



Helping from the heart: Voluntary upregulation of heart rate variability predicts altruistic behavior



Boris Bornemann^{a,*}, Bethany E. Kok^a, Anne Böckler^{a,b}, Tania Singer^a

^a Department of Social Neuroscience, Max Planck Institute for Human Cognitive and Brain Sciences, Germany

^b Department of Psychology, Würzburg University, Germany

ARTICLE INFO

Article history:

Received 26 February 2016

Received in revised form 30 June 2016

Accepted 1 July 2016

Available online 2 July 2016

Keywords:

Vagus

Parasympathetic nervous system

Vagal flexibility

Heart rate variability

Biofeedback

Regulation

Altruism

Prosocial behavior

ABSTRACT

Our various daily activities continually require regulation of our internal state. These regulatory processes covary with changes in High Frequency Heart Rate Variability (HF-HRV), a marker of parasympathetic activity. Specifically, incidental increases in HF-HRV accompany positive social engagement behavior and prosocial action. Little is known about deliberate regulation of HF-HRV and the role of voluntary parasympathetic regulation in prosocial behavior. Here, we present a novel biofeedback task that measures the ability to deliberately increase HF-HRV. In two large samples, we find that a) participants are able to voluntarily upregulate HF-HRV, and b) variation in this ability predicts individual differences in altruistic prosocial behavior, but not non-altruistic forms of prosociality, assessed through 14 different measures. Our findings suggest that self-induction of parasympathetic states is involved in altruistic action. The biofeedback task may provide a measure of deliberate parasympathetic regulation, with implications for the study of attention, emotion, and social behavior.

© 2016 Elsevier B.V. All rights reserved.

1. Introduction

As we go through the various activities of our day, our internal milieu continually changes. The adaptations of our internal states are mirrored in changes of autonomic system activity (Kreibig, 2010; Porges, 2007; Thayer & Lane, 2009). In this paper, we focus on changes in parasympathetic activity, particularly activity of the vagus nerve, which can be estimated by measuring the high frequency band of heart rate variability (HF-HRV; e.g., Task-Force, 1996). Some behaviors, such as solving a cognitively demanding task or coping with a stressful situation, are accompanied by reductions in HF-HRV, indicative of vagal withdrawal (Duschek, Muckenthaler, Werner, & del Paso, 2009; Graziano & Derefinko, 2013; Luque-Casado, Perales, Cárdenas, & Sanabria, 2015). Other behaviors, such as positive social engagement, have been linked to increases in HF-HRV, indicative of vagal upregulation (Bazhenova, Plonskaia, & Porges, 2001; Hastings et al., 2008; Miller et al., 2013; Porges, 2003). The degree to which people show these situation-dependent adaptations in HF-HRV, termed vagal flexibility (Muhtadie, Koslov, Akinola, & Mendes, 2014), has been

hypothesized to relate to psychological health (Beauchaine, 2001). Indeed, it has been found that people who exhibit lower HF-HRV in stressful situations and higher HF-HRV during positive social engagement show better stress coping (Bazhenova et al., 2001), fewer depressive symptoms (Oppenheimer, Measelle, Laurent, & Ablow, 2013), and are less likely to be diagnosed with psychopathology (Musser et al., 2011; Shahrestani, Stewart, Quintana, Hickie, & Guastella, 2014).

The role of vagal upregulation in positive social engagement led researchers to pursue the hypothesis that it is also involved in altruistic feelings and behaviors (e.g., Barraza, Alexander, Beavin, Terris, & Zak, 2015; Miller, Kahle, & Hastings, 2015). Following Batson, (2014, p.6), we define behaviors as altruistically motivated if they follow from a “motivational state with the ultimate goal of increasing another’s welfare”. A link between altruism and vagal upregulation is in line with the implication of the vagus in the mammalian “care-system” (Panksepp, 2006, 2011; also called “affiliative system”, Depue & Morrone-Strupinsky, 2005), a biological system that evolved in mammals for the care of the offspring but may lie at the basis of caring or altruistic acts in general (Eisenberger & Cole, 2012; Gordon, Martin, Feldman, & Leckman, 2011; Panksepp, 2011; Preston, 2013). In rodents, the vagus nerve closely interacts with the neuropeptide oxytocin, which is a hallmark of the care/affiliative system (Charpak, Armstrong, Mühlethaler, & Dreifuss, 1984; Depue & Morrone-Strupinsky, 2005;

* Corresponding author at: Max Planck Institute for Human Cognitive and Brain Sciences, Stephanstraße 1a, 04103 Leipzig, Germany.

E-mail address: bornemann@cbs.mpg.de (B. Bornemann).

Dreifuss, Raggenbass, Charpak, Dubois-Dauphin, & Tribollet, 1988; Panksepp, 2011; Tribollet, Charpak, Schmidt, Dubois-Dauphin, & Dreifuss, 1989) to bring about the state of quiescence that is involved in care-giving behaviors (McCall & Singer, 2012; Porges, 2003; Uvnäs-Moberg, 1998). In humans, intranasal administration of oxytocin increases HF-HRV (Kemp et al., 2012; Norman et al., 2011) and facilitates parasympathetic responses to social stimuli (Gamer & Büchel, 2012), underlining the implication of vagal activation in the care/affiliative system. Several studies support the hypothesis that altruistic feelings and behaviors are accompanied by increases in vagal activity. Intraindividual increases in HF-HRV accompany the experience of compassion, induced by videos on human suffering (Oveis, 2002; Stellar, Cohen, Oveis, & Keltner, 2015), and HF-HRV is elevated when people witness the altruistic actions of others (Hutchinson, 2012). Children who show less HF-HRV reduction when exposed to a toddler in distress display more empathetic concern (Gill & Calkins, 2003), and those who maintain higher HF-HRV when hearing about sick and incapacitated children are more willing to share their own resources with them (Miller et al., 2015). Similarly, in adults, the degree of HF-HRV upsurge when viewing a video depicting human suffering positively predicts their readiness to donate money to a related charity (Barraza et al., 2015).

All of these studies demonstrate that adjustments in HF-HRV co-occur with certain emotions and behaviors. In particular, incidental increases in HF-HRV accompany altruistic feelings and behaviors. A possible explanation is that the upsurges in vagal activity reflect *deliberate* self-regulatory efforts, specifically the activation of emotional-motivational systems related to positive social engagement and care-giving (Panksepp, 2011; Porges, 2003; Thayer & Lane, 2009). This claim, however, has never been directly tested. We therefore designed a task to measure deliberate upregulation of vagal activity. We hypothesized that people who more readily activate the vagus in such a deliberate self-regulation paradigm would also be more inclined to activate it in social interaction situations. Thus, higher ability to self-induce vagal activity should relate to more altruistic behavior. This would indicate that the biological processes which accompany altruistic actions are at least partially under conscious regulatory control.

To study voluntary upregulation of vagal activity, we developed a procedure that continually (roughly every 2.5 s) feeds back a short term estimate of HF-HRV to participants as the altitude of a ball on a computer screen. We informed participants that the ball mirrors some aspect of their mental-bodily state and asked them to make it go up (which happened when HF-HRV increased). Participants were not told which parameter is indicated by the ball nor suggested any strategies to influence it (see Supplementary material for full instructions). This procedure is different from previous HF-HRV feedback procedures (see Wheat & Larkin, 2010 for a review), in all of which participants were told to attain regulation by slower breathing (e.g., Druschky & Druschky, 2015; Dziembowska et al., 2015; Karavidas et al., 2007; Lehrer et al., 2003; Nolan et al., 2005), or participants' attention was drawn to breathing as a possible way to take influence in the biofeedback (Cowan, Kogan, Burr, Hendershot, & Buchanan, 1990; Lehrer et al., 1997). First, an open instruction to regulate one's mental-bodily state is more conducive to measuring individual differences in participant's inclination and ability to increase vagal activity than a purely physiological approach. Second, and more importantly, restricting regulation of HF-HRV to breathing related strategies may be problematic because of the complex relationship of breathing, HF-HRV, and vagal activity: Although slower breathing may indeed have stimulating effects on the vagus (Bernardi, Porta, Gabutti, Spicuzza, & Sleight, 2001; Grossman, 1983; Pal & Velkumary, 2004; Vaschillo, Vaschillo, & Lehrer, 2006), it may also be an artifact of the measurement of vagal activity through HF-HRV because there is a

negative relationship between respiration rate and HF-HRV even in the absence of changes in vagal activity (Grossman & Taylor, 2007; Quintana & Heathers, 2014). Of course, in our task, participants may also use breathing changes to influence HF-HRV. We therefore measured respiration rate throughout the experiment and control for it when using individual differences in the biofeedback as an approximate measure for vagal upregulation. As this type of HF-HRV biofeedback without any strategy instruction is novel, a first aim of this study was to investigate whether people are able to self-induce increases in HF-HRV in this task.

To assess aspects of prosociality and particularly altruistic behavior, we used a large battery of classical behavioral measures and self-reports that have been assessed in the context of the ReSource project, a longitudinal study on mental training, from which we used baseline data for the purposes of the present paper (for details Singer et al., *in press*). This task battery included game theoretical paradigms (Berg, Dickhaut, & McCabe, 1995; Camerer, 2003; Fehr & Fischbacher, 2004), ecologically valid computer tasks (Hare, Camerer, Knoepfle, O'Doherty, & Rangel, 2010; Leiber, Klimecki, & Singer, 2011), hypothetical distribution tasks (Jones & Rachlin, 2006; Van Lange, 1999), and self-reports on socio-emotional dispositions (Caprara, Steca, Zelli, & Capanna, 2005; Davis, 1983; Henning & Six, 1977). In a previous study (Böckler, Tusche, & Singer, 2016), a factor analysis on these measures yielded four factors representing largely independent subcomponents of prosociality, namely Altruistically Motivated Behavior (AMB), Norm Motivated Behavior (NMB), Strategically Motivated Behavior (SMB), and Self-Reports (SR) of socio-emotional dispositions. The first three factors are all comprised of different types of behavioral measures that assess aspects of human prosociality, whereas the last factor contained only trait-level questionnaires. The first three factors distinguish between the motivations that underlie prosocial behavior. In the case of NMB and SMB, prosocial behaviors are motivated by adherence to social norms and strategic considerations to maximize one's own profits, respectively. In contrast, behaviors subsumed in the AMB factor involve unconditional giving and helping based on generosity and altruistic motivation. AMB thus has the ultimate goal of fostering the well-being of another (cf. Batson, 2014). Because of the association of vagal upregulation with the care-system and altruism, we hypothesized that the ability to activate the vagus would be related to individual differences in AMB, but not other types of prosocial behaviors, which are not based in care-motivation but rather in norm-adherence or self-focused motivation. When it comes to the fourth factor, the self-report factor, an association to HF-HRV upregulation seems unlikely, as self-reports of socio-emotional dispositions had previously been found to be only weakly related to actual behavior (Böckler et al., 2016) and furthermore, no previous study had shown any relationship between increases in HF-HRV and self-reports of socio-emotional dispositions.

2. Methods

2.1. Participants

All measures were provided by participants in the ReSource Project, a large scale study on the effects of meditation and mental training, conducted in Leipzig and Berlin. Detailed descriptions of the overall study design and participant recruitment procedure are available in Singer et al. (*in press*). Briefly, all participants were selected to be mentally and physically healthy and between 20 and 55 years of age. The present study only utilizes data that were collected before the training began. Of the 332 participants enrolled in the study, 248 (age $M = 39.94$, $SD = 9.32$; 138 female) had complete data on all measures relevant to this paper (see Supplementary

material, Section A, for details on missing data). Weight and height of participants were assessed to compute the Body Mass Index (BMI) which was included as a covariate because of its possible influence on measures of heart rate variability (Koenig et al., 2014; but also see Antelmi et al., 2004). BMI data of 5 participants were missing due to scheduling reasons. Half of the sample was recruited and tested in Berlin ($n = 126$, age $M = 41.75$, $SD = 8.66$, 75 females) the other half in Leipzig ($n = 122$, M age = 38.07, $SD = 9.64$, 63 female). Data collection at each location was run by a different team of experimenters with parallel technical setups.

2.2. Ethics

The study was approved by the Research Ethics Committee of the University of Leipzig, number 376/12-ff and the Research Ethics Committee of the Humboldt University in Berlin, numbers 2013-02, 2013-29, and 2014-10. All participants gave written informed consent.

The study was registered with the Protocol Registration System of ClinicalTrials.gov under the title “Plasticity of the Compassionate Brain” with the [ClinicalTrials.gov](https://clinicaltrials.gov/ct2/show/study/NCT01833104) Identifier: NCT01833104.

2.3. Physiological recordings

Heart rate and respiration rate were assessed throughout baseline measurement and the biofeedback task. For heart rate measurement, a standard Lead-II electrocardiogram was acquired by placing disposable Ag/AgCl Electrodes on the right mid-clavicle, left ribcage, and left outer clavicle. To measure respiration, a strain gauge was attached around the torso of participants at the position of the lower ribs to capture both chest and abdominal breathing. Signals were recorded at 1000 Hz using a Biopac® (BIOPAC Systems Inc., Santa Barbara, CA) MP150 data acquisition system and the software AcqKnowledge 4.3. Data were processed and cleaned for artifacts with ARTiiFACT (Kaufmann, Sütterlin, Schulz, & Vögele, 2011) and custom MATLAB scripts (available on request).

2.4. Vagal activity parameter

The most commonly used parameter to estimate vagal activity is the power of the high frequency band of heart rate variability (HF-HRV), derived via Fourier transformation of interbeat interval (IBI) series. As Fourier transformation requires a minimum length of approximately two minutes of IBI series to be accurate (Task-Force, 1996), such a measure is unfeasible for biofeedback, in which information about physiological activity should be minimally delayed. Peak-to-trough RSA (Grossman, van Beek, & Wientjes, 1990), another common measure, proved unfeasible in pilot studies because online assessment of respiratory peaks and troughs was prone to error. We thus developed a short term estimate of HF-HRV that can be calculated and fed back to the participant in real time. This measure, which we term Local Power (LP), quantifies the power of the high frequency oscillations in heart period twice per oscillation cycle (see Fig. 1 for an explanation of the algorithm). Specifically, each time the heart period reaches a local maximum, the differences to the preceding local minimum is computed and vice versa. During a 5 min baseline measurement, mean LP was highly correlated with HF-HRV ($r = 0.853$, $p < 0.001$) and with RSA ($r = 0.976$, $p < 0.001$). The correlations remained high during biofeedback (with HF-HRV: $r = 0.818$, $p < 0.001$; with RSA: $r = 0.968$, $p < 0.001$). The intercorrelations of HF-HRV and RSA were $r = 0.821$ and $r = 0.785$ at baseline and biofeedback, respectively. Across both measurement periods, the LP measurement was thus able to capture between 69.83% (HF-HRV) and 94.5% (RSA) of the information represented by established measures of vagal activity. Given that, in this sample, RSA and HF-HRV shared between 61.6%

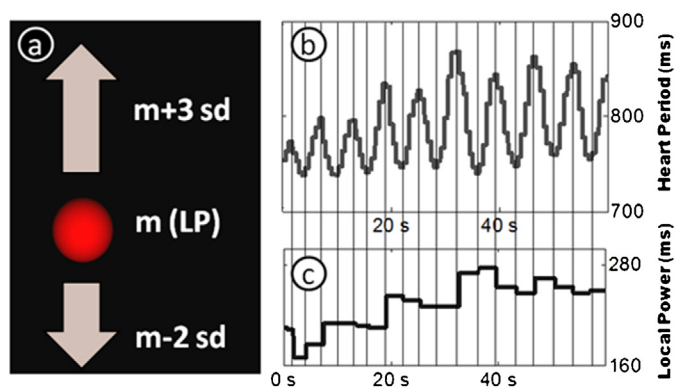


Fig. 1. Panel a shows the display of the biofeedback task. A spinning ball is displayed on the screen. Its height is determined by Local Power (LP). Panel b and c illustrate the computation of LP: Shown is the heart period (HP) of a single subject over the course of 1 min (Panel b). Every time the direction of the HP curve shifts (vertical lines), a new LP value (Panel c) is assigned, computed as the difference in HP to the previous shifting point. An average of the last two LP values is used for feedback.

and 67.4% of variance over the same periods, we consider LP an acceptable method for the assessment of vagal activity. The limits of agreement (Bland & Altman, 1986) between LP and RSA were $[-0.431$ sd; 0.431 sd]. Between LP and HRV they were $[-1.063$ sd; 1.063 sd]. Further details about the interrelationship between LP, peak-to-trough RSA, and HF-HRV derived by Fast Fourier transform can be found in the Supplementary material, section F.

2.5. Tasks

The baseline measurement and the biofeedback task were recorded in a single session. Between one and four participants were tested at the same time. When tested in groups, participants were separated by wooden blinds (in Leipzig) or placed several meters apart (in Berlin) to avoid distraction. Participants always started with the baseline measurement and then performed the biofeedback task either directly afterwards or following a heart beat perception task and/or a short video task not reported here. Task order did not influence any of the results. During both baseline and biofeedback, participants were asked to assume identical postures, with both feet on the ground and both hands separate from each other in their lap.

The tasks assessing social behavior were administered in three separate sessions in a multi-computer-lab (see Böckler et al., 2016; for details). Questionnaires were assessed via an online platform.

2.5.1. Baseline measurement

For assessment of baseline HF-HRV, participants were asked to just sit still and “not think of anything in particular” for 5 min, as common for resting HF-HRV assessment (Task-Force, 1996).

2.5.2. Biofeedback task

Before the biofeedback task, participants were told that they will see a ball on the screen which is related to some aspect of their mental-bodily activity. They were informed that the more they come into the desired mental-bodily state, the more the ball will rise. They were asked to make the ball go up while remaining physically still, without any further information about the target state or advice about strategies to achieve it (see Supplementary material, Section B, for exact instructions).

Then the biofeedback was started. A python-based program (available on request), written in Vizard 4.0 (WorldViz, Santa Barbara, CA) was used to display a red, spinning, three-dimensional ball in the horizontal center of the screen. The vertical position of the ball was determined by participant’s Local Power (Fig. 1). Based

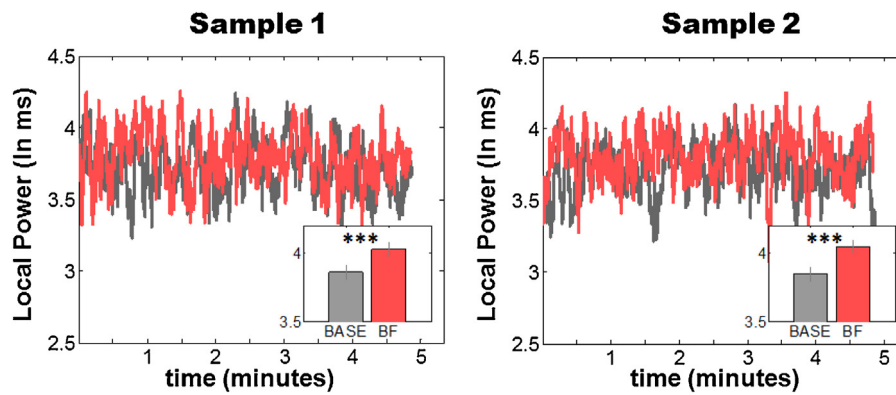


Fig. 2. Local Power during baseline measurement (BASE) and the biofeedback task (BF). Bigger Panels: raw data. Smaller Panels: aggregated data. Sample 1 from Berlin, Sample 2 from Leipzig.

on the algorithm described in Fig. 1, LP could be computed every 2.46 s ($SD = 0.64s$), on average. To individualize the feedback range, average LP and intraindividual standard deviation of LP was computed for every participant during baseline measurement. During the biofeedback task, when LP was at the participant's baseline-derived mean, the ball was two fifth of a screen length above the lower screen boundary. The lowest possible ball position (at lower screen boundary) represented an LP of $M - 2SD$. The highest possible ball position (upper screen boundary) represented an LP of $M + 3SD$ (see Fig. 1a). Lower and higher values were cut at these boundaries so that the ball never left the screen. The position was always determined by an average of the last two LP values, to make the signal more stable. The biofeedback task lasted 5 min.¹

After the biofeedback, participants were asked to freely describe (in a text field on the screen) how they had approached the task (see Supplementary material, Section D, for details).

2.5.3. Prosociality measures

Prosociality was assessed with 14 different measures (see Böckler et al., 2016, for details on the task procedures). These were acquired in the context of five game theoretical paradigms, namely the Dictator Game (Forsythe, Horowitz, Savin, & Sefton, 1994), a Trust Game and a Risk Game (Berg et al., 1995; Bohnet & Zeckhauser, 2004; Coleman, 1994), and a 2nd and a 3rd Person Punishment Game (Fehr & Fischbacher, 2004); two interactive computer tasks, namely the Zurich Prosocial Game (Leiberg et al., 2011) and a Donation Task (Harbaugh, Mayr, & Burghart, 2007; Hare et al., 2010); two hypothetical distribution tasks, namely the Social Discounting Task (Jones & Rachlin, 2006) and the Social Value Orientation Scale (Van Lange, 1999); and three trait questionnaires, namely the Prosocialness Scale (Caprara et al., 2005), the Machiavelli Scale (Henning & Six, 1977), and the Interpersonal Reactivity Index (Davis, 1983). In a previous study (Böckler et al., 2016), all of these measures have been subduced to a factor analysis (Principal Component Analysis with oblique rotation) to identify the underlying structure of human prosociality. The analyses yielded four factors. The first factor was composed of the overall percentage of helping in the Zurich Prosocial Game, the amount of money given to charitable organizations in the Donation Game, the amount of money given in the Dictator Game, the amount of money given in the Trust Game minus money given in the Risk Game, the degree

to which participants maximize group payoffs rather than individual payoffs in the Social Value Orientation Scale, and the degree to which participants favor an equal distribution of wealth over a distribution to close others in the Social Discounting Questionnaire. As all of these measures reflect pure generosity or willingness to help another person without the possibility to receive money in return (with the exception of the Trust Game), this factor was termed *Altruistically Motivated Behavior*. The second factor was composed of the extent of punishment in the 2nd and 3rd Person Punishment Game and of the reciprocity effect in the Zurich Prosocial Game (how much more participants help if they have been helped before). As these measures reflect adherence to or enforcement of social norms, it was termed *Norm Motivated Behavior*. The third factor was comprised of strategic giving in the game theoretical paradigms and the cost effect in the Zurich Prosocial Game (how much less participants help if it is costly). This factor was called *Strategically Motivated Behavior*. The fourth factor was comprised of all three trait questionnaire measures in the study, in which participants described their socio-emotional dispositions. It was called *Self-Reports*.

To assign individual scores to participants, all measures were z-transformed and added within their respective dimension (Altruistically Motivated Behavior, Norm Motivated Behavior, Strategically Motivated Behavior, and Self-Reports).

3. Results

3.1. Local Power during baseline and the biofeedback task

Our first hypothesis was that participants would be able to upregulate LP in the biofeedback task. To assess this, LP values were transformed using \log_e to reduce skew, following common procedures for analyzing vagal activity measures (Berntson et al., 1997; Grossman & Taylor, 2007). LP was significantly higher during the biofeedback (BF) than during baseline measurement (BASE), paired-sample $t(247) = 6.29$, $p < 0.001$, *Cohen's d* = 0.283. To test for replicability, we split the sample according to the study sites, Berlin (B) and Leipzig (L). Effects were reproduced in both sites (Fig. 2): The differences in LP between BF and BASE were significant, $p < 0.001$, and of similar magnitude, $d_B = 0.295$, $d_L = 0.270$, $ps < 0.001$. Note that higher LP does not necessarily mean higher vagal activity. Lower respiration rate may also cause increases in LP without always leading to increases in vagal activity (Grossman & Taylor, 2007; Quintana & Heathers, 2014). An interindividual difference score to index vagal upregulation should be controlled for respiratory effects and should be related to individual differences in behaviors which are theoretically linked to vagal activity.

¹ For the initial 72 participants, we ran the biofeedback task for 10 min. However, analyses revealed that information about the ability to self-induce increases in LP could be gained in the first 5 min of the task (see Supplementary material, Section C). The task was thus cut to 5 min for the remaining participants. All analyses reported here use only the first 5 min of the BF task. As detailed in the Supplementary Material, this does not influence any results.

Table 1
Correlations between vuLP_R and measures of prosociality.

	Altruistically Motivated Behavior (AMB)	Norm Motivated Behavior (NMB)	Strategically Motivated Behavior (SMB)	Self-Reports of Prosociality (SR)
vuLP_R	0.234***	−0.136*	−0.079	0.023
AMB		−0.006	−0.427***	0.191**
NMB			−0.088	0.009
SMB				−0.058

Note: vuLP_R denotes voluntary upregulation of Local Power controlled for respiration. The four factors of prosociality are derived from 14 different behavioral and self-report measures (see Böckler et al., 2016).

*** $p < 0.001$.

** $p < 0.01$

* $p < 0.05$.

3.2. Calculating upregulatory success

In the next step we calculated an individual upregulation success parameter for each participant. In creating this parameter, we were mindful of the role of respiration, which can be both a way to change autonomic activity and a confound to the measurement. On the one hand, breathing may have powerful effects on the autonomous nervous system, with slower breathing inducing relaxation and increases in vagal activity (Bernardi et al., 2001; Pal & Velkumary, 2004; Vaschillo et al., 2006). On the other hand, slower breathing may cause increases in measures of vagal activity, such as LP, without actually affecting the vagus (Grossman & Taylor, 2007; Quintana & Heathers, 2014). To avoid this confound we controlled increases in LP for changes in respiration rate as follows. We first computed voluntary upregulation of Local Power (vuLP) as an increase in Local Power in BF compared to BASE, that is $\text{vuLP} = \text{LP}_{\text{BF}} - \text{LP}_{\text{BASE}}$. We then computed the same difference score for change in respiration rate, $\text{RSPchange} = \text{RSP}_{\text{BF}} - \text{RSP}_{\text{BASE}}$. These scores, increase in LP and increase in respiration rate, were correlated at $r = -0.615$, $p < 0.001$. To obtain a score that approximates vagal upregulation, we computed a regulation success score that is residualized for respiration rate changes (vuLP_R = the residual of a regression of RSPchange on vuLP). We then analyzed the relationships of voluntary upregulation of Local Power, residualized for changes in respiration (vuLP_R), to our indices of prosociality (Table 1).

3.3. Relation of voluntary upregulation of Local Power to prosociality

VuLP_R was correlated with Altruistically Motivated Behavior (AMB), $r = 0.234$, $p < 0.001$ (a medium sized effect of Cohen's $d = 0.481$). Again, we split the analyses according to study site to check for replicability (Fig. 3). We found the correlation to be significant in both samples with similar effect sizes, $r_B = 0.250$ ($d = 0.516$), $p = 0.005$, and $r_L = 0.220$ ($d = 0.451$), $p = 0.015$. There was a weak negative association of vuLP_R with Norm Motivated Behavior (NMB), $r = -0.136$ ($d = 0.274$), $p = 0.032$. This correlation did not hold when splitting for study site to test for replicability, $r_B = -0.117$, $p = 0.191$, $r_L = -0.155$, $p = 0.088$. There were no correlations of vuLP_R with Strategically Motivated Behavior (SMB), $r = -0.079$, $p = 0.216$, or self reports (SR) of socio-emotional dispositions, $r = -0.023$, $p = 0.717$. None of the constituent questionnaires of the SR factor or their subscales were significantly related to vuLP_R , all $ps > 0.05$ (see Supplementary material for a full correlation matrix). The correlation of vuLP_R to AMB was significantly higher than the correlation of vuLP_R to NMB, $z = 4.174$, $p < 0.001$, SMB, $z = 2.95$, $p = 0.003$, or SR, $z = 3.222$, $p = 0.001$.

The correlation between voluntary upregulation and AMB also holds when using commonly used vagal activity estimates instead of LP such as RSA, $r = 0.219$, $p < 0.001$, RMSSD, $r = 0.253$, $p < 0.001$, or HF-HRV, $r = 0.173$, $p = 0.006$ (note though that use of traditional

Fourier-derived HF-HRV may underestimate the effects because for some participants respiratory rate during BF is lower than the conventionally used boundary of 0.15 Hz; also see Karavidas et al., 2007). The correlation also holds when including 50 additional participants who had incomplete data on the measures of AMB, $r = 0.184$, $p = 0.001$.

We followed up on this correlational analysis by a regression analysis with AMB as the criterion, where age, sex, and BMI were entered as predictors in the first step, and vuLP_R was entered in the second step. The first step of the regression was significant, $F(3,239) = 3.824$, $p = 0.011$, $R^2 = 0.046$. Specifically, the effect of age was significant, $\beta = -0.161$, $p = 0.017$, whereas sex and BMI did not significantly predict AMB, $ps > 0.15$. The second step of the regression was significant, too, $F(4,238) = 5.403$, $p < 0.001$, $R^2 = 0.068$ and vuLP_R , significantly predicted AMB, $\beta = 0.198$, $p = 0.002$. This indicates that the relationship of vuLP_R and AMB persists when controlling for the effects sex, age, and BMI. When repeating these analysis with NMB, SMB, or SR as the criterion, vuLP_R was never a significant predictor in the second step of the regression, $\beta = -0.116$, $p = 0.075$ (NMB), $\beta = -0.096$, $p = 0.139$ (SMB), $\beta = 0.039$, $p = 0.535$ (SR). When using voluntary regulation measures based on other measures of vagal activity in the second step of the regression to predict AMB, voluntary regulation was always a significant predictor, $\beta = 0.184$, $p = 0.004$ (RSA), $\beta = 0.209$, $p = 0.001$ (RMSSD), $\beta = 0.161$, $p = 0.011$ (HF-HRV).

3.4. The role of breathing

Participants breathed more slowly in the biofeedback task ($M = 0.175$ Hz, $SD = 0.056$) than during BASE ($M = 0.200$ Hz, $SD = 0.060$), $t(247) = 9.314$, $p < 0.001$. However, AMB was uncorrelated with changes in respiration rate from BASE to BF, $r = 0.016$, $p = 0.800$, indicating that respiration rate changes do not explain the observed relationship of vuLP_R and AMB. When voluntary upregulation of LP was not corrected for respiration changes, the correlation to AMB was slightly diminished, $r = 0.174$, $p = 0.006$. This decrease in correlation magnitude is marginally significant (Fisher's $z = 1.537$, $p_{\text{one-tailed}} = 0.062$), suggesting that controlling for respiration helps to carve out the portion of vuLP variance that is related to AMB.

3.5. Relationship of AMB to LP at BASE

AMB was uncorrelated to LP at BASE, $r = -0.028$, $p = 0.661$. Following up on findings by Kogan et al. (2014), we also checked for a quadratic relationships between LP at BASE and AMB, but found this to be absent, $r = 0.028$, $p = 0.661$.

3.6. The role of heart rate

Heart rate was significantly lower during BF ($M = 75.17$ bpm, $SD = 10.37$) than during BASE ($M = 76.07$, $SD = 10.97$), $t(247) = 3.43$,

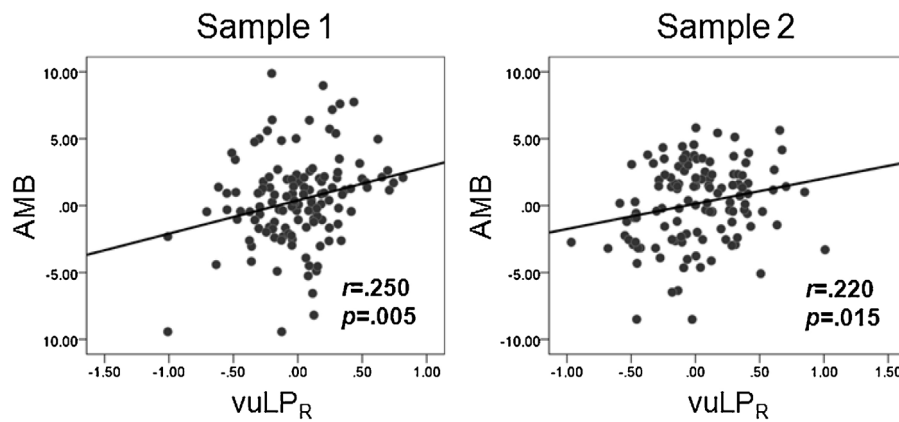


Fig. 3. Correlation of voluntary upregulation of Local Power, controlled for respiration ($vuLP_R$) to Altruistically Motivated Behavior (AMB) as assessed by a multi-method factor score. Sample 1 from Berlin, Sample 2 from Leipzig.

$p < 0.001$. Moreover, there was a strong correlation of $vuLP_R$ with decreases in heart rate from BASE to BF, $r = 0.424$, $p < 0.001$, also when controlling for heart rate at BASE, $r = 0.354$, $p < 0.001$. This finding indicates that participants who successfully upregulated LP decreased in tonic cardiac arousal, supporting the idea of vagal regulation, as upregulation of the vagus leads to decreased heart rate (Parker, Celler, Potter, & McCloskey, 1984).

3.7. Upregulatory strategy analyses

After the completion of the biofeedback task, participants were asked to freely describe how they had approached the task. Two independent raters classified the described strategies according to a fine grained categorical system (e.g., breathing changes, observation of the body, induction of positive or negative emotion, relaxation), which was applied with good inter-rater reliability (88.78% flag-wise congruency). The Supplementary material (Section D) contains this categorical system and details on the analyses. To summarize, there were no clear associations of employed strategy with $vuLP_R$. This finding indicates that no specific strategy was more successful in influencing vagal activity than other strategies. Importantly, the association of $vuLP_R$ to AMB is preserved across all strategies. This result indicates that within subjects who used a certain strategy for regulation, those who attained higher $vuLP_R$ showed more altruistic behavior.

4. Discussion

In this study, we assessed the ability to deliberately upregulate parasympathetic activity and its relation to prosociality, particularly altruistically motivated behavior. We employed a novel biofeedback procedure in which participants were asked to upregulate Local Power (LP). LP is an ECG-derived measure that is closely related to High Frequency Heart Rate Variability (HF-HRV; e.g., Task-Force, 1996) and peak-to-trough RSA (Grossman et al., 1990) and indexes activity of the vagus, the body's largest parasympathetic nerve. Participants exhibited higher LP during the biofeedback task than during a sitting baseline measurement, indicating successful upregulation.

Secondly, based on the theorized role of the vagus in social engagement (Bazhenova et al., 2001; Hastings et al., 2008; Miller et al., 2013; Porges, 2003) and the motivational systems of care and affiliation (Depue & Morrone-Strupinsky, 2005; Feldman & Eidelman, 2003; Kemp et al., 2012; Norman et al., 2011; Panksepp, 2011; Tribollet et al., 1989; Uvnäs-Moberg, 1994, 1998), as well as earlier studies which had linked incidental upregulation of HF-HRV to altruistic feelings and behaviors (Barraza et al., 2015; Miller

et al., 2015; Stellar et al., 2015) we hypothesized that individual differences in the ability to deliberately up-regulate LP would be linked to individual differences in altruistic behavior. We operationalized altruistic behavior through a multi-method approach that identified a latent construct called Altruistically Motivated Behavior (AMB) which includes several commonly-used behavioral measures of altruistic behavior (Böckler et al., 2016). Specifically, AMB entails helping behavior in the Zurich Prosocial Game (Leiberg et al., 2011), charitable donations (Harbaugh et al., 2007; Hare et al., 2010), generosity expressed in a Dictator Game (Forsythe et al., 1994) and in other-oriented distribution decisions in the Social Value Orientation Scale (Van Lange, 1999), a measure of interpersonal trust (measured in a Trust and a Risk game, Berg et al., 1995; Bohnet & Zeckhauser, 2004; Coleman, 1994), and the degree to which participants favor an equal distribution of wealth over a distribution to close others in the Social Discounting Task (Jones & Rachlin, 2006). Indeed, we found voluntary upregulation of Local Power ($vuLP_R$) in the biofeedback task, controlled for respiratory confounds (Grossman & Taylor, 2007; Quintana & Heathers, 2014), to be positively correlated to AMB. Also in line with and extending previous literature (Barraza et al., 2015; Stellar et al., 2015), LP during baseline was unrelated to AMB. This pattern of results was found in two different matched samples assessed at two different study sites (Berlin and Leipzig), where participants were measured using identical procedures administered by different experimenters in different facilities.

Furthermore, we had hypothesized that other types of prosociality, which are not altruistically motivated would not be related to voluntary regulation of LP. This was ascertained by relating $vuLP_R$ to three non-altruistic dimensions of prosociality which had emerged from the factor analyses of Böckler et al. (2016). These were Norm Motivated Behavior (e.g., helping behavior which can be explained by adherence to reciprocity norms and punishment behavior to enforce social norms; Fehr & Fischbacher, 2004; Leiberg et al., 2011), Strategically Motivated Behavior (e.g., giving more money if a lack of generosity could be potentially punished and helping more if it is not costly for oneself; Fehr & Fischbacher, 2004; Forsythe et al., 1994) and Self-Reports of socio-emotional dispositions (Caprara et al., 2005; Davis, 1983; Henning & Six, 1977). Norm Motivated Behavior showed a negative association with $vuLP_R$. However, this association was weak and did not replicate across the two samples. Interindividual differences in Strategically Motivated Behavior were uncorrelated to differences in $vuLP_R$. Self-Reports of socio-emotional dispositions were also uncorrelated to $vuLP_R$ and only weakly related to Altruistically Motivated Behavior (also see Böckler et al., 2016). Our findings are in line with previous studies that have demonstrated associations between incidental HF-HRV

upregulation and altruistically motivated behavior (Miller et al., 2015; Barraza et al., 2015), whereas no such association has been reported for trait measures of socio-emotional dispositions based on self-report. Taken together, our data indicate that the propensity to upregulate HF-HRV is primarily related to social behaviors which are oriented towards the well-being of others (i.e., altruistic acts, cf., Batson, 2014), not other types of prosocial behavior which are not based in altruistic motivation.

These findings underline the importance of HF-HRV flexibility (Muhtadie et al., 2014) as a physiological correlate of regulated behavior (Butler, Wilhelm, & Gross, 2006; Duschek et al., 2009; Graziano & Derefinko, 2013; Oppenheimer et al., 2013; Segerstrom & Nes, 2007). More specifically, we corroborate earlier findings on a relationship between increases in HF-HRV and altruistic behavior (Barraza et al., 2015; Miller et al., 2015). Unlike earlier studies which employed a single task to index altruism, our measure relies on a validated multi-method factor score of altruistic behavior across a variety of tasks (Böckler et al., 2016). Importantly, we extend earlier work which had shown that HF-HRV increases *incidentally* when people exhibit altruistic feelings and behaviors (e.g., Barraza et al., 2015; Stellar et al., 2015), by demonstrating that individual differences in the ability to *deliberately* induce changes in HF-HRV predict individual differences in altruistic behavior. Such a link between the ability for deliberate physiological self-regulation and altruistic behavior suggests that the emotional and behavioral adjustments required to engage in altruistic action are at least partially grounded in consciously accessible processes that regulate parasympathetic functions.

We assume that both incidental and deliberate regulation of HF-HRV demonstrate the readiness of an individual to transition into an emotional-motivational state of caregiving. This is suggested by the vagus' role in the mammalian care- or affiliative system (Depue & Morrone-Strupinsky, 2005; Kemp et al., 2012; Norman et al., 2011; Panksepp, 2011; Tribollet et al., 1989), that is, the biological systems underlying caregiving behaviors toward offspring which are also implicated in generosity and altruistic acts toward strangers (Eisenberger & Cole, 2012; Feldman, Weller, Zagoory-Sharon, & Levine, 2007; Gordon et al., 2011; Kosfeld, Heinrichs, Zak, Fischbacher, & Fehr, 2005; Lee, Macbeth, Pagani, & Scott Young, 2009; Panksepp, 2011; Preston, 2013; Uvnäs-Moberg, 1998; Zak, Stanton, & Ahmadi, 2007). In the case of incidental upregulation, the activation of this motivational system is triggered by outer cues such as the sound of a crying baby (Gill & Calkins, 2003), a narrative about a severely ill child (Barraza et al., 2015) or visual depictions of human suffering (Klimecki, Leiberg, Lamm, & Singer, 2013; Klimecki, Leiberg, Ricard, & Singer, 2014; Stellar et al., 2015). In the case of the biofeedback task, interindividual differences in HF-HRV upregulation may be based on interindividual differences in the degree to which the vagus as part of this care/affiliative system can be called online by deliberate internal regulation. Our data suggest that the availability of vagal activation is a physiological characteristic of individuals which can be measured independently from situations that would typically elicit it.

Previous studies (Barraza et al., 2015; Miller et al., 2015) have attributed the incidental upregulations of HF-HRV that precede altruistic behaviors to the activation of the Social Engagement System (Porges, 2007). Our explanation in terms of the human care/affiliative system (Depue & Morrone-Strupinsky, 2005; Panksepp, 2011) is clearly commensurable with this account. Our account may however be a bit more specific in explaining why caring and altruistic behaviors are related to HF-HRV upregulation, whereas other prosocial behaviors (such as strategic or norm motivated giving) are not. Future theoretical and empirical work is warranted to more closely investigate the specific function that vagal upregulation subserves or indexes in the context of caregiving and altruistic behaviors. This should incorporate findings on

the role of HF-HRV upregulation in impulse control (Segerstrom & Nes, 2007) and emotion regulation (Butler et al., 2006), both of which may be implicated in altruistic action (Eisenberg, 2000; Kanfer, 1979).

Our study has several limitations and stimulates further questions. First, our analyses of relationships between employed strategy and biofeedback success did not provide evidence for certain strategies to elicit stronger vagal activity increases than others (see Supplementary material, Section D). However, the fact that participants used strategies only briefly and mixed many different strategies limits the scope of this finding. Future studies that assign participants to the use of a certain strategy and prompt them to stick with it for a longer duration could shed more light on the differential efficiency of self-regulation methods to induce parasympathetic activity. Second, we found the predictive validity of the BF task for altruistic behavior to be equally good across different subsets of participants that used the same strategy. This indicates that irrespective of strategy, those who are more successful in recruiting parasympathetic activity show more altruistic behavior. It is, however, well possible that restricting participants to certain regulatory strategies reduces the “error variance” induced by strategy choice and makes the task even more predictive of altruistic or other behaviors that are under parasympathetic control. Third, our parameter of voluntary regulation ($vuLP_R$) is statistically controlled for changes in HF-HRV that covary with changes in respiration rate, which is an important concern when using HF-HRV changes to estimate changes in vagal activity (Grossman & Taylor, 2007; Quintana & Heathers, 2014). We also find $vuLP_R$ to be correlated with reductions in heart rate, which further supports the assumption that our parameter actually indexes vagal regulation (Grossman & Taylor, 2007; Parker et al., 1984). However, it remains an indirect measure. Higher certainty about the contribution of vagal activity in the observed cardiac regulation would require more complex regimes of respiration control (Schulz, Ayala, Dahme, & Ritz, 2009) or pharmacological blockade of other (sympathetic) contributors to heart rate variability (Cacioppo et al., 1994). Fourth, we only investigated upregulation of LP. Although upregulation is clearly more relevant in the context of altruistic behavior, in other contexts (e.g., when coping with stress) the degree of LP downregulation may be more informative to predict adaptive behavior (Duschek et al., 2009; Graziano & Derefinko, 2013). It is an open question whether ‘upwards flexibility’ is related to ‘downwards flexibility’ – both when measured incidentally or in deliberate regulation paradigms as presented here – and whether they predict different psychological abilities. Fifth and finally, our study is correlational in nature and the two parameters of interest, $vuLP_R$ and AMB, were measured in separate experimental sessions. Thus, we cannot determine the temporal sequence of or causal relationship between increases in HF-HRV and altruistically motivated behavior in naturalistic settings. We assume that increases in vagal activity occur when an individual activates an emotional-motivational state related to care and affiliation (Depue & Morrone-Strupinsky, 2005; Kemp et al., 2012; Norman et al., 2011; Panksepp, 2011; Tribollet et al., 1989) and that these physiological adaptations play a role in preparing the organism for behaviors related to this motivation, i.e. altruistic behavior (e.g. Porges, 2003; Segerstrom & Nes, 2007; Butler et al., 2006; Eisenberg, 2000; Kanfer, 1979). Typically, we would expect activation of a motivational system and its respective physiological adaptations to precede corresponding behavior, but in some cases the reverse causality may also occur, such that an action increases the activity of a motivational system (e.g. Harbaugh et al., 2007; Huang, Galinsky, Gruenfeld, & Guillory, 2011; Reddish, Bulbulia, & Fischer, 2014). Whether increases in vagal activity are by themselves sufficient to increase the likelihood of altruistic behavior could be investigated in future studies by experimentally manip-

ulating states of vagal activity and then studying the effects on subsequent behavior.

To summarize, we have demonstrated that people are able to self-regulate LP, a short term estimate of HF-HRV, when provided with continuous feedback about LP. Furthermore, individual differences in the ability to up-regulate LP, indicative of parasympathetic self-regulation, are related to individual differences in altruistic behavior. This has important implications for the study of altruistic behavior and the field of cooperation and prosociality in general as it points to underlying physiological mechanisms of other-regarding behaviors. Because HF-HRV flexibility has been linked to many other psychological processes such as attention and emotion regulation (Butler et al., 2006; Duschek et al., 2009), the employed LP biofeedback procedure may prove to be a useful measure of regulatory abilities across a broad range of psychological study purposes. Due to its relatively fast assessment (5 min), LP biofeedback may be easily added as a complement to traditional baseline measures of heart rate variability in cross-sectional studies on the regulation of attention, emotion, or behavior. It may also be a valuable measure for longitudinal studies to both predict and index change, particularly in studies on loving-kindness and compassion meditation or self-compassion programs which have been found to affect affiliative feelings (Jazaieri et al., 2013; Klimecki et al., 2013) prosocial behavior (Leiberg et al., 2011; Weng et al., 2013) and parasympathetic function (Arch et al., 2014; Kemeny et al., 2012; Kok et al., 2013). Higher HF-HRV has also been linked to better physiological health, particularly lower rates of inflammation (De Couck, Maréchal, Moorthamers, Van Laethem, & Gidron, 2016; Frasure-Smith, Lespérance, Irwin, Talajic, & Pollock, 2009; Thayer, 2009) and cardiovascular problems (Kleiger, Miller, Bigger, & Moss, 1987; Thayer, Yamamoto, & Brosschot, 2010; Tsuji et al., 1996). The task may be useful in training programs for people at risk for such problems, or to recover the reduced HF-HRV in patients after cardiac infarct (Fei, Copie, Malik, & Camm, 1996). Investigating the dynamics by which people activate biological systems related to care-giving, such as self-induction of parasympathetic activity, could generate important insights that help in fostering individual health and building a more caring and cooperative society.

Acknowledgments

The ReSource Project in which this study was conducted is a collaborative effort by the Department of Social Neuroscience at the Max Planck Institute of Human Cognitive and Brain Science. We are thankful to all members of the department as well as countless outside collaborators who have supported us. We are particularly thankful to Astrid Ackermann, Christina Bochow, Matthias Bolz, and Sandra Zurborg for managing the study, to Hannes Niederhausen, Henrik Grunert, and Thorsten Kästner for their technical support, and to Sylvia Tydecks, Elisabeth Murzik, and Kerstin Träger for their help with recruitment and data collection. Tania Singer, as principal investigator, received funding for the ReSource Project from a) the European Research Council under the European Community's Seventh Framework Program (FP7/2007–2013/ERC Grant Agreement Number 205557), and b) from the Max Planck Society.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biopsycho.2016.07.004>.

References

Antelmi, I., De Paula, R. S., Shinzato, A. R., Peres, C. A., Mansur, A. J., & Grupi, C. J. (2004). Influence of age, gender, body mass index, and functional capacity on

- heart rate variability in a cohort of subjects without heart disease. *The American Journal of Cardiology*, 93(3), 381–385.
- Arch, J. J., Brown, K. W., Dean, D. J., Landy, L. N., Brown, K. D., & Laudenslager, M. L. (2014). Self-compassion training modulates alpha-amylase, heart rate variability, and subjective responses to social evaluative threat in women. *Psychoneuroendocrinology*, 42, 49–58. <http://dx.doi.org/10.1016/j.psyneuen.2013.12.018>
- Böckler, A., Tusche, A., & Singer, T. (2016). The structure of human prosociality: differentiating altruistically motivated, norm motivated, strategically motivated and self-reported prosocial behavior. *Social Psychological and Personality Science*, 1–12. <http://dx.doi.org/10.1177/1948550616639650>
- Barraza, J. A., Alexander, V., Beavin, L. E., Terris, E. T., & Zak, P. J. (2015). The heart of the story: peripheral physiology during narrative exposure predicts charitable giving. *Biological Psychology*, 105, 138–143. <http://dx.doi.org/10.1016/j.biopsycho.2015.01.008>
- Batson, C. D. (2014). *The altruism question: toward a social-psychological answer*. New York: Psychology Press.
- Bazhenova, O. V., Plonskaia, O., & Porges, S. W. (2001). Vagal reactivity and affective adjustments in infants during interacting challenges. *Child Development*, 72(5), 1314–1326.
- Beauchaine, T. P. (2001). Vagal tone, development, and Gray's motivational theory: toward an integrated model of autonomic nervous system functioning in psychopathology. *Development and Psychopathology*, 13(02), 183–214.
- Berg, J., Dickhaut, J., & McCabe, K. (1995). Trust, reciprocity, and social history. *Games and Economic Behavior*, 10(1), 122–142.
- Bernardi, L., Porta, C., Gabutti, A., Spicuzza, L., & Sleight, P. (2001). Modulatory effects of respiration. *Autonomic Neuroscience*, 90(1), 47–56.
- Berntson, G. G., Bigger, T., Eckberg, D. L., Grossman, P., Kaufmann, P., Malik, M., . . . & Van der Molen, M. (1997). Heart rate variability: origins methods and interpretative caveats. *Psychophysiology*, 34, 623–648.
- Bland, J. M., & Altman, D. G. (1986). Statistical methods for assessing agreement between two methods of clinical measurement. *The Lancet*, 1, 307–310.
- Bohnet, I., & Zeckhauser, R. (2004). Trust, risk and betrayal. *Journal of Economic Behavior & Organization*, 55(4), 467–484.
- Butler, E. A., Wilhelm, F. H., & Gross, J. J. (2006). Respiratory sinus arrhythmia, emotion, and emotion regulation during social interaction. *Psychophysiology*, 43(6), 612–622. <http://dx.doi.org/10.1111/j.1469-8986.2006.00467.x>
- Cacioppo, J. T., Berntson, G. G., Binkley, P. F., Quigley, K. S., Uchino, B. N., & Fieldstone, A. (1994). Autonomic cardiac control. II. Noninvasive indices and basal response as revealed by autonomic blockades. *Psychophysiology*, 31(6), 586–598. <http://dx.doi.org/10.1111/j.1469-8986.1994.tb02351.x>
- Camerer, C. (2003). *Behavioral game theory*. Princeton: Princeton University Press.
- Caprara, G. V., Steca, P., Zelli, A., & Capanna, C. (2005). A new scale for measuring adults' prosocialness. *European Journal of Psychological Assessment*, 21(2), 77–89.
- Charpak, S., Armstrong, W., Mühlenthaler, M., & Dreifuss, J.-J. (1984). Stimulatory action of oxytocin on neurones of the dorsal motor nucleus of the vagus nerve. *Brain Research*, 300(1), 83–89.
- Coleman, J. S. (1994). *Foundations of social theory*. Boston: Harvard University Press.
- Cowan, M. J., Kogan, H., Burr, R., Hendershot, S., & Buchanan, L. (1990). Power spectral analysis of heart rate variability after biofeedback training. *Journal of Electrocardiology*, 23, 85–94.
- Davis, M. H. (1983). Measuring individual differences in empathy: evidence for a multidimensional approach. *Journal of Personality and Social Psychology*, 44(1), 113.
- De Couck, M., Maréchal, R., Moorthamers, S., Van Laethem, J.-L., & Gidron, Y. (2016). Vagal nerve activity predicts overall survival in metastatic pancreatic cancer: mediated by inflammation. *Cancer Epidemiology*, 40, 47–51.
- Depue, R. A., & Morrone-Strupinsky, J. V. (2005). A neurobehavioral model of affiliative bonding: implications for conceptualizing a human trait of affiliation. *Behavioral and Brain Sciences*, 28(3), 313–395. <http://dx.doi.org/10.1017/s0140525x05000063>
- Dreifuss, J.-J., Raggenbass, M., Charpak, S., Dubois-Dauphin, M., & Tribollet, E. (1988). A role of central oxytocin in autonomic functions: its action in the motor nucleus of the vagus nerve. *Brain Research Bulletin*, 20(6), 765–770.
- Druschky, K., & Druschky, A. (2015). Mobile biofeedback of heart rate variability in patients with diabetic polyneuropathy: a preliminary study. *Clinical Physiology and Functional Imaging*, 35(5), 332–337.
- Duschek, S., Muckenthaler, M., Werner, N., & del Paso, G. A. (2009). Relationships between features of autonomic cardiovascular control and cognitive performance. *Biological Psychology*, 81(2), 110–117. <http://dx.doi.org/10.1016/j.biopsycho.2009.03.003>
- Dziembowska, I., Izdebski, P., Rasmus, A., Brudny, J., Grzelczak, M., & Cysewski, P. (2015). Effects of heart rate variability biofeedback on EEG alpha asymmetry and anxiety symptoms in male athletes: a pilot study. *Applied Psychophysiology and Biofeedback*, 1–10.
- Eisenberg, N. (2000). Emotion, regulation, and moral development. *Annual Review of Psychology*, 51(1), 665–697.
- Eisenberger, N. I., & Cole, S. W. (2012). Social neuroscience and health: neurophysiological mechanisms linking social ties with physical health. *Nature Neuroscience*, 15(5), 669–674. <http://dx.doi.org/10.1038/nn.3086>
- Fehr, E., & Fischbacher, U. (2004). Third-party punishment and social norms. *Evolution and Human Behavior*, 25(2), 63–87. [http://dx.doi.org/10.1016/S1090-5138\(04\)00005-4](http://dx.doi.org/10.1016/S1090-5138(04)00005-4)
- Fei, L., Copie, X., Malik, M., & Camm, A. J. (1996). Short- and long-term assessment of heart rate variability for risk stratification after acute myocardial infarction.

- The American Journal of Cardiology*, 77(9), 681–684. [http://dx.doi.org/10.1016/S0002-9149\(97\)89199-0](http://dx.doi.org/10.1016/S0002-9149(97)89199-0)
- Feldman, R., & Eidelman, A. I. (2003). Skin-to-skin contact (Kangaroo Care) accelerates autonomic and neurobehavioural maturation in preterm infants. *Developmental Medicine & Child Neurology*, 45(04), 274–281.
- Feldman, R., Weller, A., Zagoory-Sharon, O., & Levine, A. (2007). Evidence for a neuroendocrinological foundation of human affiliation. *Psychological Science*, 18(11), 965–970. <http://dx.doi.org/10.1111/j.1467-9280.2007.02010.x>
- Forsythe, R., Horowitz, J. L., Savin, N. E., & Sefton, M. (1994). Fairness in simple bargaining experiments. *Games and Economic Behavior*, 6(3), 347–369.
- Frasure-Smith, N., Lespérance, F., Irwin, M. R., Talajic, M., & Pollock, B. G. (2009). The relationships among heart rate variability, inflammatory markers and depression in coronary heart disease patients. *Brain, Behavior, and Immunity*, 23(8), 1140–1147.
- Gamer, M., & Büchel, C. (2012). Oxytocin specifically enhances valence-dependent parasympathetic responses. *Psychoneuroendocrinology*, 37(1), 87–93.
- Gill, K. L., & Calkins, S. D. (2003). Do aggressive/destructive toddlers lack concern for others? Behavioral and physiological indicators of empathic responding in 2-year-old children. *Development and Psychopathology*, 15, 55–71.
- Gordon, I., Martin, C., Feldman, R., & Leckman, J. F. (2011). Oxytocin and social motivation. *Developmental Cognitive Neuroscience*, 1(4), 471–493. <http://dx.doi.org/10.1016/j.dcn.2011.07.007>
- Graziano, P., & Derefinko, K. (2013). Cardiac vagal control and children's adaptive functioning: a meta-analysis. *Biological Psychology*, 94(1), 22–37. <http://dx.doi.org/10.1016/j.biopsycho.2013.04.011>
- Grossman, P., & Taylor, E. W. (2007). Toward understanding respiratory sinus arrhythmia: relations to cardiac vagal tone, evolution and biobehavioral functions. *Biological Psychology*, 74(2), 263–285. <http://dx.doi.org/10.1016/j.biopsycho.2005.11.014>
- Grossman, P., Beek, J. V., & Wientjes, C. (1990). A comparison of three quantification methods for estimation of respiratory sinus arrhythmia. *Psychophysiology*, 27(6), 702–714.
- Grossman, P. (1983). Respiration, stress, and cardiovascular function. *Psychophysiology*, 20(3), 284–300.
- Harbaugh, W. T., Mayr, U., & Burghart, D. R. (2007). Neural responses to taxation and voluntary giving reveal motives for charitable donations. *Science*, 316(5831), 1622–1625.
- Hare, T. A., Camerer, C. F., Knopfle, D. T., O'Doherty, J. P., & Rangel, A. (2010). Value computations in ventral medial prefrontal cortex during charitable decision making incorporate input from regions involved in social cognition. *The Journal of Neuroscience*, 30(2), 583–590.
- Hastings, P. D., Nuselovici, J. N., Utendale, W. T., Coutya, J., McShane, K. E., & Sullivan, C. (2008). Applying the polyvagal theory to children's emotion regulation: social context, socialization, and adjustment. *Biological Psychology*, 79(3), 299–306. <http://dx.doi.org/10.1016/j.biopsycho.2008.07.005>
- Henning, H.-J., & Six, B. (1977). Konstruktion einer Machiavellismus-Skala. *Zeitschrift für Sozialpsychologie*, 8, 185–198.
- Huang, L., Galinsky, A. D., Gruenfeld, D. H., & Guillory, L. E. (2011). Powerful postures versus powerful roles which is the proximate correlate of thought and behavior? *Psychological Science*, 22(1), 95–102. <http://dx.doi.org/10.1177/0956797610391912>
- Hutchinson, J. S. (2012). *The heart of elevation: investigating the physiological and neural mechanisms underlying moral elevation*. Oregon State University (Doctor).
- Jazaieri, H., Jinpa, G. T., McGonigal, K., Rosenberg, E. L., Finkelstein, J., Simon-Thomas, E., ... & Goldin, P. R. (2013). Enhancing compassion: a randomized controlled trial of a compassion cultivation training program. *Journal of Happiness Studies*, 14(4), 1113–1126.
- Jones, B., & Rachlin, H. (2006). Social discounting. *Psychological Science*, 17(4), 283–286.
- Kanfer, F. H. (1979). Personal control, social control, and altruism: can society survive the age of individualism? *American Psychologist*, 34(3), 231–239. <http://dx.doi.org/10.1037/0003-066X.34.3.231>
- Karavidas, M. K., Lehrer, P. M., Vaschillo, E., Vaschillo, B., Marin, H., Buyske, S., ... & Hassett, A. (2007). Preliminary results of an open label study of heart rate variability biofeedback for the treatment of major depression. *Applied Psychophysiology and Biofeedback*, 32(1), 19–30.
- Kaufmann, T., Sütterlin, S., Schulz, S., & Vögele, C. (2011). ARTiiFACT: a tool for heart rate artifact processing and heart rate variability analysis. *Behavior Research Methods*, 43(4), 1161–1170. <http://dx.doi.org/10.3758/s13428-011-0107-7>
- Kemeny, M. E., Foltz, C., Cavanagh, J. F., Cullen, M., Giese-Davis, J., Jennings, P., ... & Wallace, B. A. (2012). Contemplative/emotion training reduces negative emotional behavior and promotes prosocial responses. *Emotion*, 12(2), 338.
- Kemp, A. H., Quintana, D. S., Kuhert, R. L., Griffiths, K., Hickie, I. B., & Guastella, A. J. (2012). Oxytocin increases heart rate variability in humans at rest: implications for social approach-related motivation and capacity for social engagement. *Public Library of Science*, 7(8), e44014. <http://dx.doi.org/10.1371/journal.pone.0044014>
- Kleiger, R. E., Miller, J. P., Bigger, J. T., Jr., & Moss, A. J. (1987). Decreased heart rate variability and its association with increased mortality after acute myocardial infarction. *The American Journal of Cardiology*, 59(4), 256–262. [http://dx.doi.org/10.1016/0002-9149\(87\)90795-8](http://dx.doi.org/10.1016/0002-9149(87)90795-8)
- Klimecki, O. M., Leiberg, S., Lamm, C., & Singer, T. (2013). Functional neural plasticity and associated changes in positive affect after compassion training. *Cerebral Cortex*, 23(7), 1552–1561. <http://dx.doi.org/10.1093/cercor/bhs142>
- Klimecki, O. M., Leiberg, S., Ricard, M., & Singer, T. (2014). Differential pattern of functional brain plasticity after compassion and empathy training. *Social Cognitive and Affective Neuroscience*, 9(6), 873–879. <http://dx.doi.org/10.1093/scan/nst060>
- Koenig, J., Jarczok, M. N., Warth, M., Ellis, R. J., Bach, C., Hillecke, T. K., et al. (2014). Body mass index is related to autonomic nervous system activity as measured by heart rate variability—a replication using short term measurements. *The Journal of Nutrition, Health & Aging*, 18(3), 300–302.
- Kogan, A., Oveis, C., Carr, E. W., Gruber, J., Mauss, I. B., Shallcross, A., ... & Keltner, D. (2014). Vagal activity is quadratically related to prosocial traits, prosocial emotions, and observer perceptions of prosociality. *Journal of Personality and Social Psychology*, 107(6), 1051–1063. <http://dx.doi.org/10.1037/a0037509>
- Kok, B. E., Coffey, K. A., Cohn, M. A., Catalino, L. I., Vacharkulksemsuk, T., Algeo, S. B., & Fredrickson, B. L. (2013). How positive emotions build physical health: perceived positive social connections account for the upward spiral between positive emotions and vagal tone. *Psychological Science*, 24(7), 1123–1132. <http://dx.doi.org/10.1177/0956797612470827>
- Kosfeld, M., Heinrichs, M., Zak, P. J., Fischbacher, U., & Fehr, E. (2005). Oxytocin increases trust in humans. *Nature*, 435(7042), 673–676.
- Kreibitz, S. D. (2010). Autonomic nervous system activity in emotion: a review. *Biological Psychology*, 84(3), 394–421. <http://dx.doi.org/10.1016/j.biopsycho.2010.03.010>
- Lee, H.-J., Macbeth, A. H., Pagani, J. H., & Scott Young, W. (2009). Oxytocin: the great facilitator of life. *Progress in Neurobiology*, 88(2), 127–151. <http://dx.doi.org/10.1016/j.pneurobio.2009.04.001>
- Lehrer, P. M., Carr, R. E., Smetankine, A., Vaschillo, E., Peper, E., Porges, S., ... & Hochron, S. (1997). Respiratory sinus arrhythmia versus neck/trapezius EMG and incentive spirometry biofeedback for asthma: a pilot study. *Applied Psychophysiology and Biofeedback*, 22(2), 95–109.
- Lehrer, P. M., Vaschillo, E., Vaschillo, B., Lu, S.-E., Eckberg, D. L., Edelberg, R., & Tahvanainen, K. U. (2003). Heart rate variability biofeedback increases baroreflex gain and peak expiratory flow. *Psychosomatic Medicine*, 65(5), 796–805.
- Leiberg, S., Klimecki, O., & Singer, T. (2011). Short-term compassion training increases prosocial behavior in a newly developed prosocial game. *Public Library of Science*, 6(3), e17798. <http://dx.doi.org/10.1371/journal.pone.0017798>
- Luque-Casado, A., Perales, J. C., Cárdenas, D., & Sanabria, D. (2015). Heart rate variability and cognitive processing: the autonomic response to task demands. *Biological Psychology*, <http://dx.doi.org/10.1016/j.biopsycho.2015.11.013>
- McCall, C., & Singer, T. (2012). The animal and human neuroendocrinology of social cognition, motivation and behavior. *Nature Neuroscience*, 15(5), 681–688.
- Miller, J. G., Choccol, C., Nuselovici, J. N., Utendale, W. T., Simard, M., & Hastings, P. D. (2013). Children's dynamic RSA change during anger and its relations with parenting, temperament, and control of aggression. *Biological Psychology*, 92(2), 417–425. <http://dx.doi.org/10.1016/j.biopsycho.2012.12.005>
- Miller, J. G., Kahle, S., & Hastings, P. D. (2015). Roots and benefits of costly giving: children who are more altruistic have greater autonomic flexibility and less family wealth. *Psychological Science*, 26(7), 1038–1045. <http://dx.doi.org/10.1177/0956797615578476>
- Muhtadie, L., Koslov, K., Akinola, M., & Mendes, W. B. (2014). Vagal flexibility: a physiological predictor of social sensitivity. *Journal of Personality and Social Psychology*, <http://dx.doi.org/10.1037/pspp0000016>
- Musser, E. D., Backs, R. W., Schmitt, C. F., Ablow, J. C., Measelle, J. R., & Nigg, J. T. (2011). Emotion regulation via the autonomic nervous system in children with attention-deficit/hyperactivity disorder (ADHD). *Journal of Abnormal Child Psychology*, 39(6), 841–852. <http://dx.doi.org/10.1007/s10802-011-9499-1>
- Nolan, R. P., Kamath, M. V., Floras, J. S., Stanley, J., Pang, C., Picton, P., et al. (2005). Heart rate variability biofeedback as a behavioral neurocardiac intervention to enhance vagal heart rate control. *American Heart Journal*, 149(6), 1137. [e1137-1137. e1137.](http://dx.doi.org/10.1177/0956797615578476)
- Norman, G. J., Cacioppo, J. T., Morris, J. S., Malarkey, W. B., Berntson, G. G., & Devries, A. C. (2011). Oxytocin increases autonomic cardiac control: moderation by loneliness. *Biological Psychology*, 86(3), 174–180. <http://dx.doi.org/10.1016/j.biopsycho.2010.11.006>
- Oppenheimer, J. E., Measelle, J. R., Laurent, H. K., & Ablow, J. C. (2013). Mothers' vagal regulation during the Still-Face Paradigm: normative reactivity and impact of depression symptoms. *Infant Behavior and Development*, 36(2), 255–267. <http://dx.doi.org/10.1016/j.infbeh.2013.01.003>
- Oveis, C. S. (2002). *Vagal tone, positive emotion, and pro-sociality*. Berkeley: University of California, Berkeley [Doctoral Dissertation].
- Pal, G., & Velkumary, S. (2004). Effect of short-term practice of breathing exercises on autonomic functions in normal human volunteers. *The Indian Journal of Medical Research*, 120(2), 115–121.
- Panksepp, J. (2006). The core emotional systems of the mammalian brain: the fundamental substrates of human emotions. In J. Corrigan, H. Payne, & H. Wilkinson (Eds.), *About a Body: working with the embodied mind in psychotherapy*. Routledge: Hove, UK & NYC.
- Panksepp, J. (2011). Cross-species affective neuroscience decoding of the primal affective experiences of humans and related animals. *Public Library of Science*, 6(9), e21236. <http://dx.doi.org/10.1371/journal.pone.0021236>
- Parker, P., Celler, B., Potter, E. K., & McCloskey, D. (1984). Vagal stimulation and cardiac slowing. *Journal of the Autonomic Nervous System*, 11(2), 226–231.
- Porges, S. W. (2003). Social engagement and attachment. *Annals of the New York Academy of Sciences*, 1008(1), 31–47.

- Porges, S. W. (2007). The polyvagal perspective. *Biological Psychology*, 74(2), 116–143. <http://dx.doi.org/10.1016/j.biopsycho.2006.06.009>
- Preston, S. D. (2013). The origins of altruism in offspring care. *Psychological Bulletin*, 139(6), 1305.
- Quintana, D. S., & Heathers, J. A. (2014). Considerations in the assessment of heart rate variability in biobehavioral research. *Frontiers in Psychology*, 5, 805. <http://dx.doi.org/10.3389/fpsyg.2014.00805>
- Reddish, P., Bulbulia, J., & Fischer, R. (2014). Does synchrony promote generalized prosociality? *Religion, Brain & Behavior*, 4(1), 3–19.
- Schulz, S. M., Ayala, E., Dahme, B., & Ritz, T. (2009). A MATLAB toolbox for correcting within-individual effects of respiration rate and tidal volume on respiratory sinus arrhythmia during variable breathing. *Behavioral Research Methods*, 41(4), 1121–1126. <http://dx.doi.org/10.3758/BRM.41.4.1121>
- Seegerstrom, S. C., & Nes, L. S. (2007). Heart rate variability reflects self-regulatory strength, effort, and fatigue. *Psychological Science*, 18(3), 275–281. <http://dx.doi.org/10.1111/j.1467-9280.2007.01888.x>
- Shahrestani, S., Stewart, E. M., Quintana, D. S., Hickie, I. B., & Guastella, A. J. (2014). Heart rate variability during social interactions in children with and without psychopathology: a meta-analysis. *Journal of Child Psychology and Psychiatry*, 55(9), 981–989. <http://dx.doi.org/10.1111/jcpp.12226>
- Singer T., Kok B.E., Bornemann B., Zurborg S., Bolz M., Bochow C.A. (in press). The ReSource Project: background, design, samples, and measurements. Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany.
- Stellar, J. E., Cohen, A. B., Oveis, C., & Keltner, D. (2015). Affective and physiological responses to the suffering of others: compassion and vagal activity. *Journal of Personality and Social Psychology*, 108(4), 572–585.
- Task-Force. (1996). Heart rate variability—standards of measurement, physiological interpretation, and clinical use. Task Force of the European Society of Cardiology and the North American Society of Pacing and Electrophysiology. *Circulation*, 93, 1043–1065.
- Thayer, J. F., & Lane, R. D. (2009). Claude Bernard and the heart-brain connection: further elaboration of a model of neurovisceral integration. *Neuroscience and Biobehavioral Reviews*, 33(2), 81–88. <http://dx.doi.org/10.1016/j.neubiorev.2008.08.004>
- Thayer, J. F., Yamamoto, S. S., & Brosschot, J. F. (2010). The relationship of autonomic imbalance, heart rate variability and cardiovascular disease risk factors. *International Journal of Cardiology*, 141(2), 122–131. <http://dx.doi.org/10.1016/j.ijcard.2009.09.543>
- Thayer, J. F. (2009). Vagal tone and the inflammatory reflex. *Cleveland Clinic Journal of Medicine*, 76(Suppl. 2), 23–26.
- Tribollet, E., Charpak, S., Schmidt, A., Dubois-Dauphin, M., & Dreifuss, J. (1989). Appearance and transient expression of oxytocin receptors in fetal, infant, and peripubertal rat brain studied by autoradiography and electrophysiology. *The Journal of Neuroscience*, 9(5), 1764–1773.
- Tsuji, H., Larson, M. G., Venditti, F. J., Manders, E. S., Evans, J. C., Feldman, C. L., et al. (1996). Impact of reduced heart rate variability on risk for cardiac events: the framingham heart study. *Circulation*, 94(11), 2850–2855. <http://dx.doi.org/10.1161/01.cir.94.11.2850>
- Uvnäs-Moberg, K. (1994). Role of efferent and afferent vagal nerve activity during reproduction: integrating function of oxytocin on metabolism and behaviour. *Psychoneuroendocrinology*, 19(5), 687–695.
- Uvnäs-Moberg, K. (1998). Oxytocin may mediate the benefits of positive social interaction and emotions. *Psychoneuroendocrinology*, 23(8), 819–835. [http://dx.doi.org/10.1016/s0306-4530\(98\)00056-0](http://dx.doi.org/10.1016/s0306-4530(98)00056-0)
- Van Lange, P. A. (1999). The pursuit of joint outcomes and equality in outcomes: an integrative model of social value orientation. *Journal of Personality and Social Psychology*, 77(2), 337.
- Vaschillo, E. G., Vaschillo, B., & Lehrer, P. M. (2006). Characteristics of resonance in heart rate variability stimulated by biofeedback. *Applied Psychophysiology and Biofeedback*, 31(2), 129–142. <http://dx.doi.org/10.1007/s10484-006-9009-3>
- Weng, H. Y., Fox, A. S., Shackman, A. J., Stodola, D. E., Caldwell, J. Z. K., Olson, M. C., . . . & Davidson, R. J. (2013). Compassion training alters altruism and neural responses to suffering. *Psychological Science*, 24(7), 1171–1180. <http://dx.doi.org/10.1177/0956797612469537>
- Wheat, A. L., & Larkin, K. T. (2010). Biofeedback of heart rate variability and related physiology: a critical review. *Applied Psychophysiology and Biofeedback*, 35(3), 229–242.
- Zak, P. J., Stanton, A. A., & Ahmadi, S. (2007). Oxytocin increases generosity in humans. *Public Library of Science*, 2(11), e1128.