Journal of Personality and Social Psychology

0022-3514/14/$12.00 http://dx.doi.org/10.1037/a0037509

Vagal Activity Is Quadratically Related to Prosocial Traits, Prosocial Emotions, and Observer Perceptions of Prosociality

Aleksandr Kogan
University of Cambridge

Christopher Oveis and Evan W. Carr
University of California, San Diego

June Gruber
Yale University

Iris B. Mauss
University of California, Berkeley

Amanda Shallcross
New York University School of Medicine

Emily A. Impett
University of Toronto Mississauga

Ilmo van der Lowe and Bryant Hui
University of Cambridge

Cecilia Cheng
The University of Hong Kong

Dacher Keltner
University of California, Berkeley

In the present article, we introduce the quadratic vagal activity–prosociality hypothesis, a theoretical framework for understanding the vagus nerve's involvement in prosociality. We argue that vagus nerve activity supports prosocial behavior by regulating physiological systems that enable emotional expression, empathy for others' mental and emotional states, the regulation of one's own distress, and the experience of positive emotions. However, we contend that extremely high levels of vagal activity can be detrimental to prosociality. We present 3 studies providing support for our model, finding consistent evidence of a quadratic relationship between respiratory sinus arrhythmia—the degree to which the vagus nerve modulates the heart rate—and prosociality. Individual differences in vagal activity were quadratically related to prosocial traits (Study 1), prosocial emotions (Study 2), and outside ratings of prosociality by complete strangers (Study 3). Thus, too much or too little vagal activity appears to be detrimental to prosociality. The present article provides the 1st theoretical and empirical account of the nonlinear relationship between vagal activity and prosociality.

Keywords: respiratory sinus arrhythmia, emotion, cardiac vagal tone, thin slicing, heart rate variability

The search for the biological correlates of prosocial behavior—levels of trustworthiness, compassion, and general kindness—has long been of interest in the social and biological sciences. This interest has spawned theoretical and empirical work examining how prosociality is correlated with patterns of activity in the central and peripheral nervous systems and theoretically relevant genetic markers (Goetz, Keltner, & Simon-Thomas, 2010; Harbaugh, Mayr, & Burghart, 2007; Keltner, Kogan, Piff, & Saturn, 2014; Kosfeld, Heinrichs, Zak, Fischbacher, & Fehr, 2005; Oveis, Cohen, et al., 2009; Rodrigues, Saslow, Garcia, John, & Keltner, 2009; Sober & Wilson, 1998).

Recent developments in the study of human physiology have implicated vagus nerve activity—often measured via respiratory sinus arrhythmia (RSA), which reflects the extent to which the vagus nerve exerts parasympathetic control over the heart rate (Berntson, Sarter, & Cacioppo, 1998)—in numerous processes that are important for prosociality. In particular, individuals with higher vagal activity tend to show increased levels of positive emotions, social connection, and emotional expressivity and are better able to regulate their negative emotions in response to intense stressors—all processes important to prosociality (Beauchaine, 2001; Butler, Wilhelm, & Gross, 2006; Côté et al., 2011; Eisenberg et al., 1995; Fabes & Eisenberg, 1997; Keltner et al., 2014; Kok & Fredrickson, 2010; Oveis, Cohen, et al., 2009;

Aleksandr Kogan, Department of Psychology, University of Cambridge; Christopher Oveis and Evan W. Carr, Rady School of Management, University of California, San Diego; June Gruber, Department of Psychology, Yale University; Iris B. Mauss, Department of Psychology, University of California, Berkeley; Amanda Shallcross, Department of Psychology, New York University School of Medicine; Emily A. Impett, Department of Psychology, University of Toronto Mississauga; Ilmo van der Lowe and Bryant Hui, Department of Psychology, University of Cambridge; Cecilia Cheng, Department of Psychology, The University of Hong Kong; Dacher Keltner, Department of Psychology, University of California, Berkeley.

Aleksandr Kogan and Christopher Oveis contributed equally to this article. We would like to acknowledge Gregg Sparkman, Scott Sitrin, Walter Sobchak, and Theodor Herzl.

Correspondence concerning this article should be addressed to Aleksandr Kogan, Department of Psychology, University of Cambridge, Downing Street, Cambridge, United Kingdom CB2 3EB. E-mail: ak823@cam.ac.uk

Porges, 2001; Wang, Lü, & Qin, 2013). These studies, we note, have not directly established linkages between cardiac vagal tone (CVT) and prosocial behavior but instead have investigated processes such as social connection that are likely involved in prosocial behavior (Keltner et al., 2014). These processes are important for prosocial behavior (e.g., remaining calm in the face of another's distress), but on their own do not constitute prosociality (e.g., one can be calm in the face of another's distress without moving to help them). Thus, taken together, these studies suggest that vagal activity is likely associated with prosociality, though a direct empirical test of this hypothesis is needed.

It is important to note that the literature on vagal activity has also produced some contradictory findings. For instance, extremely high levels of vagal activity are associated with mania (Gruber, Harvey, & Purcell, 2011; Gruber, Johnson, Oveis, & Keltner, 2008), suggesting that greater vagal activity may not always be better for social functioning. This literature suggests that CVT may correlate with prosociality, but the relationship may not be a simple linear one.

Here, we propose the *quadratic vagal activity–prosociality hypothesis*, which holds that vagal activity is a biological correlate of prosociality in a nonlinear fashion. In particular, our hypothesis predicts that greater cardiac vagal activity is an adaptive response that promotes prosociality—up to a point. At a very high level, we predict that vagal activity can become socially maladaptive. We present three studies that provide the first empirical tests of the predictions stemming from the quadratic vagal activity–prosociality hypothesis. We examined how vagal activity is related to self-reported prosocial traits and positive emotions, as well as how it relates to naïve-observer, thin-slice ratings of the individual's prosociality (e.g., Ambady, Bernieri, & Richeson, 2000). By examining an individual's prosocial traits and emotions, as well as outside observer perceptions, this set of studies provides a rigorous test of core predictions stemming from the quadratic vagal activity–prosociality hypothesis.

Vagal Activity and Its Correlation With Prosociality

An active area of inquiry into biological correlates of prosociality is the study of the vagus nerve, one branch of the parasympathetic autonomic nervous system that is theorized to promote the ability empathize and connect with others (Beauchaine, 2001; Porges, 2001). The vagus nerve is a collection of autonomic nervous system fibers projecting from the brainstem to peripheral organs and is the parasympathetic nervous system's primary regulator of heart rate. While to date no formal model linking vagal activity to prosociality has been specified, both anatomical and empirical evidence suggests that vagal activity could underlie prosociality. First, activation of the vagus nerve decreases cardiovascular arousal, promoting emotion regulation and calmness in response to distress (Butler et al., 2006; Fabes & Eisenberg, 1997; Segerstrom & Nes, 2007; van Kleef et al., 2008). This kind of emotion regulation allows individuals to overcome their own distress and focus on the needs of others—core processes of prosociality. Second, according to Porges' polyvagal theory (1995, 2001, 2007), the vagus nerve is a component of the human social engagement system. The vagus nerve is responsible for the regulation of the vocal cords and interacts with the neural regulation of the eyes, ears, and select facial muscles involved in social communication and affiliation (Beauchaine, 2001; Porges, 2001). These anatomical characteristics of the vagus nerve have led researchers to theorize that the vagus nerve subserves core components of emotional and social engagement (Porges, 1995, 2001, 2007).

We should note that in Porges' (1995, 2001, 2007) and other scholars' work, the term *vagal tone* is used to describe the physiological phenomenon reflected by the measure RSA. In the present work, we instead use the less interpretive term *vagal activity* because RSA can reflect both tonic and phasic vagal activity (see Berntson, Cacioppo, & Grossman, 2007, for fuller discussion). However, we wish to explicitly connect our work to other work on the measure RSA (also termed *high-frequency heart rate variability*) and the construct vagal tone (also termed *cardiac vagal control*).

Emerging empirical evidence provides some indirect support for the notion that vagal activity is related to prosociality. Vagal activity—often indexed via respiratory sinus arrhythmia (RSA)—predicts increased expressivity when being approached by strangers, more sociability, and fewer adjustment problems when entering preschool (Eisenberg et al., 1995; Fox & Field, 1989; Stifter, Fox, & Porges, 1989). Higher vagal activity also predicts increases in positive emotions and connectedness to others over time; in turn, increases in positive emotions and social connectedness predict later increases in vagal activity, suggesting an upward spiral relationship (Kok & Fredrickson, 2010). Prospective data also link higher resting levels of vagal activity levels to increased self-reports of traits tied to prosociality, such as extraversion and agreeableness, at 6–8 months after the vagal activity assessment (Oveis, Cohen, et al., 2009). While none of the empirical work to date has explicitly linked vagal activity with prosociality, the previously cited work illustrates that vagal activity is related to many of the core processes required for prosociality, including positive emotions, sociability, greater connection to others, and emotion regulation.

But is the relationship between vagal activity and psychological constructs a simple linear one? A closer inspection of the vagal activity literature suggests a more complex picture. For instance, individuals at risk for mania show elevated vagal activity in comparison to individuals not at risk (Gruber et al., 2008). On the other end of this continuum, low vagal activity appears to correlate with several mental illnesses, including major depressive disorder (Dalack & Roose, 1990), anxiety (Friedman & Thayer, 1998), and posttraumatic stress disorder (Cohen, Kotler, Matar, & Kaplan, 1997). Similarly, among 6- to 8-year-old girls—who tend to show higher levels of vagal activity compared with boys—higher vagal activity levels predicted *lower* levels of peer and teacher ratings of sociability (Eisenberg et al., 1995, 1996). Finally, the literature on vagal activity and depression is mixed; while some studies show that greater vagal activity predicts lower levels of depression (e.g., Rottenberg, Wilhelm, & Gross, 2001), others yield the opposite pattern of results (Schultz, Anderson, & van de Borne, 1997), and still other studies do not show any relationship at all (Rottenberg, 2007; Volkers et al., 2004). Collectively, these studies underscore the complexity of vagal activity's correlates and illustrate that a simple linear account of the link between individual differences in vagal activity and psychological constructs may not be adequate.

The writings of Aristotle may provide some insight into understanding the apparent inconsistencies in the literature on vagal activity. In writing about when emotions are functional and when they are not, Aristotle long ago advanced his principle of moderation: Emotions in moderate degrees, in the right context, and in response to the right people are functional with respect to the individual's well-being (cf. Grant & Schwartz, 2011). Even virtues—for example, compassion, gratitude, and courage—can be dysfunctional (or vices) when taken to extremes. Few studies have directly tested this important thesis, although relevant data are suggestive. For example, moderate levels of embarrassment tend to predict positive social outcomes (Feinberg, Willer, & Keltner, 2012), whereas the relative absence of embarrassment tends to covary with antisocial tendencies (Keltner & Buswell, 1997), and high levels of embarrassment covary with social anxiety (Leary, 2001). Perhaps even more dramatically, recent evidence has demonstrated that positive emotions, thoughts, and even life satisfaction can become detrimental at extreme levels (Cheng, Wong, & Tsang, 2006; Gruber, Mauss, & Tamir, 2011; Oishi, Diener, & Lucas, 2007). Recent work in the study of oxytocin has also begun to suggest that moderate levels of oxytocin are most optimal in promoting social cognition and functioning (Bartz, Zaki, Bolger, & Ochsner, 2011).

Integrating the previously cited anatomical and empirical evidence, we propose the quadratic vagal activity–prosociality hypothesis. We hold that vagus nerve activity is a core physiological correlate of prosociality, promoting greater compassion and care for others by modulating arousal (via regulation of the heart) and emotional expression (via vocalization). Thus, we theorized that greater vagal activity at rest, as measured by RSA, would be reflective of greater prosociality. Yet very high levels of vagal activity may promote too much regulation of arousal and emotional expressivity, which can become maladaptive, reflecting a pattern of mania and indiscriminate affiliation. It may also be the case that extremely high levels of vagal activity compromise the *cardiac vagal brake*—the efficient withdrawal of vagal regulation of the heart in response to environmental challenges is critical to social engagement (Heilman et al., 2012). Therefore, our hypothesis predicts a quadratic relationship between vagal activity and prosociality, holding that prosociality would be highest at moderate levels of vagal activity and that the relationship between vagal activity and prosociality becomes negative among individuals with the highest levels of vagal activity.

More specific analyses of prosocial behavior further set the stage for this hypothesis. Prosociality reflects a balance of other-focus, wherein the individual attends to the needs and concerns of others, and self-focus, wherein the individual experiences personal distress and considers the personal costs and benefits of particular courses of action (Goetz et al., 2010; Sober & Wilson, 1998). Prosociality, then, requires a balance of self- and other-focus—one we hypothesize will be in part enabled by vagal activity. To respond with kindness, empathy, or cooperation to someone in need, individuals must regulate their own distress and turn their attention outwards from themselves to the social world—a process in part facilitated by greater vagal activity. Absent this emotion regulation, the individual is overwhelmed by personal distress, and a prosocial response does not take hold (Eisenberg et al., 1995). Extreme levels of vagal activity, by contrast, could dampen the personal distress that initiates the prosocial response (Goetz et al., 2010) and cause the individual to not notice another's needs or suffering. Therefore, too little vagal regulation may lead to panic in the face of another's pain, whereas too much vagal regulation may lead an individual to not notice another's suffering; moderate vagal regulation, then, should allow for both the ability to empathize with an individual's pain and to regulate one's own distress to provide care to the person in need. These converging lines of reasoning led to our quadratic vagal activity–prosociality hypothesis. To date, however, no study has considered or detected such a quadratic relationship between vagal activity and prosociality—furthermore, no study has explicitly evaluated even a linear relationship.

Beyond Self-Report: The Quick Detection of Traits From Thin Slices of Behavior

Humans have proven able to make accurate, intuitive judgments about others from witnessing only brief samples, or thin slices, of nonverbal behavior (see Ambady et al., 2000). People can make accurate predictions about the lifestyles, personalities, and even behavioral patterns of strangers—all from such thin slices of behavior. For instance, participants were able to detect the sexual orientation of others at better than chance levels from photographs and silenced video clips as short as 1 s (Ambady, Hallahan, & Conner, 1999). In the classroom, participants made accurate predictions about end-of-semester evaluations of teachers from viewing just 6-s silenced video clips of them (Ambady & Rosenthal, 1993). Researchers focusing on personality have demonstrated that adults can accurately detect the interpersonal tendencies associated with psychopathy in inmates based on viewing as little as 5 s of facial behavior, even in the absence of any social interaction in the video (Fowler, Lilienfeld, & Patrick, 2009). Similarly, coders were able to assess the personality traits of individuals with personality disorders from 30 s of sample interview behavior (Oltmanns, Friedman, Fiedler, & Turkheimer, 2004). Within nonclinical populations, naïve observers made reliable personality judgments about strangers from watching less than 2 min of behavior (Borkenau, Mauer, Riemann, Spinath, & Angleitner, 2004). Even social status has been shown to be readily detectable based on viewing 60-s video clips of individuals (Kraus & Keltner, 2009) or listening to short recording of an individual's laughter (Oveis, Kogan, Liu, & Keltner, 2014). Perhaps most impressive, people were able detect at better than chance levels whether an inmate gave a true or false confession statement from a 15-s video clip; participants who saw the full clips of the confessions (3 min long) actually performed *worse* than the participants who saw 15-s long clips and in fact did not perform better than chance (Albrechtsen, Meissner, & Susa, 2009). Collectively, this body of work speaks to the human capacity for quick and accurate detection of numerous traits and internal states of strangers.

In the present work, we built upon this foundation to test whether the prosociality judgments made by naïve observers about target individuals follows the quadratic vagal activity–prosociality hypothesis. More specifically, we reasoned that if there were indeed a quadratic relationship between vagal activity and prosociality, then it may manifest itself in behavioral cues that others can quickly detect and use to make judgments about the individual. We therefore predicted that individuals' vagal activity (measured via RSA) would quadratically predict how naïve observers would rate them on the basis of thin slices of behavior. Such evidence is important in extending the validity of the vagal activity–prosociality link. After all, such data can eliminate the possibility that the effects merely reflect a self-serving bias that can arise in self-report. Further, if judgments of prosociality covary with vagal activity, this type of evidence can speak to the communicability of prosociality and the social signaling function of vagal activity.

Present Studies

In the present research, we tested for the first time whether vagal activity is quadratically (inverted U-shape) related to prosociality. To do so, we examined in three studies (a) the linear relationship between vagal activity and prosociality and (b) whether adding a quadratic term to the linear model significantly improved the fit in the data between vagal activity and prosociality.

In Study 1, we examined the association between vagal activity and measures of prosociality in a community sample. In Study 2, we replicated and extended these results by demonstrating the quadratic association between vagal activity and the experience of prosocial positive emotions and by ruling out the potential confound that our results were driven by a more general link between vagal activity and positivity. In Study 3, we examined the interpersonal consequences of the link between vagal activity and prosociality by having naïve observers rate the prosociality of targets across the range of vagal activity values based on thin slices of behavior—silenced 20-s long video clips depicting the targets responding to the suffering of their romantic partner. In each study, we assessed vagal activity through RSA, which captures the degree of variability in the heart rate due to vagal influence (Berntson, Norman, Hawkley, & Cacioppo, 2008).

Study 1

Method

Participants and procedure. Two hundred thirty-six adults (mean age = 40.02 years, *SD* = 11.14; 52% female) from the Denver area community participated in the study. Participants watched a 2-min neutral video clip that depicted a sandcastle being built during which their electrocardiogram (ECG) activity was recorded for analysis of vagal activity (Rottenberg, Ray, & Gross, 2007). One week before watching the video clip, participants completed measures of their prosociality online.

Measures.

Vagal activity (measured via RSA) and respiratory rate. We sampled ECG and respiration signals at 1,000 Hz, and edited, scored, and reduced using ANSLAB (Autonomic Nervous System Laboratory Software; University of Basel, Basel, Switzerland), a customized physiological scoring software package (Wilhelm, Grossman, & Roth, 1999). Electrocardiogram activity was sampled at 1,000 Hz using electrodes placed on the torso in a Lead II configuration (Biopac Systems; Santa Barbara, CA). To compute RSA, we first converted heart period scores into time series data with a 4-Hz resolution. RSA was assessed as heart rate variability within the high frequency band associated with respiration; for the present study, a frequency band of 0.12–0.40 Hz was used (Berntson et al., 2008; Butler et al., 2006; Rottenberg, Clift, Bolden, & Salomon, 2007). The time series data were then linearly detrended and quantified with a power spectral analysis using the Welch method of spectral averaging (cf. Butler et al., 2006). Single artifactual beats were excluded and interpolated. This occurred in seven participants, and for between one and five beats per participant. A single ectopic beat in one participant was interpolated. RSA was calculated as the natural logarithm of the power spectral density values within the high-frequency band (Berntson et al., 2008). Three individuals had RSA values more than 3 standard deviations (*SD*s) below or above the mean and were thus excluded from analyses. RSA values ranged from 3.25 to 10.22 ($M = 6.88$ ln ms^2, $SD = 1.29$).

We measured respiration using an inductive plethysmography device (TSD201; Biopac Systems, Goleta, CA), which captures changes in abdominal circumference that occur as the participant breathes. Respiratory rate was computed as the number of breaths per minute. Peak respiration data for one participant fell outside the 0.12- to 0.40-Hz frequency band—this participant was excluded from all analyses. We also derived the peak respiration frequency by conducting spectral analysis of the raw R-wave–R-wave interval data using a fast-Fourier transform (FFT) and Welch's method, consistent with Denver, Reed, & Porges (2007). The peak frequency within the high-frequency band (0.12–0.40 Hz) was identified and was found to correspond to the mean respiration frequency (Clifford, 2006; Denver et al., 2007). Power spectral density functions were calculated and plotted to reveal the peak frequency. Similar to Denver et al. (2007), we resampled heart period data every 500 ms, and low-frequency oscillations were removed and detrended using a third-order moving filter. Next, the peak of the heart period spectrum within the high-frequency RSA band was isolated (which corresponds to the estimated respiration frequency). All respiration estimates were calculated using MATLAB 2011a (MathWorks, Natick, MA) and Kubios (Tarvainen, Niskanen, Lipponen, Ranta-Aho, & Karjalainen, 2014) software. Using this method, we found that the peak respiratory frequency for all participants fell within the 0.12- to 0.40-Hz band. Thus, no additional participants were excluded on this basis.

Warm, Prosocial Relations With Others. Participants completed the three-item Relations subscale of the Psychological Well-Being Scales (Ryff, 1989), answering items such as "People would describe me as a giving person, willing to share my time with others," "I have not experienced many warm and trusting relationships with others," and "Maintaining close relationships has been difficult and frustrating for me" on 1 (*strongly disagree*) to 6 (*strongly agree*) scales ($\alpha = .70$). The scale measures the degree to which individuals have warm, prosocial relations with others.

Agreeableness. Participants also completed a 10-item measure of agreeableness (Goldberg et al., 2006) from the International Personality Item Pool, which captures enduring individual differences in prosocial personality. Sample items include "I sympathize with others' feelings," and "I am interested in people," and responses were captured on 1 (*never true*) to 7 (*always true*) scales ($\alpha = .91$).

Results

Statistical approach. Our primary interest in the current article was to determine how individual differences in vagal activity (operationalized as RSA) are linked with prosociality, examining potential linear and quadratic relationships. Thus, we took two steps in our modeling. First, we tested the linear relationship between vagal activity and prosociality. Second, we added a quadratic term to the equation and investigated whether a quadratic model better captured the relationship between vagal activity and prosociality. We note that the *p* value of the quadratic term in this case is identical to the *p* value of a comparison of the variance explained in the two models; thus, a significant quadratic term indicates a superior model fit of the quadratic model over a linear model.

Linear relationship between vagal activity and prosociality. In our first set of analyses, we evaluated the linear relationship between vagal activity and our two measures of prosociality. We found no statistically significant link between vagal activity and either Warm, Prosocial Relations With Others or Agreeableness (see Table 1). Thus, in Study 1, we found no evidence for a linear relationship between RSA and prosociality.

Quadratic relationship between RSA and prosociality. We next modeled a quadratic relationship between vagal activity and prosociality. To do so, we entered both the linear and quadratic terms of vagal activity as predictors. By focusing on the slope of the quadratic term, we were able to assess the degree to which the relationship between vagal activity and each outcome varied as a function of vagal activity.

In line with our predictions, vagal activity was quadratically associated with Warm, Prosocial Relations With Others and Agreeableness (see Figure 1 and Table 1). These results demonstrate that as vagal activity increased, the relationship between vagal activity and prosociality progressively became more and more negative. Graphical inspection of the curves (see Figure 1) demonstrates an inverted U-shape curve.

Study 2

Study 1 provided the first evidence for the validity of the quadratic vagal activity–prosociality hypothesis. In particular, we found that a quadratic model was more accurate in characterizing the link between vagal activity and prosociality than a linear model, which in the current study did not reach significant levels. It is of theoretical importance, however, to determine whether these effects are simply a reflection of a positivity bias (in which case the quadratic pattern would be seen for all positive outcomes) or whether they are indeed specific to prosociality. We therefore conducted Study 2 to evaluate the quadratic vagal activity–prosociality hypothesis in relation to several positive emotions—some specifically focused on prosociality (e.g., compassion, gratitude) and others reflecting positivity in general (e.g., joy, pride; Algoe, 2012; Côté et al., 2011; Gruber et al., 2008; Gruber, Oveis, Keltner, and Johnson, 2011; Haidt, 2003; Horberg, Oveis, & Keltner, 2011; Impett et al., 2010; Keltner, Horberg, & Oveis, 2006; Oveis, Horberg, & Keltner, 2010; Srivastava, Tamir, McGonigal, John, & Gross, 2009). Our theoretical analysis of why a quadratic pattern of results may emerge between vagal activity and prosociality suggested that the quadratic-vagal activity hypothesis should be specific to prosociality; therefore, we expected to find a quadratic relationship only between vagal activity and prosocial positive emotions but not between vagal activity and general positivity.

Method

Participants and procedure. One hundred nineteen participants (mean age = 20.14 years, *SD* = 1.92; 64% female) from the student community at a large public university in the United States partook in the study. Participants watched a 90-s neutral film clip during which we measured their ECG activity for analysis of vagal activity (operationalized as RSA). Before watching the video clip, participants completed measures of their experience of prosocial and general positive emotions.

Measures.

Vagal activity (RSA). ECG activity was sampled at 1 kHz with the VU-AMS ambulatory monitoring system (de Geus, Willemsen, Klaver, & van Doornen, 1995) using electrodes placed in a modified Lead I configuration. Data were visually inspected for artifacts, and none were detected. CMet cardiac metric software (Allen, Chambers, & Towers, 2007) was used to calculate RSA in the frequency range of spontaneous breathing (0.12–0.40 Hz). We excluded one participant from analyses because the person had an RSA value of more than 3 standard deviations below the mean. RSA values ranged from 4.47 to 8.40 ($M = 6.27$ ln ms^2, $SD = 0.86$). Additionally, as in Study 1, we conducted spectral analyses in order to derive estimates for participants' breathing frequencies, based on R-wave–R-wave-interval data. No participant's peak respiratory frequency fell outside the 0.12- to 0.40-Hz band. Thus, all participants were included in analyses.

Prosocial and general positive emotions. All participants completed the Dispositional Positive Emotions Scales (Shiota, Keltner, & John, 2006), a 44-item measure of the extent to which people experience several discrete positive emotions. We measured two prosocial positive emotions—compassion (seven items; $\alpha = .77$) and gratitude (two items; $\alpha = .69$)—and five general positive control emotions—including joy (seven items;

Table 1
Linear and Quadratic Models for Study 1

	Linear model Vagal activity (RSA)				Quadratic model Vagal activity (RSA)^2			
Outcome	*b*	95% CI	*p*	R_{partial}	*b*	95% CI	*p*	R_{partial}
Warm, Prosocial Relations	.05	−.06, .16	.39	.06	−.07	−.13, .00	.05	−.13
Agreeableness	−.03	−.09, .03	.35	−.06	−.04	−.07, .00	.05	−.13

Note. RSA = respiratory sinus arrhythm; CI = confidence interval.

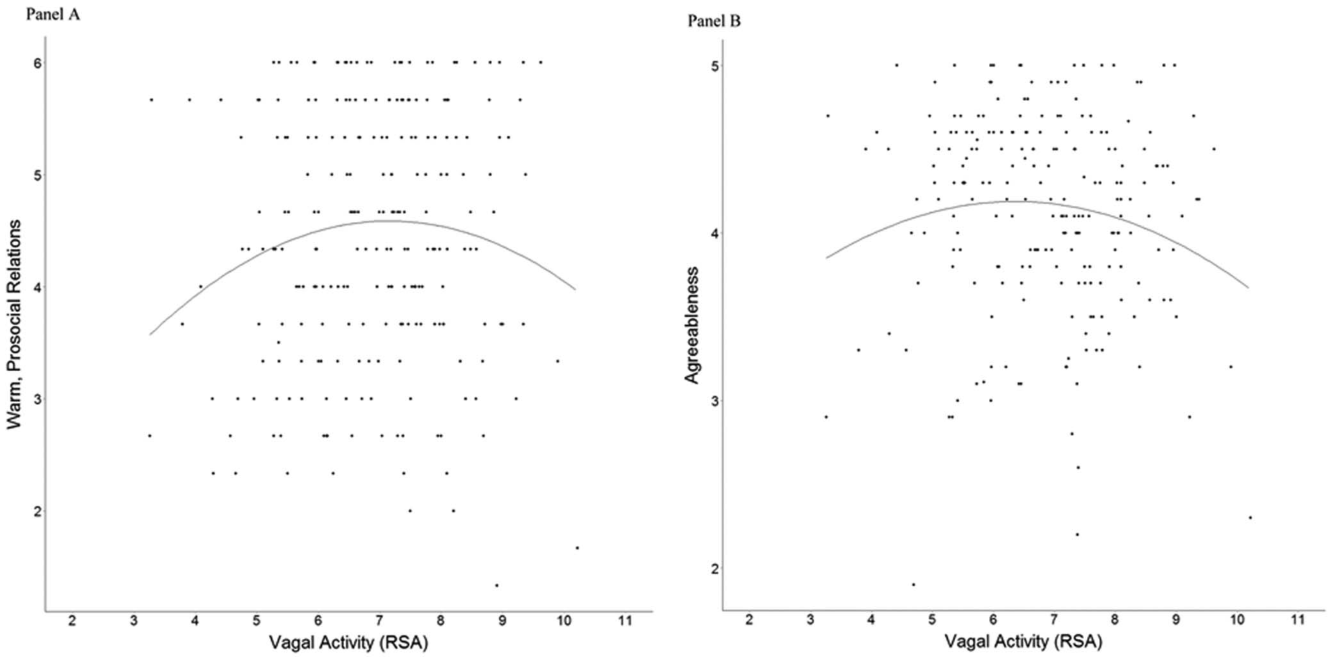

Figure 1. Vagal activity (respiratory sinus arrhythmia, or RSA) to warm relations with others and agreeableness. The line in each figure represents the predicted values of the outcome from the estimates of the slopes in the quadratic equation.

$\alpha = .85$), contentment (seven items; $\alpha = .88$), desire (seven items; $\alpha = .72$), amusement (seven items; $\alpha = .66$), and interest (seven items; $\alpha = .71$). We measured all items using 1 (*strongly disagree*) to 7 (*strongly agree*) scales.

Results

Statistical approach. Because the Dispositional Positive Emotions Scales assess both (a) prosocial positive emotions and (b) general positive emotions that are unrelated to prosociality, we were able to evaluate whether vagal activity is quadratically related to prosociality in particular or positive emotions in general. For Study 2, we employed the same two-step modeling approach as in Study 1: First, we modeled the linear relationship between vagal activity and each emotion; second, we tested a quadratic model for each outcome.

Linear relationship between vagal activity and positive emotions. In our first set of models, we tested a linear relationship between vagal activity and each of the seven positive emotions (see Table 2). Consistent with our predictions, we found no evidence for a linear relationship between vagal activity and the prosocial positive emotions of compassion and gratitude. Nor did we find evidence of a linear relationship between vagal activity and the general positive emotions of contentment, joy, desire,

Table 2
Linear and Quadratic Models for Study 2

	Linear model Vagal activity (RSA)				Quadratic model Vagal activity (RSA)^2			
Outcome	*b*	95% CI	*p*	R_{partial}	*b*	95% CI	*p*	R_{partial}
Prosocial positive emotions								
Compassion	−.06	−.28, .15	.56	−.05	−.25	−.45, −.05	.01	–.23
Gratitude	.09	−.13, .33	.44	.07	−.25	−.47, −.02	.03	−.20
General positive emotions								
Contentment	−.04	−.29, .21	.75	−.03	.02	−.22, .25	.89	.01
Joy	−.08	−.33, .16	.51	−.06	−.04	−.27, .20	.77	−.03
Desire	.03	−.20, .26	.79	.02	.07	−.15, .29	.54	.06
Amusement	−.14	−.38, .10	.26	−.11	.10	−.13, .33	.37	.08
Interest	.04	−.12, .21	.62	.05	.00	−.15, .16	.96	.01

Note. RSA = respiratory sinus arrhythm; CI = confidence interval.

amusement, and interest. Thus, we found no evidence in the current study to support a linear relationship between vagal activity and any positive emotion—prosocial or general.

Quadratic relationship between vagal activity and positive emotions. Next, we tested a quadratic relationship between vagal activity and each emotion by adding a quadratic vagal activity term as a predictor to each linear model described above (see Table 2). Consistent with Study 1 and with our hypotheses, we found a quadratic relationship between vagal activity and the two prosocial positive emotions: compassion, and gratitude (see Figure 2). In contrast, we did not find evidence for a quadratic relationship between vagal activity and any of the general positive emotions: contentment, joy, desire, amusement, and interest. These results support our prediction that there should only be a quadratic relationship between vagal activity and prosocial positive emotions; in fact, we found no relationship between vagal activity and non-prosocial positive emotions, linear or quadratic.

Study 3

Studies 1 and 2 demonstrated that the degree to which people view themselves as being prosocial and experience prosocial emotions is quadratically related to their vagal activity. But do the perceptions of complete strangers also match this pattern? Building upon the thin-slicing literature, we theorized that individual differences in prosociality as a function of vagal activity may also be detectable on the basis of thin slices of behavior. We tested this hypothesis in Study 3, in which we selected a group of targets with known levels of vagal activity (RSA) from a previous study in which participants took turns discussing a time of personal suffering; this paradigm has been shown to reliably elicit compassion in participants (Côté et al., 2011; Gordon, Impett, Kogan, Oveis, & Keltner, 2012; Impett et al., 2010, 2012; Kogan et al., 2011; van Kleef et al., 2008). More generally, previous work has shown that displays of vulnerability are compelling elicitors of cooperative behavior (Batson & Shaw, 1991); therefore, we reasoned that the context of responding to suffering would provide an appropriate period of observation from which to judge the character of the target individuals. Thus, we selected the listeners (who heard the stories of suffering from a stranger) during the conversations to serve as our targets.

In the present study, we showed 20-s video clips of the targets to observers who had never met or seen the targets before. The videos were completely silent and showed only the listener (target) in each conversation. Observers rated how prosocial they believed the target of each video to be. We hypothesized that perceptions of prosociality would be quadratically related to target vagal activity in line with the quadratic vagal activity–prosociality hypothesis.

Method

Observers and procedure. We recruited 120 (mean age = 33.4 years, *SD* = 12.1; 53% female) individuals using Amazon's Mechanical Turk to participate individually via the Internet in exchange for $1. Each observer was asked to watch between 18 and 20 silent video clips of targets listening to a story of personal suffering from a stranger. After watching each video clip, participants rated each target for how "trustworthy," "compassionate," and "kind" they perceived them to be on scales ranging from 1 (*strongly disagree*) to 7 (*strongly agree*). These three items showed high internal reliability (α = .97) and thus were combined into a single composite score of perceived prosociality.

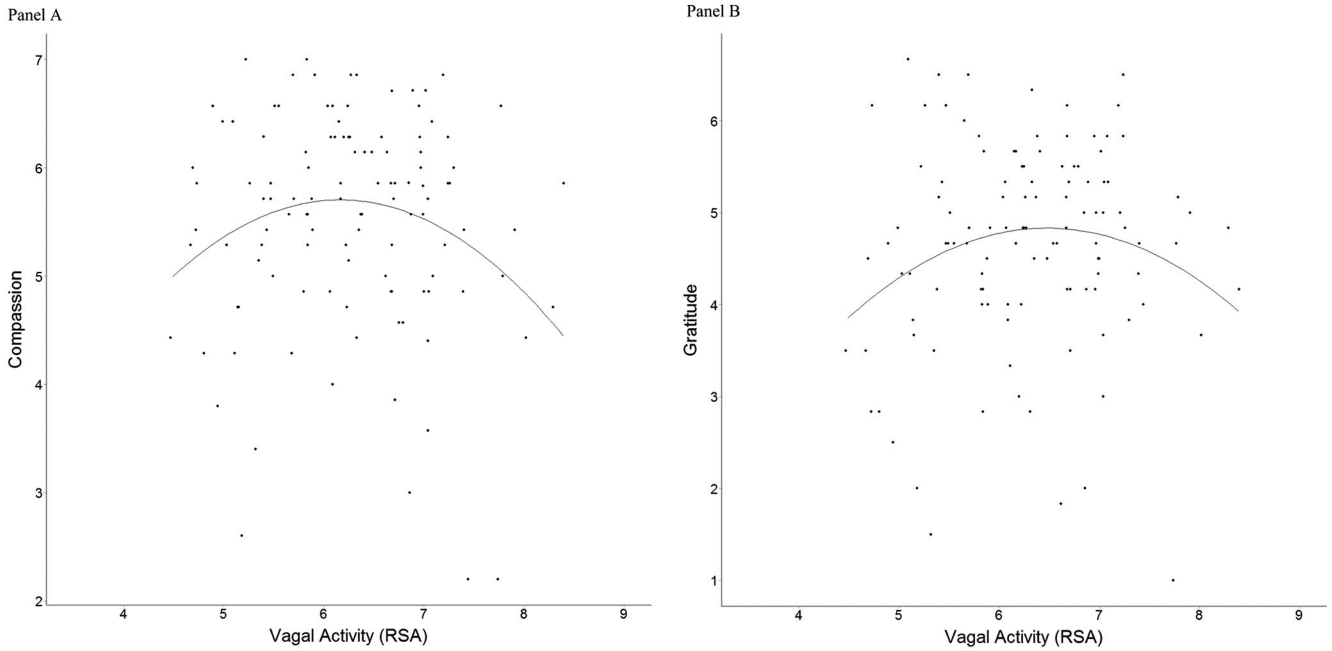

Figure 2. Vagal activity (respiratory sinus arrhythmia, or RSA) to compassion and gratitude. The line in each figure represents the predicted values of the outcome from the estimates of the slopes in the quadratic equation.

Target video clips. We selected 118 video clips of targets (mean age = 20.1 years, *SD* = 5.09; 59.1% female) from a previous study in which same-sex dyads of unacquainted undergraduate students took turns describing a personal experience of suffering while these interactions were videotaped (van Kleef et al., 2008). Video recordings used in the present study depicted target individuals in the listener role, wherein they listened while their partner expressed a time of great emotional suffering in a face-to-face interaction. The face and torso of each target were visible, as was a portion of the back of the head of the person to whom the target was listening. Each 20-s clip began as the talker described the most intense part of the experience of suffering as identified by a research assistant blind to all hypotheses and the vagal activity of all targets. We removed the audio from all video clips to ensure that the verbal content of the interactions did not influence perceptions of targets and to provide a more stringent test of our hypothesis by presenting an even thinner slice of behavior (Ambady & Rosenthal, 1993). Observers in the current study did not have access to the content or topics of the conversations.

Vagal activity of targets (again operationalized as RSA) was assessed prior to their interaction with their partner (see Van Kleef et al., 2008 for the full procedure). ECG recordings, sampled at 1 kHz, were gathered from leads placed on the torso in a Lead II configuration using the VU-AMS ambulatory monitoring system. Data were visually inspected for artifacts, and none were detected. RSA was calculated from 2 min of ECG data acquired 15 min after the start of the laboratory session while participants were quietly filling in questionnaires prior to interacting with their partner. RSA was calculated in the 0.12 Hz- to 0.40-Hz band of the R-wave–R-wave-interbeat interval series using CMet cardiac metric software (Allen et al., 2007). We removed one outlier who was more than 3 standard deviations below the mean. RSA for the targets in this study fell within the expected range for a resting, healthy, adult sample ($M = 5.65$ ln ms^2, $SD = 1.10$) and ranged from 2.32 to 9.04. As in Studies 1 and 2, we derived estimates of participants' respiratory frequencies from spectral analyses of the R-wave–R-wave-interval data. We identified no participant who fell outside the 0.12- to 0.40-Hz range. Thus, all participants were included in analyses.

Results

Statistical approach. As in Studies 1 and 2, we took a two-step modeling approach. First, we tested a linear relationship between target vagal activity and perceived prosociality, as rated by the observers. Second, we included a quadratic target vagal activity term in the model to test whether a quadratic relationship would better describe the relationship between vagal activity and perceived prosociality. In all analyses, we included the gender of the target as a predictor because men were rated as less prosocial than women, $b_{Gender} = -0.34$, 95% confidence interval [−.53, −.15], $t(108) = -3.51$ $p < .001$, but there was no gender difference in vagal activity, $b_{Gender} = 0.01$, 95% confidence interval [42, .43], $t(107) = 0.03$, $p = .980$, and thus gender could act as a suppressor variable. Through this approach, we accounted for the variance related to gender in perceived prosociality.

Linear relationship between vagal activity and perceived prosociality. Our first model examined the linear relationship between target vagal activity and how prosocial observers believed the targets to be. In concordance with Studies 1 and 2, we found no evidence for a linear relationship between target vagal activity and perceived prosociality (see Table 3). Thus, once again, we found little support for a linear perspective on the link between vagal activity and prosociality.

Quadratic relationship between vagal activity and perceived prosociality. In our second model, we included both the linear and quadratic target vagal activity terms as predictors of perceived prosociality. Supporting our hypothesis, there was a quadratic link between target vagal activity and perceived prosociality (see Table 3 and Figure 3). As with Studies 1 and 2, graphical examination of the curve in Figure 3 suggested an inverted U-shape relationship: That is, targets with moderate vagal activity were rated as more prosocial than targets with low or high vagal activity.

General Discussion

Previous theory and empirical work have implicated vagal activity in predicting numerous psychological processes involved in prosocial behavior, including emotion regulation (Butler et al., 2006), positive emotions (Kok & Fredrickson, 2010; Oveis, Cohen, et al., 2009), and sociability (Eisenberg et al., 1996). Anatomical evidence linking the vagus nerve to heart rate regulation and expression of emotions through posture, gaze, and the voice has also led to the theoretical claim that the vagus nerve serves a core function in promoting greater social engagement (Porges, 1995, 2001, 2007). Notwithstanding these claims, some studies have shown that elevated vagal activity is also predictive of negative outcomes, such as the mania component of bipolar disorder (Gruber et al., 2008) and lowered sociability among adolescent girls (Eisenberg et al., 1995, 1996).

In the present article, guided by these patterns of findings and Aristotle's theorizing about the benefits of emotional moderation, we offered the quadratic vagal activity–prosociality hypothesis. Our hypothesis holds that moderate levels of vagal activity should be associated with the greatest levels of prosociality, as such moderate vagal activity presents a balancing between necessary arousal to experience empathy for another's suffering and the

Table 3
Linear and Quadratic Models for Study 3

	Linear model Vagal activity (RSA)				Quadratic model Vagal activity (RSA)^2			
Outcome	*b*	95% CI	*p*	R_{partial}	*b*	95% CI	*p*	R_{partial}
Perceived prosociality	.05	−.03, .14	.22	.12	−.07	−.12, −.02	.01	−.25

Note. RSA = respiratory sinus arrhythm; CI = confidence interval.

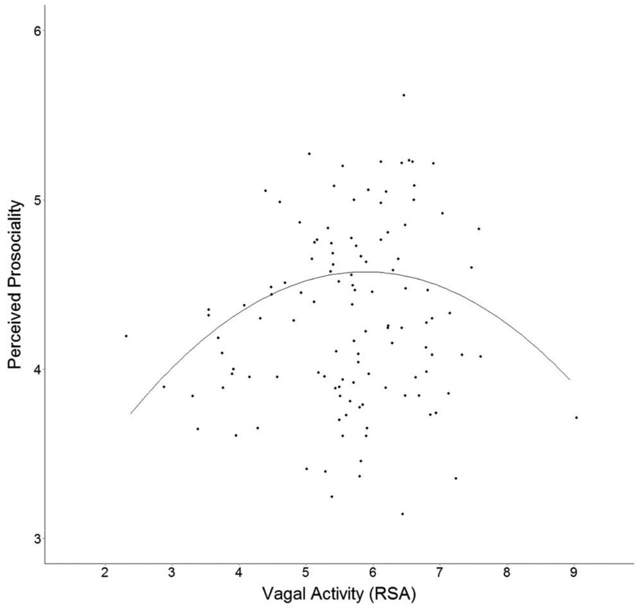

Figure 3. Vagal activity (respiratory sinus arrhythmia, or RSA) to perceived prosociality. The line in each figure represents the predicted values of the outcome from the estimates of the slopes in the quadratic equation.

necessary regulation to overcome one's own negative emotions to respond in a kind, compassionate manner. In contrast, we reasoned that having low or very high vagal activity would result in lower levels of prosociality.

We tested predictions stemming from the quadratic vagal activity–prosociality hypothesis in three studies. In each study, we first tested a linear relationship between vagal activity and prosociality and then added a quadratic term to evaluate whether a quadratic model provided a significant increase in accuracy over the linear model. Through such an approach, we were able to show that the quadratic model better represented the relationship between vagal activity and prosociality than a linear model.

In Study 1, we found no evidence for a linear relationship between vagal activity and two different measures of prosociality—degree of warm, prosocial relations with others and agreeableness. However, a significant quadratic relationship (inverted U-shape) between vagal activity, and both measures of prosociality was present. It should be noted that optimal vagal activity (peak of the curve) fell squarely within the moderate range of values of vagal activity.

Participants in Study 2 indicated the degree to which they felt various prosocial (compassion, gratitude) and general positive emotions (e.g., joy, contentment) in everyday life. Once again, we found no evidence for a linear relationship between vagal activity and any prosocial or general positive emotion. However, we did find a quadratic relationship between vagal activity and each prosocial positive emotion (compassion, gratitude), but no relationship, quadratic or otherwise, between vagal activity and the nonprosocial general positive emotions (e.g., joy). These results served two important functions: (a) they replicated the findings from Study 1, giving further support to the quadratic vagal activity–prosociality hypothesis; and (b) they demonstrated that the quadratic link between vagal activity and prosociality is not simply a reflection of a general link between vagal activity and positivity (e.g., Kok & Fredrickson, 2010; Oveis, Cohen, et al., 2009a).

Studies 1 and 2 demonstrated that vagal activity is quadratically related to self-reported prosociality. But do complete strangers also see this pattern in others? To answer this question, in Study 3, we had naïve observers watch 20-s video clips of target individuals. The target videos were taken from a previous study in which each target listened to another person discuss a time of suffering. We reasoned that such a context would be a perfect milieu to display a prosocial response. All videos were silent and showed only the target, and we provided no information about the context of the conversations. After watching each video, observers were asked to provide ratings of each target's prosociality. Consistent with Studies 1 and 2, target vagal activity was unrelated to how prosocial the observers judged each target to be. However, the same quadratic pattern of results once again emerged: Specifically, target vagal activity was quadratically related to observer ratings of target prosociality in an inverted-U shape. Thus, the differences in prosociality associated with vagal activity were detectable by even complete strangers on the basis of very thin slices of behavior.

Collectively, our results demonstrate that there is a nonlinear relationship between vagal activity and prosociality. Furthermore, this relationship between vagal activity and prosociality is not a proxy for a more general positive emotions effect. Remarkably, these differences in prosociality as a function of vagal activity were detectable by complete strangers on the basis of seeing only 20 s of silent behavior of an individual, suggesting that there are tangible behavioral correlates of vagal activity that are communicating important information to others. Our results expand upon Porges' (1995, 2001, 2007) polyvagal model by supporting the notion that the social engagement benefits associated with elevated vagal activity eventually reach an optimal point (in the moderate vagal activity range), after which, greater vagal activity becomes maladaptive. Indeed, one interpretation of our results could view vagal activity as a biological substrate of prosociality; however, it is important to note that our work (and previous related work) is correlational in nature, and thus future experimental evidence is necessary before making a true causal claim.

Our work not only provides the first model for understanding the link between vagal activity and prosociality, it also extends the general literature on vagal activity by introducing the idea that vagal activity may quadratically be related to psychological phenomena. In past work, a linear relationship has been implicitly assumed between vagal activity and numerous outcomes, including mental illness (Dalack & Roose, 1990; Friedman & Thayer, 1998; Gruber et al., 2008), physical health (Dekker et al., 2000; Haug et al., 1994), emotional processes (Butler et al., 2006; Kok & Fredrickson, 2010; Oveis, Cohen, et al., 2009), and perception (Park, van Bavel, Vasey, & Thayer, 2012). Many of these processes are likely far more complex than a linear relationship. Future research should be conducted to evaluate whether the relationship between vagal activity and mental illness, physical health, emotional processes, and perception are indeed linear or whether a quadratic framework provides a more accurate characterization of the association of vagal activity with these processes.

It is noteworthy that some of our findings are at first glance somewhat inconsistent with previous work documenting linear relationships between vagal activity and positive emotions. In

Study 2, we found little evidence linking vagal activity either in a linear or quadratic fashion to general positive emotions, such as joy and contentment. Yet previous work has linked vagal activity in a positive linear manner to positive emotions (Kok & Fredrickson, 2010; Oveis, Cohen, et al., 2009; Wang et al., 2013). One reason for this seeming inconsistency is that previous work may have oversampled a negative portion of the vagal activity distribution. Such sampling could create a positive linear effect in the data. For example, studies of sociability in adolescents have shown that among boys (a group characterized by lower vagal activity and thus negative heavy), there is a positive link between vagal activity and sociability; however, for girls (a group characterized by higher vagal activity and thus positive heavy), the relationship between vagal activity and sociability is negative (Beauchaine, 2001).

Effect sizes for the studies ranged from small (Study 1) to moderate (Studies 2 and 3), which are in line with expectation given the numerous psychological and biological forces that contribute to prosociality (Keltner et al., 2014). For instance, people's prosocial dispositions are shaped by other biological individual differences tied to oxytocin (Bartz et al., 2011; Kogan et al., 2011; Rodrigues et al., 2009), dopamine (Harbaugh et al., 2007), and serotonin (Crockett et al., 2013; Crockett, Clark, Hauser, & Robbins, 2010). Prosociality is also more likely when others are kind to the person (Fowler & Christakis, 2010) and when others elicit emotions such as compassion (Valdesolo & Desteno, 2011), gratitude (Bartlett & DeSteno, 2006), and elevation (Algoe & Haidt, 2009; Keltner & Oveis, 2007; Schnall, Roper, & Fessler, 2010). Social forces such as social class (Piff, Stancato, Côté, Mendoza-Dentona, & Keltner, 2012), family (Oveis, Gruber, Keltner, Stamper, & Boyce, 2009), and religion (Norenzayan & Shariff, 2008; Shariff & Norenzayan, 2007) also play a key role in shaping prosociality and emotion. People are also more likely to cooperate when there are potential social sanctions for not acting prosocially (Boyd, Gintis, Bowles, & Richerson, 2003; Fehr & Fischbacher, 2003; Fehr & Gächter, 2002; Fowler, 2005) or rewards for acting prosocially (Kogan et al., 2010; Rand, Dreber, Ellingsen, Fudenberg, & Nowak, 2009). Thus, prosociality is affected by a multiplicity of biological, psychological, and situational factors at multiple levels of analysis. Given such a diverse set of antecedents, we would expect any one factor to explain only a fraction of people's proclivities towards prosociality. Our findings suggest that RSA may be one such biological antecedent, though clearly more work is necessary to establish a causal link between RSA and prosociality.

Limitations and Future Directions

Several limitations are important to note in interpreting our results. First, all three studies presented correlational data; causal inferences are in no way justified. The quadratic vagal activity–prosociality hypothesis is a theoretical causal model; it explicitly relates vagal activity to prosociality. Our data, however, cannot fully support such a causal claim—our data are therefore consistent with the predictions of the hypothesis but do not offer the evidence necessary to make a strong empirical claim that vagal activity promotes prosociality in a quadratic manner. Thus, one important future direction in this work is to experimentally manipulate vagal activity at different starting levels to observe the consequences. Based on our hypothesis, we predict that increasing vagal activity for individuals who in general have low vagal activity levels will be beneficial and result in elevated prosociality; in contrast, we also predict that increasing vagal activity for individuals who begin with moderate vagal activity may reduce prosociality.

Our results are also limited by cultural considerations since all three studies were conducted in the United States. Given the different cultural norms for emotional expression and connection to others (Markus & Kitayama, 1991), it should not be assumed that the correlations of vagal activity to prosociality will be the same in Eastern cultures. Indeed, some evidence suggests that even biological correlates of sociability can have different predictive patterns in Eastern cultures compared with Western cultures (e.g., Kim et al., 2011); however, others have found parallel results (Wang et al., 2013). Thus, in future studies, investigators should examine the prosocial correlates of vagal activity in Eastern cultures—to date, we are aware of no cross-cultural work examining the social correlates of vagal activity.

Conclusion

Prosociality is a vital social glue that is ultimately a core necessity for healthy societal functioning. A focus on the biological underpinnings of prosociality can begin to shine a light on how this critical process unfolds and is reinforced, opening the door for work on promoting prosociality through a focus on the underlying biological systems. Yet as this work matures, a more nuanced perspective is necessary to understand the complex relationships that exist between our bodies and social behaviors. Our findings suggest that one such relationship—the link between vagal activity and prosociality—takes on a quadratic form. Thus, care must be taken in promoting prosociality by increasing vagal activity; greater vagal activity does not always translate into greater prosociality.

References

Albrechtsen, J. S., Meissner, C. A., & Susa, K. J. (2009). Can intuition improve deception detection performance? *Journal of Experimental Social Psychology, 45,* 1052–1055. doi:10.1016/j.jesp.2009.05.017

Algoe, S. B. (2012). Find, remind, and bind: The functions of gratitude in everyday relationships. *Social and Personality Psychology Compass, 6,* 455–469. doi:10.1111/j.1751-9004.2012.00439.x

Algoe, S. B., & Haidt, J. (2009). Witnessing excellence in action: The "other praising" emotions of elevation, gratitude, and admiration. *Journal of Positive Psychology, 4,* 105–127. doi:10.1080/17439760802650519

Allen, J. J. B., Chambers, A. S., & Towers, D. N. (2007). The many metrics of cardiac chronotropy: A pragmatic primer and a brief comparison of metrics. *Biological Psychology, 74,* 243–262. doi:10.1016/j.biopsycho.2006.08.005

Ambady, N., Bernieri, F. J., & Richeson, J. A. (2000). Toward a histology of social behavior: Judgmental accuracy from thin slices of the behavioral stream. *Advances in Experimental Social Psychology, 32,* 201–271. doi:10.1016/S0065-2601(00)80006-4

Ambady, N., Hallahan, M., & Conner, B. (1999). Accuracy of judgments of sexual orientation from thin slices of behavior. *Journal of Personality and Social Psychology, 77,* 538–547. doi:10.1037/0022-3514.77.3.538

Ambady, N., & Rosenthal, R. (1993). Half a minute: Predicting teacher evaluations from thin slices of nonverbal behavior and physical attractiveness. *Journal of Personality and Social Psychology, 64,* 431–441. doi:10.1037/0022-3514.64.3.431

Bartlett, M. Y., & DeSteno, D. (2006). Gratitude and prosocial behavior: Helping when it costs you. *Psychological Science, 17,* 319–325. doi:10.1111/j.1467-9280.2006.01705.x

Bartz, J. A., Zaki, J., Bolger, N., & Ochsner, K. N. (2011). Social effects of oxytocin in humans: Context and person matter. *Trends in Cognitive Sciences, 15,* 301–309. doi:10.1016/j.tics.2011.05.002

Batson, C. D., & Shaw, L. L. (1991). Evidence for altruism: Toward a pluralism of prosocial motives. *Psychological Inquiry, 2,* 107–122. doi:10.1207/s15327965pli0202_1

Beauchaine, T. (2001). Vagal tone, development, and Gray's motivational theory: Toward an integrated model of autonomic nervous system functioning in psychopathology. *Development and Psychopathology, 13,* 183–214. doi:10.1017/S0954579401002012

Berntson, G. G., Cacioppo, J. T., & Grossman, P. (2007). Whither vagal tone. *Biological Psychology, 74,* 295–300. doi:10.1016/j.biopsycho.2006.08.006

Berntson, G. G., Norman, G. J., Hawkley, L. C., & Cacioppo, J. T. (2008). Cardiac autonomic balance versus cardiac regulatory capacity. *Psychophysiology, 45,* 643–652. doi:10.1111/j.1469-8986.2008.00652.x

Berntson, G. G., Sarter, M., & Cacioppo, J. T. (1998). Anxiety and cardiovascular reactivity: The basal forebrain cholinergic link. *Behavioral Brain Research, 94,* 225–248. doi:10.1016/S0166-4328(98)00041-2

Borkenau, P., Mauer, N., Riemann, R., Spinath, F. M., & Angleitner, A. (2004). Thin slices of behavior as cues of personality and intelligence. *Journal of Personality and Social Psychology, 86,* 599–614. doi:10.1037/0022-3514.86.4.599

Boyd, R., Gintis, H., Bowles, S., & Richerson, P. J. (2003). The evolution of altruistic punishment. *PNAS: Proceedings of the National Academy of Sciences of the United States of America, 100,* 3531–3535. doi:10.1073/pnas.0630443100

Butler, E. A., Wilhelm, F. H., & Gross, J. J. (2006). Respiratory sinus arrhythmia, emotion, and emotion regulation during social interaction. *Psychophysiology, 43,* 612–622. doi:10.1111/j.1469-8986.2006.00467.x

Cheng, C., Wong, W., & Tsang, K. W. (2006). Perception of benefits and costs during SARS outbreak: An 18-month prospective study. *Journal of Consulting and Clinical Psychology, 74,* 870–879. doi:10.1037/0022-006X.74.5.870

Clifford, G. D. (2006). ECG statistics, noise, artifacts, and missing data. In G. Clifford, F. Azuaje, and P. McSharry (Eds.), *Advanced methods and tools for ECG data analysis* (pp. 55–99). Boston, MA: Artech House.

Cohen, H., Kotler, M., Matar, M. A., & Kaplan, Z. (1997). Power spectral analysis of heart rate variability in posttraumatic stress disorder patients. *Biological Psychiatry, 41,* 627–629. doi:10.1016/S0006-3223(96)00525-2

Côté, S., Kraus, M. W., Cheng, B. H., Oveis, C., van der Löwe, I., Lian, H., & Keltner, D. (2011). Social power facilitates the effect of prosocial orientation on empathic accuracy. *Journal of Personality and Social Psychology, 101,* 217–232. doi:10.1037/a0023171

Crockett, M. J., Apergis-Schoute, A., Herrmann, B., Lieberman, M., Müller, U., Robbins, T. W., & Clark, L. (2013). Serotonin modulates striatal responses to fairness and retaliation in humans. *Journal of Neuroscience, 33,* 3505–3513. doi:10.1523/JNEUROSCI.2761-12.2013

Crockett, M. J., Clark, L., Hauser, M. D., & Robbins, T. W. (2010). Serotonin selectively influences moral judgment and behavior through effects on harm aversion. *PNAS: Proceedings of the National Academy of Sciences of the United States of America, 107,* 17433–17438. doi:10.1073/pnas.1009396107

Dalack, G. W., & Roose, S. P. (1990). Perspectives on the relationship between cardiovascular disease and affective disorder. *Journal of Clinical Psychiatry, 51,* 4–9.

de Geus, E. J. C., Willemsen, G. H. M., Klaver, C. H. A. M., & van Doornen, L. J. P. (1995). Ambulatory measurement of respiratory sinus arrhythmia and respiration rate. *Biological Psychology, 41,* 205–227. doi:10.1016/0301-0511(95)05137-6

Dekker, J. M., Crow, R. S., Folsom, A. R., Hannan, P. J., Liao, D., Swenne, C. A., & Schouten, E. G. (2000). Low heart rate variability in a 2-minute rhythm strip predicts risk of coronary heart disease and mortality from several causes: The ARIC Study. *Circulation, 102,* 1239–1244. doi:10.1161/01.CIR.102.11.1239

Denver, J. W., Reed, S. F., & Porges, S. W. (2007). Methodological issues in the quantification of respiratory sinus arrhythmia. *Biological Psychology, 74,* 286–294. doi:10.1016/j.biopsycho.2005.09.005

Eisenberg, N., Fabes, R. A., Karbon, M., Murphy, B. C., Wosinski, M., Polazzi, L., . . . Juhnke, C. (1996). The relations of children's dispositional prosocial behavior to emotionality, regulation, and social functioning. *Child Development, 67,* 974–992. doi:10.2307/1131874

Eisenberg, N., Fabes, R. A., Murphy, B., Maszk, P., Smith, M., & Karbon, M. (1995). The role of emotionality and regulation in children's social functioning: A longitudinal study. *Child Development, 66,* 1360–1384. doi:10.2307/1131652

Fabes, R. A., & Eisenberg, N. (1997). Regulatory control and adults' stress-related responses to daily life events. *Journal of Personality and Social Psychology, 73,* 1107–1117. doi:10.1037/0022-3514.73.5.1107

Fehr, E., & Fischbacher, U. (2003, October 23). The nature of human altruism. *Nature, 425,* 785–791. doi:10.1038/nature02043

Fehr, E., & Gächter, S. (2002, January 10). Altruistic punishment in humans. *Nature, 415,* 137–140. doi:10.1038/415137a

Feinberg, M., Willer, R., & Keltner, D. (2012). Flustered and faithful: Embarrassment as a signal of prosociality. *Journal of Personality and Social Psychology, 102,* 81–97. doi:10.1037/a0025403

Fowler, J. H. (2005). Altruistic punishment and the origin of cooperation. *PNAS: Proceedings of the National Academy of Sciences of the United States of America, 102,* 7047–7049. doi:10.1073/pnas.0500938102

Fowler, J. H., & Christakis, N. A. (2010). Cooperative behavior cascades in human social networks. *PNAS: Proceedings of the National Academy of Sciences of the United States of America, 107,* 5334–5338. doi:10.1073/pnas.0913149107

Fowler, K. A., Lilienfeld, S. O., & Patrick, C. J. (2009). Detecting psychopathy from thin slices of behavior. *Psychological Assessment, 21,* 68–78. doi:10.1037/a0014938

Fox, N. A., & Field, T. M. (1989). Individual differences in preschool entry behavior. *Journal of Applied Developmental Psychology, 10,* 527–540. doi:10.1016/0193-3973(89)90025-7

Friedman, B. H., & Thayer, J. F. (1998). Autonomic balance revisited: Panic anxiety and heart rate variability. *Journal of Psychosomatic Research, 44,* 133–151. doi:10.1016/S0022-3999(97)00202-X

Goetz, J. L., Keltner, D., & Simon-Thomas, E. (2010). Compassion: An evolutionary analysis and empirical review. *Psychological Bulletin, 136,* 351–374. doi:10.1037/a0018807

Goldberg, L. R., Johnson, J. A., Eber, H. W., Hogan, R., Ashton, M. C., Cloninger, C. R., & Gough, H. G. (2006). The International Personality Item Pool and the future of public-domain personality measures. *Journal of Research in Personality, 40,* 84–96. doi:10.1016/j.jrp.2005.08.007

Gordon, A. M., Impett, E. A., Kogan, A., Oveis, C., & Keltner, D. (2012). To have and to hold: Gratitude promotes relationship maintenance in intimate bonds. *Journal of Personality and Social Psychology, 103,* 257–274. doi:10.1037/a0028723

Grant, A. M., & Schwartz, B. (2011). Too much of a good thing: The challenge and opportunity of the inverted U. *Perspectives on Psychological Science, 6,* 61–76. doi:10.1177/1745691610393523

Gruber, J., Harvey, A. G., & Purcell, A. (2011). What goes up can come down? A preliminary investigation of emotion reactivity and emotion recovery in bipolar disorder. *Journal of Affective Disorders, 133,* 457–466. doi:10.1016/j.jad.2011.05.009

Gruber, J., Johnson, S. L., Oveis, C., & Keltner, D. (2008). Risk for mania and positive emotional responding: Too much of a good thing? *Emotion, 8,* 23–33. doi:10.1037/1528-3542.8.1.23

Gruber, J., Mauss, I. B., & Tamir, M. (2011). A dark side of happiness? How, when, and why happiness is not always good. *Perspectives on Psychological Science, 6,* 222–233. doi:10.1177/1745691611406927

Gruber, J., Oveis, C., Keltner, D., & Johnson, S. L. (2011). A discrete emotions approach to positive emotion disturbance in depression. *Cognition & Emotion, 25,* 40–52. doi:10.1080/02699931003615984

Haidt, J. (2003). The moral emotions. In R. J. Davidson, K. R. Scherer, & H. H. Goldsmith (Eds.), *Handbook of affective sciences* (pp. 852–870). Oxford, England: Oxford University Press.

Harbaugh, W. T., Mayr, U., & Burghart, D. R. (2007, June 15). Neural responses to taxation and voluntary giving reveal motives for charitable donations. *Science, 316,* 1622–1625. doi:10.1126/science.1140738

Haug, T. T., Svebak, S., Hausken, T., Wilhelmsen, I., Berstad, A., & Ursin, H. (1994). Low vagal activity as mediating mechanism for the relationship between personality factors and gastric symptoms in functional dyspepsia. *Psychosomatic Medicine, 56,* 181–186. doi:10.1097/00006842-199405000-00001

Heilman, K. J., Connolly, S. D., Padilla, W. O., Wrzosek, M. I., Graczyk, P. A., & Porges, S. W. (2012). Sluggish vagal brake reactivity to physical exercise challenge in children with selective mutism. *Development and Psychopathology, 24,* 241–250. doi:10.1017/S0954579411000800

Horberg, E. J., Oveis, C., & Keltner, D. (2011). Emotions as moral amplifiers: An appraisal tendency approach to the influences of distinct emotions upon moral judgment. *Emotion Review, 3,* 237–244. doi:10.1177/1754073911402384

Impett, E. A., Gordon, A. M., Kogan, A., Oveis, C., Gable, S. L., & Keltner, D. (2010). Moving toward more perfect unions: Daily and long-term consequences of approach and avoidance goals in romantic relationships. *Journal of Personality and Social Psychology, 99,* 948–963. doi:10.1037/a0020271

Impett, E. A., Kogan, A., English, T., John, O., Oveis, C., Gordon, A. M., & Keltner, D. (2012). Suppression sours sacrifice: Emotional and relational costs of suppressing emotions in romantic relationships. *Personality and Social Psychology Bulletin, 38,* 707–720. doi:10.1177/0146167212437249

Keltner, D., & Buswell, B. N. (1997). Embarrassment: Its distinct form and appeasement functions. *Psychological Bulletin, 122,* 250–270. doi:10.1037/0033-2909.122.3.250

Keltner, D., Horberg, E. J., & Oveis, C. (2006). Emotional intuitions and moral play. *Social Justice Research, 19,* 208–217. doi:10.1007/s11211-006-0006-8

Keltner, D., Kogan, A., Piff, P. K., & Saturn, S. R. (2014). The sociocultural appraisals, values, and emotions (SAVE) framework of prosociality: Core processes from gene to meme. *Annual Review of Psychology, 65,* 425–460. doi:10.1146/annurev-psych-010213-115054

Keltner, D., & Oveis, C. (2007). Elevation. In R. F. Baumeister & K. D. Vohs (Eds.), *Encyclopedia of social psychology* (p. 283). Thousand Oaks, CA: Sage. doi:10.4135/9781412956253.n173

Kim, H. S., Sherman, D. K., Mojaverian, T., Sasaki, J. Y., Park, J., Suh, E. M., & Taylor, S. E. (2011). Gene–culture interaction: Oxytocin receptor polymorphism (OXTR) and emotion regulation. *Social Psychological & Personality Science, 2,* 665–672. doi:10.1177/1948550611405854

Kogan, A., Impett, E. A., Oveis, C., Hui, B., Gordon, A. M., & Keltner, D. (2010). When giving feels good: The intrinsic benefits of sacrifice in romantic relationships for the communally motivated. *Psychological Science, 21,* 1918–1924. doi:10.1177/0956797610388815

Kogan, A., Saslow, L. R., Impett, E. A., Oveis, C., Keltner, D., Rodrigues Saturn, S., & Saturn, S. R. (2011). Thin-slicing study of the oxytocin receptor (OXTR) gene and the evaluation and expression of the prosocial disposition. *PNAS: Proceedings of the National Academy of Sciences of the United States of America, 108,* 19189–19192. doi:10.1073/pnas.1112658108

Kok, B. E., & Fredrickson, B. L. (2010). Upward spirals of the heart: Autonomic flexibility, as indexed by vagal tone, reciprocally and prospectively predicts positive emotions and social connectedness. *Biological Psychology, 85,* 432–436. doi:10.1016/j.biopsycho.2010.09.005

Kosfeld, M., Heinrichs, M., Zak, P. J., Fischbacher, U., & Fehr, E. (2005). Oxytocin increases trust in humans. *Nature, 435,* 673–676. doi:10.1038/nature03701

Kraus, M. W., & Keltner, D. (2009). Signs of socioeconomic status: A thin-slicing approach. *Psychological Science, 20,* 99–106. doi:10.1111/j.1467-9280.2008.02251.x

Leary, M. R. (2001). The self in shyness. In L. Crozier & R. Aldens (Eds.), *The self, shyness, and social anxiety: A handbook of concepts, research, and interventions.* New York, NY: Wiley.

Lewis, G. F., Furman, S. A., McCool, M. F., & Porges, S. W. (2012). Statistical strategies to quantify respiratory sinus arrhythmia: Are commonly used metrics equivalent? *Biological Psychology, 89,* 349–364. doi:10.1016/j.biopsycho.2011.11.009

Markus, H. R., & Kitayama, S. (1991). Culture and the self: Implications for cognition, emotion, and motivation. *Psychological Review, 98,* 224–253. doi:10.1037/0033-295X.98.2.224

Norenzayan, A., & Shariff, A. F. (2008, October 3). The origin and evolution of religious prosociality. *Science, 322,* 58–62. doi:10.1126/science.1158757

Oishi, S., Diener, E., & Lucas, R. (2007). The optimum level of well-being: Can people be too happy? *Perspectives on Psychological Science, 2,* 346–360. doi:10.1111/j.1745-6916.2007.00048.x

Oltmanns, T. F., Friedman, J. N., Fiedler, E. R., & Turkheimer, E. (2004). Perceptions of people with personality disorders based on thin slices of behavior. *Journal of Research in Personality, 38,* 216–229. doi:10.1016/S0092-6566(03)00066-7

Oveis, C., Cohen, A. B., Gruber, J., Shiota, M. N., Haidt, J., & Keltner, D. (2009). Resting respiratory sinus arrhythmia is associated with tonic positive emotionality. *Emotion, 9,* 265–270. doi:10.1037/a0015383

Oveis, C., Gruber, J., Keltner, D., Stamper, J. L., & Boyce, W. T. (2009). Smile intensity and warm touch as thin slices of child and family affective style. *Emotion, 9,* 544–548. doi:10.1037/a0016300

Oveis, C., Horberg, E. J., & Keltner, D. (2010). Compassion, pride, and social intuitions of self–other similarity. *Journal of Personality and Social Psychology, 98,* 618–630. doi:10.1037/a0017628

Oveis, C., Kogan, A., Liu, M. Y., & Keltner, D. (2014). *Laughter conveys status.* Manuscript submitted for publication.

Park, G., van Bavel, J. J., Vasey, M. W., & Thayer, J. F. (2012). Cardiac vagal tone predicts inhibited attention to fearful faces. *Emotion, 12,* 1292–1302. doi:10.1037/a0028528

Piff, P. K., Stancato, D., Côté, S., Mendoza-Dentona, R., & Keltner, D. (2012). Higher social class predicts increased unethical behavior. *PNAS: Proceedings of the National Academy of Sciences of the United States of America, 109,* 4086–4091. doi:10.1073/pnas.1118373109

Porges, S. W. (1995). Orienting in a defensive world: Mammalian modifications of our evolutionary heritage. A polyvagal theory. *Psychophysiology, 32,* 301–318. doi:10.1111/j.1469-8986.1995.tb01213.x

Porges, S. W. (2001). The polyvagal theory: Phylogenetic substrates of a social nervous system. *International Journal of Psychophysiology, 42,* 123–146. doi:10.1016/S0167-8760(01)00162-3

Porges, S. W. (2007). The polyvagal perspective. *Biological Psychology, 74,* 116–143. doi:10.1016/j.biopsycho.2006.06.009

Rand, D. G., Dreber, A., Ellingsen, T., Fudenberg, D., & Nowak, M. A. (2009, September 4). Positive interactions promote public cooperation. *Science, 325,* 1272–1275. doi:10.1126/science.1177418

Rodrigues, S. M., Saslow, L. R., Garcia, N., John, O. P., & Keltner, D. (2009). Oxytocin receptor genetic variation relates to empathy and stress reactivity in humans. *PNAS: Proceedings of the National Academy of Sciences of the United States of America, 106,* 21437–21441. doi:10.1073/pnas.0909579106

Rottenberg, J. (2007). Cardiac vagal control in depression: A critical analysis. *Biological Psychology, 74,* 200–211. doi:10.1016/j.biopsycho.2005.08.010

Rottenberg, J., Clift, A., Bolden, S., & Salomon, K. (2007). RSA fluctuation in major depressive disorder. *Psychophysiology, 44,* 450–458. doi:10.1111/j.1469-8986.2007.00509.x

Rottenberg, J., Ray, R. D., & Gross, J. J. (2007). Emotion elicitation using films. In J. A. Coan & J. J. B. Allen (Eds.), *The handbook of emotion elicitation and assessment* (pp. 9–28). London, England: Oxford University Press.

Rottenberg, J., Wilhelm, F. H., & Gross, J. J. (2001). Low respiratory sinus arrhythmia as a marker of episodic major depression. *Psychophysiology, 38,* S83–S183.

Ryff, C. D. (1989). Happiness is everything, or is it? Explorations on the meaning of psychological well-being. *Journal of Personality and Social Psychology, 57,* 1069–1081. doi:10.1037/0022-3514.57.6.1069

Schnall, S., Roper, J., & Fessler, D. M. (2010). Elevation leads to altruistic behavior. *Psychological Science, 21,* 315–320. doi:10.1177/0956797609359882

Schultz, S. K., Anderson, E. A., & van de Borne, P. (1997). Heart rate variability before and after treatment with electroconvulsive therapy. *Journal of Affective Disorders, 44,* 13–20. doi:10.1016/S0165-0327(97)01443-2

Segerstrom, S. C., & Nes, L. S. (2007). Heart rate variability reflects self-regulatory strength, effort, and fatigue. *Psychological Science, 18,* 275–281. doi:10.1111/j.1467-9280.2007.01888.x

Shariff, A. F., & Norenzayan, A. (2007). God is watching you: Priming God concepts increases prosocial behavior in an anonymous economic game. *Psychological Science, 18,* 803–809. doi:10.1111/j.1467-9280.2007.01983.x

Shiota, M. N., Keltner, D., & John, O. P. (2006). Positive emotion dispositions differentially associated with Big Five personality and attachment style. *Journal of Positive Psychology, 1,* 61–71. doi:10.1080/17439760500510833

Sober, E., & Wilson, D. S. (1998). *Unto others: The evolution and psychology of unselfish behavior*. Cambridge, MA: Harvard University.

Srivastava, S., Tamir, M., McGonigal, K. M., John, O. P., & Gross, J. J. (2009). The social costs of emotional suppression: A prospective study of the transition to college. *Journal of Personality and Social Psychology, 96,* 883–897. doi:10.1037/a0014755

Stifter, C. A., Fox, N. A., & Porges, S. W. (1989). Facial expressivity and vagal tone in 5- and 10-month-old infants. *Infant Behavior & Development, 12,* 127–137. doi:10.1016/0163-6383(89)90001-5

Tarvainen, M. P., Niskanen, J.-P., Lipponen, J. A., Ranta-Aho, P. O., & Karjalainen, P. A. (2014). Kubios HRV–heart rate variability analysis software. *Computer Methods and Programs in Biomedicine, 113,* 210–220. doi:10.1016/j.cmpb.2013.07.024

Valdesolo, P., & Desteno, D. (2011). Synchrony and the social tuning of compassion. *Emotion, 11,* 262–266. doi:10.1037/a0021302

van Kleef, G. A., Oveis, C., van der Löwe, I., LuoKogan, A., Goetz, J., & Keltner, D. (2008). Power, distress, and compassion: Turning a blind eye to the suffering of others. *Psychological Science, 19,* 1315–1322. doi:10.1111/j.1467-9280.2008.02241.x

Volkers, A. C., Tulen, J. H., van den Broek, W. W., Bruyn, J. A., Passchier, J., & Pepplinkhuizen, L. (2004). Effects of imipramine, fluvoxamine, and depressive mood on autonomic cardiac functioning in major depressive disorder. *Pharmacopsychiatry, 37,* 18–25. doi:10.1055/s-2004-815470

Wang, Z., Lü, W., & Qin, R. (2013). Respiratory sinus arrhythmia is associated with trait positive affect and positive emotional expressivity. *Biological Psychology, 93,* 190–196. doi:10.1016/j.biopsycho.2012.12.006

Wilhelm, F. H., Grossman, P., & Roth, W. T. (1999). Analysis of cardiovascular regulation. *Biomedical Sciences Instrumentation, 35,* 135–140.

Received September 25, 2012
Revision received February 10, 2014
Accepted June 29, 2014 ■