.

Self-report affect. First, we examined whether the social context manipulation would moderate the effects of vagal flexibility on self-reported shame. We predicted self-reported shame after the interview task, controlling for age, gender, BMI, and vagal tone, and self-reported shame at baseline, and observed no main effects for vagal flexibility or feedback condition. In Step 2, the vagal flexibility by social feedback condition interaction was significant, $t(59) = 3.30$, $p = .002$. Among participants assigned to receive negative social feedback, greater vagal flexibility was associated with more self-reported shame, $b = .48$, $p = .002$, but the direction of the association was reversed (though nonsignificant) for those assigned to receive positive feedback, $b = -.22$, $p = .184$ (see Figure 1).

Blood pressure reactivity. We expected that individuals with greater vagal flexibility would show more context-sensitive responses to social feedback—specifically, greater increases in blood pressure to negative feedback and smaller increases in blood

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[5] Video-recordings of 10 participants were lost in a hard drive failure.

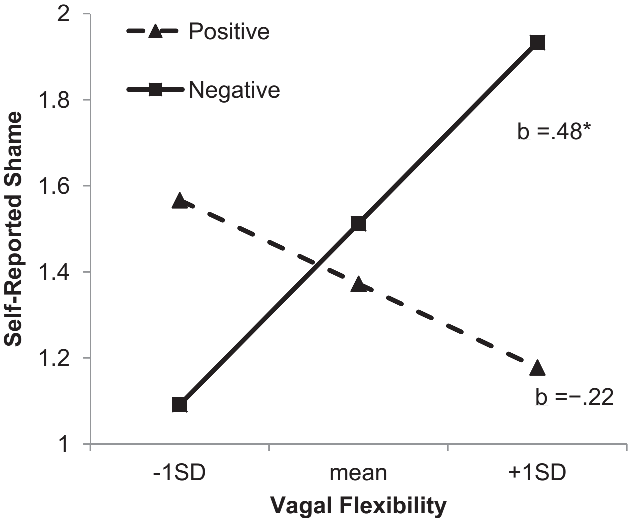

Figure 1. Estimated regression slopes predicting self-reported shame postinterview by vagal flexibility moderated by social context. Lines plotted at the mean and 1 *SD* above and below the mean.

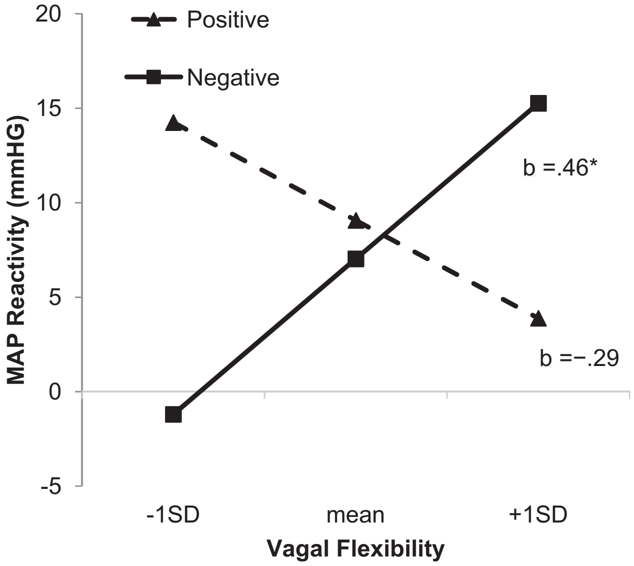

Figure 2. Estimated regression slopes predicting mean arterial blood pressure changes during the interview by vagal flexibility moderated by social context. Lines plotted at the mean and ±1 *SD* above and below the mean.

pressure to positive feedback. As before, we included the standard covariates and the main effects of vagal flexibility and feedback condition in Step 1 to predict blood pressure changes. No main effects were observed. The vagal flexibility by social feedback condition interaction in Step 2 was significant, $t(52) = 2.90$, $p = .006$. Among participants receiving positive social feedback, greater vagal flexibility was associated with lower blood pressure reactivity, $b = -.29$, $p = .138$, though not significantly so; by contrast, participants receiving negative social feedback showed the opposite pattern: greater RSA flexibility was associated with higher blood pressure reactivity, $b = .46$, $p = .015$ (see Figure 2).

Observed behavior. We then turned to the data obtained from the videos in which participants' behavior during the interview was coded for sociability. Following the same regression strategy as before, we observed a significant main effect of feedback condition on observed sociable behavior, $t(52) = -4.66$, $p < .001$. Consistent with the feedback assignment, participants who received positive social feedback ($M = 2.38$, $SD = .84$) were seen as more sociable by our observers than were participants receiving negative social feedback ($M = 1.34$, $SD = .65$). Critically, the vagal flexibility by social feedback condition interaction was significant, $t(52) = -3.07$, $p = .004$. Among participants assigned to receive positive social feedback, greater vagal flexibility was associated with more sociable behavior toward the evaluators, $b = .38$, $p = .032$, whereas among participants assigned to receive negative social feedback, greater vagal flexibility was associated with less sociable behavior, $b = -.34$, $p = .047$ (see Figure 3).

Comparison of vagal flexibility with vagal tone. We also investigated whether vagal tone would produce the same effects reported for vagal flexibility above by running parallel regression analyses predicting self-reported shame, MAP reactivity, and sociable behavior from the standard covariates (age, gender, and BMI), vagal tone, social feedback condition, and the interaction of vagal tone and feedback condition. In all three cases, the interaction of vagal tone and feedback condition was nonsignificant: shame: $t(61) = .44$, $p = .66$, MAP reactivity: $t(53) = -.50$, $p = .62$, sociable behavior: $t(54) = -.67$, $p = .51$. Thus, vagal tone does not appear to be related to the sensitivity of affective, physiological, and behavioral responses to valenced social feedback.

Specificity of parasympathetic nervous system flexibility. To more stringently test the specificity of our finding that vagal flexibility—a measure of parasympathetic nervous system influence on the heart—is a unique physiological predictor of social sensitivity, we ran similar regressions to those above (i.e., predict-

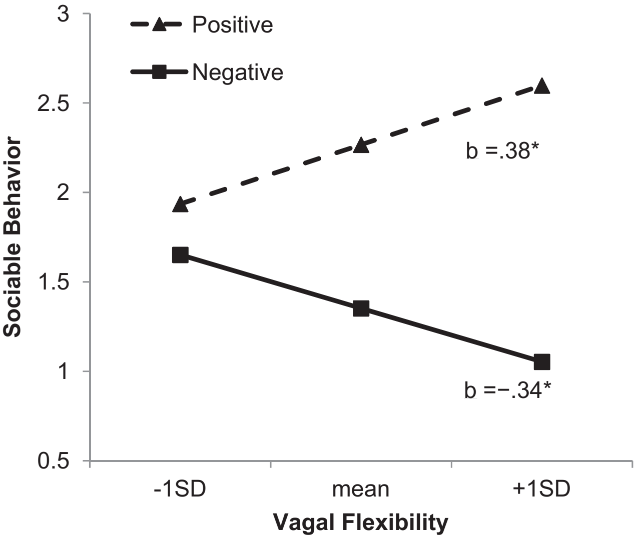

Figure 3. Estimated regression slopes predicting sociable behavior coded by observers during the interview by vagal flexibility moderated by social context. Lines plotted at the mean and ±1 *SD* above and below the mean.

ing self-reported shame, MAP reactivity, and sociable behavior) using the interaction of pre-ejection period (PEP) reactivity and feedback condition as predictors and including the same standard covariates. PEP, which is a measure of the period between the stimulation of the heart's left ventricle and the opening of the aortic valve, provides a relatively pure index of sympathetic nervous system influence on the heart. As with the analyses for vagal flexibility, we calculated PEP reactivity by subtracting PEP during baseline from PEP during the speech preparation phase and then multiplying this value by -1, so that greater decreases in PEP (indexing greater sympathetic activation) would be reflected by positive values. Our results showed that the interaction of PEP reactivity and social feedback condition significantly predicted self-reported shame, $t(55) = -4.06$, $p < .001$. Among participants receiving positive feedback, greater PEP reactivity was associated with less self-reported shame, $b = -.33$, $p = .051$. Participants receiving negative feedback showed the opposite pattern: PEP reactivity was associated with more self-reported shame, $b = .51$, $p < .001$. Consistent with a reciprocal relationship between sympathetic nervous system and parasympathetic nervous system, the sympathetic effects mirrored the parasympathetic effects for the affect reports. Nonetheless, PEP was not a significant predictor of MAP reactivity, $t(49) = -1.61$, $p = .115$, or sociable behavior, $t(47) = .93$, $p = .358$. Thus, the dynamic influence of the parasympathetic nervous system on the heart—assessed via vagal flexibility—appears to uniquely predict the full constellation of affective, physiological, and behavioral responses to valenced social feedback.

Discussion

Building on the results of Study 3, in which we showed a link between vagal flexibility and social sensitivity using static facial images, Study 4 examined this association using a richer and more ecologically meaningful task. In line with the results of Study 3, we again found that participants with greater vagal flexibility showed greater social sensitivity, as indexed by their awareness of, and affective, physiological, and behavioral responsiveness to, dynamic social feedback cues. Specifically, among individuals assigned to receive negative social feedback, greater vagal flexibility was associated with more shame, greater increases in blood pressure, and less sociable behavior. By contrast, among those assigned to receive positive social feedback, greater vagal flexibility was associated with more sociable behavior toward the evaluators. These results support the idea that vagal flexibility is related to greater social sensitivity and responsiveness to static and dynamic affective contexts. More important, we did not observe wide-ranging effects when examining either vagal tone or sympathetic (PEP) reactivity.

General Discussion

Our investigation examined whether individual differences in vagal flexibility—operationalized as the magnitude of RSA decrease from rest to mental challenge—serves as a useful trait-like physiological index that can be used to predict social sensitivity, or attunement to subtle social-emotional cues in the environment. In Studies 1 and 2, we demonstrated that individual differences in vagal flexibility show acceptable reliability across a variety of mental challenges and over time, and provide unique psychosocial information beyond that provided by vagal tone. In Study 3, we demonstrated an association between greater vagal flexibility and more accurate social-emotional perception—a relation that held after controlling for several potential confounds, including age, gender, BMI, verbal IQ, attentional capacity, and vagal tone. In Study 4, we extended the investigation from the perception of static facial images to a dynamic interaction in which subtle social feedback was manipulated. We expected that greater vagal flexibility would be associated with increased social sensitivity and that these effects would be moderated by social context. Consistent with our predictions, we found that in the context of social rejection cues, individuals with greater vagal flexibility responded with greater negative responses, including subjective states, hemodynamic changes, and observable behavior. In contrast, when perceiving cues of social acceptance, greater vagal flexibility translated into more observable sociable behavior and a trend toward lower blood pressure reactivity. More important, the strong association we repeatedly found between vagal flexibility and social sensitivity was never obtained for the more commonly used vagal tone measure, suggesting that it may be profitable for researchers interested in the biobehavioral processes underlying social sensitivity to begin including more dynamic measures of vagal functioning.

Limitations and Strengths

There are several limitations that we view as caveats to the work reported here. First, a central limitation of these studies is that all of our outcome variables and contexts were social in nature. Therefore, these data cannot help us discern whether greater vagal flexibility is simply related to better global perceptual acuity and responsiveness (i.e., irrespective of whether the percepts are of a social vs. nonsocial nature), or whether this acuity and responsiveness are specific to the social domain (though the results of Study 2 showing a unique link between greater vagal flexibility and less loneliness is a first step in the direction of isolating the social effects of vagal flexibility). Much theory has been advanced to argue for the social specificity of the vagus nerve. For example, polyvagal theory strongly argues that myelinated vagal control of the heart is specifically involved in social engagement, though Thayer and colleagues have argued that individuals with higher vagal tone at rest and greater vagal withdrawal during challenge have a better ability to engage and disengage with demands in the environment, broadly construed (Thayer & Friedman, 2004; Thayer & Lane, 2000b). We acknowledge that the present study did not allow us to test the limits of social-specificity. Second, we used a variety of tasks to engender vagal withdrawal, capitalizing on past evidence suggesting that mental challenge, broadly defined, robustly produces decreases in RSA. This can be viewed as an advantage in that we show generalizability across mental challenges, or as a shortcoming given the use of multiple tasks across studies. Third, our focus on vagal withdrawal precludes the full array of possible vagal regulatory responses, including increases in RSA from baseline that might be elicited by tasks inducing a state of relaxation, such as meditation or the induction of certain positive emotions. In future research, exploring individuals' full range of vagal flexibility (i.e., the degree to which they can both decrease and increase RSA in context-appropriate fashion) might prove even more informative as a biobehavioral predictor of social context sensitivity. Finally, given our correlational approach to measuring the associations between vagal flexibility and social sensitivity, our data stop short of uncovering the causal nature of vagal influences on social engagement processes. This type of work would only be possible by directly manipulating vagal responses— either through pharmacological blockade via the cholinergic blocker atropine or by vagal nerve stimulation—and then testing the resultant effects on social sensitivity.

Implications and Future Directions

The association between vagal flexibility and social cue sensitivity demonstrated herein has important implications for clinical, developmental, and health psychology, and points to multiple avenues for future exploration. In terms of clinical psychology, the focus on a trait-like physiological predictor of social context sensitivity aligns with the general trend in mental health research away from relying on *Diagnostic and Statistical Manual for Mental Disorders*-based diagnostic categories and toward conceptualizing psychopathologies using dimensions of observable behavior and neurobiological indices that cut across disorders (http://nimh.nih.gov/research-priorities/rdoc/index.shtml). Aberrant RSA reactivity has already been documented across a range of psychopathologies, including anxiety, depressive, attentional deficit, and autism spectrum disorders, as well as among individuals who engage in nonsuicidal self-injury and those who behave aggressively (Beauchaine et al., 2013; Cohen et al., 2000; Crowell et al., 2005; Gottman et al., 1995; Neuhaus, Bernier, & Beauchaine, 2014; Rottenberg, Wilhelm, Gross, & Gotlib, 2003; Thayer, Friedman, & Borkovec, 1996). In all these pathologies, individuals share a tendency toward behavior that is poorly calibrated to the social context. Thus, looking at these disorders through a physiologic lens—namely, one that is characterized by poor vagal flexibility—raises the possibility of better understanding their neurophysiological underpinnings and etiology, and developing more optimally matched treatments, such as somatic therapies that directly target the vagus nerve, or exercise therapy, which can improve vagal regulation.

The range of aberrant RSA responding in the aforementioned disorders—from highly restricted vagal reactivity to excessive vagal withdrawal—also raises an important question about the boundary conditions of adaptive vagal flexibility. In other words, could exaggerated or context-inappropriate RSA reactivity—particularly when paired with low vagal tone—also prove maladaptive? Indeed, several existing studies support the idea that excessive vagal withdrawal is related to negative emotional states and may be a nonspecific marker of emotional lability (Beauchaine, 2001).

In later life, physiological aging has been characterized by a progressive loss of complexity in the dynamics of all systems. In particular, age-related declines in heart rate variability have been consistently reported and are thought to stem from the dropout of sinoatrial node cells, altered β-adrenoceptor responsiveness, and an apparent reduction in parasympathetic tone (Lipsitz & Goldberger, 1992). Together, these changes impair older adults' ability to adapt to stressors, rendering them more susceptible to hypotension, sudden death, and mortality after myocardial infarction. It would be intriguing to explore the extent to which putative age-related declines in vagal flexibility are associated with decreased sensitivity to the sorts of subtle social-emotional cues that might underlie greater equanimity on the one hand, and increased gullibility on the other (e.g., Mendes, 2010).

In summary, the present investigation identified a reliable trait-like physiological marker that predicts social sensitivity in a context-dependent fashion. Our findings contribute to a growing body of literature focused on identifying neurobiological predictors of adaptive social-emotional functioning, and have important implications for research in clinical, developmental, and health psychology.

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Received January 24, 2014
Revision received June 25, 2014
Accepted July 1, 2014 ■