

Individual differences in cardiac vagal tone are associated with differential neural responses to facial expressions at different spatial frequencies: An ERP and sLORETA study

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Abstract A previous study has shown that greater cardiac vagal tone, reflecting effective self-regulatory capacity, was correlated with superior visual discrimination of fearful faces at high spatial frequency Park et al. (Biological Psychology 90:171–178, 2012b). The present study investigated whether individual differences in cardiac vagal tone (indexed by heart rate variability) were associated with different event-related brain potentials (ERPs) in response to fearful and neutral faces. Thirty-six healthy participants discriminated the *emotion* of fearful and neutral faces at broad, high, and low spatial frequencies, while ERPs were recorded. Participants with *low* resting heart rate variability—characterized by poor functioning of regulatory systems—exhibited significantly greater N200 activity in response to fearful faces at low spatial frequency and greater LPP responses to neutral faces at high spatial frequency. Source analyses—estimated by standardized low-resolution brain electromagnetic tomography (sLORETA)—tended to show that participants with low resting heart rate variability exhibited increased source activity in visual areas, such as the cuneus and the middle occipital gyrus, as compared with participants with high resting heart

rate variability. The hyperactive neural activity associated with low cardiac vagal tone may account for hypervigilant response patterns and emotional dysregulation, which heightens the risk of developing physical and emotional problems.

Keyword Cardiac vagal tone · ERPs · Spatial frequency

Facial expressions convey important social information, and the ability to accurately recognize them is crucial for making adaptive emotional responses (Ashley, Vuilleumier, & Swick, 2004). Previous research explored the relationship between the ability to efficiently process emotional expressions of face stimuli and successful self-regulation (Park, Van Bavel, Egan, Vasey, & Thayer, 2012a). Greater cardiac vagal tone, which indicates superior cognitive and emotional self-regulation, was associated with better visual discrimination of fearful faces at high spatial frequency (HSF; Park et al., 2012a). However, little is known about neural activity associated with individual differences in cardiac vagal tone for fearful and neutral facial expressions. The present study used high-density electroencephalography (EEG) to test the hypothesis that individual differences in cardiac vagal tone would be associated with differential neural responses to fearful and neutral faces at different spatial frequency ranges.

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The neurovisceral integration model and heart rate variability

The heart is innervated by both sympathetic and vagal nerves. Heart rate (HR) variability (HRV)—which refers to the differences in beat-to-beat alterations in HR—allows separating the relative contribution of sympathetic and vagal activity to the heart (Berntson et al., 1997; Task Force of the European Society of Cardiology and the North American

Society of Pacing and Electrophysiology, 1996; Thayer, Hansen, Saus-Rose, & Johnsen, 2009; Thayer & Lane, 2000). According to the neurovisceral integration model (Thayer & Lane, 2000), robust regulation of the heart via the vagal nerve (i.e., high vagally mediated HRV) is associated with effective functioning of neural networks mediating self-regulation—the ability to effectively and flexibly respond to various situational demands (Ellis & Thayer, 2010; Park et al., 2012a; Park, Van Bavel, Vasey, & Thayer, 2012b; Thayer et al., 2009). Several studies employing neuroimaging or pharmacological techniques have shown that high vagally mediated HRV (henceforth referred to as *high* resting HRV) was associated with effective prefrontal regulation of subcortical structures, which results in functional self-regulatory systems (Ahern et al., 2001; Friedman, 2007; Thayer et al., 2009; Thayer & Lane, 2000). People with high resting HRV demonstrated faster and more accurate responses on executive cognitive tasks (Hansen, Johnsen, & Thayer, 2003; Thayer et al., 2009), as well as having more adaptive physiological responses to emotional stimuli (Ruiz-Padial, Sollers, Vila, & Thayer, 2003; Thayer, Friedman, Borkovec, Johnsen, & Molina, 2000).

In contrast, low vagally mediated HRV (henceforth referred to as *low* resting HRV) was associated with poor functioning of regulatory systems, which may stem from a lack of prefrontal control of subcortical activity (Thayer et al., 2009; Thayer & Lane, 2000). People with low resting HRV showed dysfunctional emotional responses, such as the failure to recognize safety signals and to habituate to novel, neutral stimuli (Friedman, 2007; Thayer et al., 2000; Thayer et al., 2009). In one study, people with low resting HRV made undifferentiated responses to fearful and neutral stimuli, producing enhanced startle responses to neutral stimuli as if they were emotionally negative (Ruiz-Padial et al., 2003). A recent study revealed that people with low resting HRV had difficulty discriminating and inhibiting fearful faces at HSF (Park et al., 2012a; Park et al., 2012b).

The processing of faces at different spatial frequencies

Spatial frequency is defined as the energy distribution in the scale specified as the number of cycles per degree of visual angle and/or the number of cycles per image (Morrison & Schyns, 2001; Park et al., 2012a). Previous research has indicated that face stimuli at high and low spatial frequencies (LSFs) are conveyed and processed via distinctive visual pathways (Livingstone & Hubel, 1988; Merigan & Maunsell, 1993; Nieuwenhuis, Jepma, Fors, & Olivers, 2008; Vuilleumier, Armony, Driver, & Dolan, 2003). LSF information is primarily processed via the *magnocellular* visual channels that rapidly process depth, motion, and

low-contrast black-and-white information (Merigan & Maunsell, 1993; Nieuwenhuis, Jepma, Fors, & Olivers, 2008; Vuilleumier, Armony, Driver, & Dolan, 2003). LSF fearful faces, in particular, are processed via the phylogenetically old *retinotectal* pathway that conveys information from the retina through the superior colliculus and pulvinar nucleus of the thalamus to the amygdala (Livingstone & Hubel, 1988; Merigan & Maunsell, 1993; Nieuwenhuis et al., 2008; Vuilleumier et al., 2003). Previous research indicated that LSF fearful faces were processed quickly (i.e., 120 ms after stimulus onset) and elicited greater amygdala activity, as compared with LSF neutral faces (Vuilleumier, 2005; Vuilleumier et al., 2003). HSF information is primarily processed via the *parvocellular* pathway, which conveys information slowly but with high resolution (Merigan & Maunsell, 1993; Vuilleumier et al., 2003). The encoding of HSF faces was completed in the visual cortex around 170–200 ms after stimulus onset (Goffaux, Hault, Michel, Vuong, & Rossion, 2005; Goffaux & Rossion, 2006; Vuilleumier, 2005). HSF fearful faces, in particular, elicited greater activity in ventral visual cortical areas, including the bilateral fusiform and the inferior temporal-occipital cortex (Goffaux et al., 2005; Goffaux & Rossion, 2006; Vuilleumier et al., 2003).

There are several ERP studies that investigated the processing of fearful and neutral faces at different spatial frequencies (Holmes, Winston, & Eimer, 2005; Pourtois, Dan, Grandjean, Sander, & Vuilleumier, 2005; Vlamings, Goffaux, & Kemner, 2009). LSF fearful faces, relative to LSF neutral faces, elicited greater activities of early ERP components, such as P100 and N170 (Pourtois et al., 2005; Vlamings et al., 2009). The P100 component—positive deflections that occur in posterior areas around 50–165 ms after stimulus onset—is considered to reflect the early visual processing (Carretié, Hinojosa, López-Martín, & Tapia, 2007; Pourtois et al., 2005). The N170 activity—peaking at occipito-temporal regions around 170 ms after stimulus onset—has been closely linked with face processing (Heisz, Watter, & Shedden, 2006; Jacques & Rossion, 2006). A number of studies have reported that face stimuli elicited greater N170 activity than did nonface objects or scrambled faces (Heisz et al., 2006; Jacques & Rossion, 2006). Although there has been much debate on whether activity of the N170 component is modulated by emotion (Heisz et al., 2006; Jacques & Rossion, 2006), previous research suggested that LSF fearful faces elicited greater N170 amplitudes than did LSF neutral faces (Vlamings et al., 2009). In the present research, we examined ERP responses and estimated neural sources associated with individual differences in cardiac vagal tone on visual perception of fearful and neutral faces at unfiltered broad spatial frequencies (BSFs), HSFs, and LSFs.

The present study

The goal of the present research was to examine whether individual differences in cardiac vagal tone were associated with distinctive neural responses to fearful and neutral faces processed by different neurofunctional pathways (Goffaux et al., 2005). With superior temporal resolution, ERPs would be useful for studying neural activities associated with individual differences in HRV on visual perception of fearful and neutral faces at different spatial frequencies. A recent behavioral study suggested that higher HRV was correlated with superior performance discriminating the emotion of fearful faces at HSF (Park et al., 2012a). However, given the link between low HRV and amygdala hyperactivity (Ruiz-Padial et al., 2003; Thayer & Siegle, 2002), individual differences in HRV should be associated with differential neural responses to LSF fearful faces. Furthermore, hyper-vigilant response patterns associated with low HRV would be more evident with neurophysiological measures. We hypothesized that participants with low resting HRV would show enhanced P100 and N170 activities in response to LSF fearful faces, as compared with participants with high resting HRV. Also, participants with low resting HRV who were characterized by making hypervigilant responses might show greater P100 and N170 activities to LSF neutral faces, as compared with participants with high resting HRV (Ruiz-Padial et al., 2003; Thayer et al., 2000).

We also examined activity of the N200 component to directly compare the self-regulatory capacity of people with high and low resting HRV. The N200 component—peaking at frontal-midline regions around 200 to 350 ms after stimulus onset—is associated with emotional and behavioral self-regulation (e.g., Liddell, Williams, Rathjen, Shevrin, & Gordon, 2006; Williams et al., 2004). Converging evidence suggested that reduced N200 activity indicates highly functional regulatory systems (Dennis & Chen, 2007; Lamm & Lewis, 2010; Liddell et al., 2006; Williams et al., 2004). In contrast, greater N200 activity is associated with impaired regulatory systems and reflects the depletion of cognitive resources necessary to inhibit affectively significant stimuli (Dennis & Chen, 2007). For example, greater N200 amplitudes were elicited by emotional facial expressions (e.g., fearful, sad, and angry) than by neutral facial expressions (Campanella et al., 2002; Williams et al., 2004). Furthermore, people with heightened trait anxiety showed greater N200 amplitudes than did people with low trait anxiety (Dennis & Chen, 2007). Therefore, we hypothesized that participants with low resting HRV would show greater N200 activity evoked by LSF and/or HSF fearful faces, as compared with participants with high resting HRV, possibly reflecting poor self-regulatory capacity in response to affectively significant stimuli. Furthermore, people with low resting HRV might show greater N200 activity in response

to LSF and/or HSF neutral faces, as compared with participants with high resting HRV, possibly reflecting a hypervigilant response to neutral stimuli.

The slower processing of HSF information would be better captured in later ERP components, such as the late positive potential (LPP). The LPP component is a positive deflection that occurs at centro-parietal sites between 300 and 800 ms after stimulus onset (Schupp et al., 2000). The LPP component is considered to reflect greater attentional allocation and the facilitated perceptual processing of affectively significant stimuli during later stages of stimulus processing (Schupp et al., 2000; Schupp, Junghöfer, Weike, & Hamm, 2003). We hypothesized that participants with low resting HRV would show enhanced LPP activity to HSF fearful faces, as compared with participants with high resting HRV. Also, people with low resting HRV who are associated with slower habituation to neutral stimuli would exhibit greater LPP activity to HSF neutral faces, as compared with participants with high resting HRV (Thayer et al., 2000).

We did not expect that individual differences in HRV would be associated with significantly different neural responses to unfiltered BSF faces. People with severe psychiatric disorders, such as schizophrenia, were characterized by impaired neural activity in response to BSF faces (Couture, Penn, & Roberts, 2006; Lee, Kim, Kim, & Bae, 2010; Turetsky et al., 2007). We did not expect that level of neural impairment in a normal population.

Furthermore, we employed standardized low-resolution electromagnetic tomography (sLORETA) to localize potential underlying sources of ERP components. sLORETA provided three-dimensional images of brain electrical activity using a discrete linear solution for the EEG inverse problem (Pascual-Marqui, 2002; Pascual-Marqui et al., 1999).¹ We hypothesized that participants with low resting HRV would exhibit greater source activities of early ERP components to LSF fearful faces in areas associated with visual perception. Although neuroimaging studies linked LSF fearful faces with subcortical neural mechanisms, no subcortical sources should be observed in the early processing periods, because ERPs are not sensitive to deep, transient sources (Batty & Taylor, 2003). Previous source localization studies localized the N200's source to the dorsal anterior cingulate cortex (van Veen & Carter, 2002) and the ventral prefrontal cortex (Pliszka, Liotti, & Woldorff, 2000), regions that played critical roles in emotional and attentional self-regulation (e.g., Lewis, Lamm, Segalowitz, Stieben, & Zelazo, 2006; van Veen & Carter, 2002). Thus, differential N200 activity associated with individual differences in HRV

¹ However, it is theoretically impossible to find a unique solution for the inverse problem to the generators of the ERP activities. Therefore, the results from sLORETA have to be interpreted with caution.

would be traced to differential source activity in the ventral prefrontal cortex and/or the dorsal anterior cingulate cortex. Also, enhanced LPP activity to HSF fearful and/or HSF neutral faces in participants with low resting HRV would be associated with greater source activity in occipital areas (Hajcak, MacNamara, & Olivet, 2010; Sabatinelli, Lang, Keil, & Bradley, 2007).

Method

Participants

Thirty-seven healthy volunteers participated in the task. They were asked to have avoided smoking, alcohol, caffeinated beverages, and drug use for 24 h before the experiment. All participants had normal or corrected-to-normal vision (20/20 visual acuity). People with a history of vision disorders or dysfunctions, neurological or psychiatric disorders, cardiovascular disorders, or medical conditions, such as diabetes, were excluded from this experiment. One participant was identified to be left-handed. Data from 1 participant were excluded due to excessive EEG artifacts, which yielded 36 participants. The mean age of the 19 women was 25.47 ($SD = 3.20$) years, and of the men was 24.94 ($SD = 3.72$) years. Following previous research (Hansen et al., 2003; Park et al., 2012b; Thayer et al., 2000), participants were divided into two groups, high or low HRV, on the basis of the median split of root mean square successive difference (rMSSD) in milliseconds during baseline (median = 33.8; Hansen et al., 2003; Task Force, 1996; Thayer & Lane, 2000).² All participants signed a written informed consent approved by the Institutional Review Board of Inje University Ilsan Paik Hospital prior to their participation in the study.

Stimuli

We selected 104 faces (52 with fearful expressions and 52 with neutral facial expressions; 26 females and 26 males with each expression) from the Korea University Facial Expression Collection (KUFEC; Lee, Lee, Lee, Choi, & Kim, 2006). All faces were converted to grayscale. Contrast and brightness were adjusted to maintain consistency across different faces. As can be seen in Fig. 1, each face was enclosed in a circular frame using Adobe PhotoShop CS3 software (Adobe System, San Jose, CA) to exclude nonfacial features (e.g., hair). In order to produce the HSF and LSF stimuli, the original BSF pictures were

filtered through a high-pass cutoff of >24 cycles/image for the HSF stimuli and a low-pass cutoff of <8 cycles/image for the LSF stimuli. Average grayscale values for the BSF, HSF, and LSF stimuli were 128, 126, and 126, respectively. For the neutral and fearful face categories, average grayscale values were 126 and 127, respectively, on a 256 gray-level scale. These average grayscale values did not significantly differ across spatial frequency, $F(2, 309) = 1.49$, $p = .23$, $\eta_p^2 = .01$, or emotional expression, $F(1, 310) = 0.61$, $p = .44$, $\eta_p^2 = .01$. Each stimulus measured 6° horizontally and 6° vertically against a light gray background at a viewing distance of 100 cm and was displayed on a 21 in. CRT monitor with a resolution of $1,024 \times 768$ pixels.

Experimental design and procedure

All participants were tested individually in a dimly lit room. Participants were fitted with the chest band. After confirming that interbeat intervals (IBIs) were being recorded with the watch, the experimenter moved the watch (which displays beat-to-beat changes in HR) away from the participant's gaze. A stopwatch was used to time successive 5-min intervals, during which the participant sat and rested quietly in a partially sound-isolated room. After the 5-min baseline period, the chest band was removed, and EEG electrodes were attached.

Participants then performed the emotion discrimination task during EEG recording. Stimuli were presented in three separate blocks of different spatial frequencies (BSF, HSF, LSF), and blocks were presented in counterbalanced order. The task was to discriminate the emotion of faces, either fearful or neutral. In each block, participants were presented with 12 practice trials, followed by 300 experimental trials of fearful and neutral face stimuli presented in random order. After each block, participants were allowed a short break. Therefore, each face was randomly presented three times at different spatial frequency ranges. Each trial began with a fixation point for 200 ms, followed by the blank screen for 500 ms. The display with a face picture was presented for 500 ms with an inter-stimulus interval that varied randomly between 950 and 1,050 ms. Participants were told that they would be presented with a series of pictures of unfamiliar faces, and their task was to identify the emotion of the faces by pressing the "1" key for fearful and the "2" key for neutral on a number pad with their dominant hand. They were also instructed to respond as quickly and accurately as possible. Participants received "no response" feedback when they failed to respond within 3,000 ms. After the task, participants completed the Korean version of the Spielberger State-Trait Anxiety Inventory (STAI; Spielberger & Diaz-Guerrero, 1983).

² Several previous studies have used a similar approach to compare people with high and low HRV (Hansen et al., 2003; Park et al., 2012b; Ruiz-Padial et al., 2003; Thayer et al., 2000).

Fig. 1 Example stimuli: Normal broad spatial frequency fearful and neutral faces (left column), high spatial frequency faces (middle column), and low spatial frequency faces (right column)



Physiological recording and analysis

HRV data A Polar RS800cx HR monitor (Polar Electro, Finland; www.polar.fi) was used to record electrocardiographic activity. The RS800cx is a portable HR monitor tool that is sampled at 1000 Hz, which yields time and frequency domain estimates of HRV comparable to those obtained via standard 3- or 12-electrode ECG setups (e.g., Nunan et al., 2009; Vanderlei, Silva, Pastre, Azevedo, & Godoy, 2008). In the RS800cx, participants wear an elastic band around the chest, just below the sternum. A sensor attached to the elastic band detects R spikes and transmits an infrared signal to the watch, which then records the time of each R spike. Each IBI time series (in milliseconds) within the baseline period was written in a single text file and analyzed using the Kubios HRV analysis package 2.0 (<http://basmig.uku.fi/biosignal>), through which time and frequency domain indices of the heart period power spectrum were computed. Time domain indices include estimates of rMSSD and HR in beats per minute.

In the frequency domain methods, the high-frequency power (HFP) of HRV, which ranges from 0.15 to 0.4 Hz, is exclusively mediated by the vagus nerves (Park et al., 2012b; Task Force, 1996; Thayer & Friedman, 2004). The low-frequency band, which ranges from 0.04 to 0.15, is considered to be influenced by both sympathetic and vagal cardiac activity (Berntson et al., 1997; Park et al., 2012b; Task Force, 1996; Thayer & Friedman, 2004). High-frequency HRV power and rMSSD are widely used to quantify vagal cardiac activity (Task Force, 1996). For spectral analyses, we used autoregressive estimates following the Task Force of the European Society of Cardiology and the North American Society of Pacing Electrophysiology (1996) guidelines. We used rMSSD as a primary index

of the cardiac vagal tone in this study (Hansen et al., 2003).

EEG recording and data analysis EEG was recorded and processed using a NeuroScan SynAmps amplifier (Compumedics USA, El Paso, TX). Horizontal and vertical electrooculograms were recorded using four bipolar electrodes placed on the outer canthus of each eye and above and below the right eye. The scalp EEG was recorded from 62 Ag–AgCl electrodes mounted in a Quick Cap (extended 10–20 system). The impedance of EEG electrodes was kept below 5 k Ω , and EEG data were recorded with a 0.1- to 100-Hz band-pass filter at a sampling rate of 1000 Hz. The references were both mastoids. EEG data were initially processed using Scan 4.5. Before beginning the further analysis, EEG data were rereferenced offline to an average reference. Data were first corrected for eye blink artifacts using standard blink correction algorithms (Semlitsch, Anderer, Schuster, & Presslich, 1986). Trials were rejected if they included significant physiological artifacts (amplitude exceeding ± 70 μ V) at any site over all 62 electrode sites. After artifact removal, baseline correction was conducted by subtracting the mean of 300 ms before stimulus onset from the post-stimulus data for each trial. Data were band-pass filtered at 0.1–30 Hz with a steepness of 24 dB/octave and then epoched to 200 ms prestimulus and 800 ms poststimulus. ERP measures were evaluated on correct trials only. The percentage of rejected trials was 27%.

Electrode sites and time windows for each component were selected on the basis of previous literature that investigated these components and inspection of grand-average waveforms and individual participant waveforms. Each ERP was measured as mean activity, and the respective time windows of each component were

the following: P1, 70–140 ms; N170, 140–200 ms; N200, 200–300 ms; LPP, 300–600 ms. The P1 and the N170 components were examined at occipito-temporal electrodes (P7, PO7, P8, and PO8; Vlamings et al., 2009). The N200 and LPP components were obtained from midline electrodes (Fz, Cz, and Pz; Liddell et al., 2006; Williams et al., 2004). We computed separate averages for all combinations of spatial frequency (broad, high, low), HRV level (high, low), and emotional expression (fearful, neutral). Separate analyses were run for each component. Mean activity of each ERP component were subjected to an electrode site \times HRV level (high, low) \times spatial frequency (broad, high, low) \times emotion (fearful, neutral) mixed factorial analysis of variance (ANOVA). All variables were within subjects, except for HRV level.

sLORETA analysis We conducted source analyses across the time range where the ERP components were measured using sLORETA. We used the sLORETA software (<http://www.uzh.ch/keyinst/loreta.htm>), which is freely available, to calculate the source activation of the ERP waveform for each participant (Pascual-Marqui, 2002). In sLORETA, the intracerebral volume was divided into 6,239 voxels at 5-mm spatial resolution. The sLORETA computed the standardized current density at each of the 6,239 voxels in a realistic head model under the assumption that activations of neighboring neural structures would be similar to target sources (Fallgatter, Bartsch, Zielasek, & Herrmann, 2003; Fuchs, Kastner, Wagner, Hawes, & Ebersole, 2002; Mazziotta et al., 2001; Scharmüller, Leutgeb, Schäfer, Köchel, & Schienle, 2011). The source activation of the ERP waveform was calculated for each participant, using a statistical nonparametric mapping method that was provided by the sLORETA toolbox. Voxel-by-voxel independent *t*-tests of log ratio of average data were conducted. Statistical significance was assessed nonparametrically with a randomization test ($n = 5,000$) that corrected for multiple comparisons.

Results

Group characteristics

Demographic and psychological characteristics of the two groups are presented in Table 1. The two groups were significantly different in rMSSD, $t(34) = -4.95$, $p < .01$, $d = 1.91$. However, the two groups did not differ in mean HR, $t(34) = -1.47$, $p = .15$, $d = 0.57$, the trait version of the STAI (STAI-trait) scores, $t(34) = 0.21$, $p = .85$, $d = 0.08$, or the state version of the STAI (STAI-state) scores, $t(34) = 0.43$, $p = .67$, $d = 0.17$.

Table 1 Demographic and psychological characteristics of participants with high and low resting HRV (with standard deviations and the number of participants in parentheses)

Variable	HRV level	
	High ($N = 20$)	Low ($N = 16$)
HRV (rMSSD)*	56.5 (26.7)	23.1 (4.2)
Mean heart rate (HR)	73.4 (16.9)	63.2 (24.7)
Gender ratio (male: female)	9:11	8:8
Age (mean years)	24.3 (2.6)	26.4 (4.0)
STAI-T	36.5 (9.4)	38.0 (11.8)
STAI-S	38.6 (7.3)	39.1 (9.0)

Note. HRV, heart rate variability; STAI-T, trait version of the State-Trait Anxiety Inventory; STAI-S, state version of the State-Trait Anxiety Inventory

* $p < .05$

Behavioral data

Reaction times (RTs) of less than 150 ms (anticipatory responding) or more than 1,200 ms (delaying responding) were considered outliers (12% of the data). All analyses on RTs excluded incorrect trials and outliers.³ Accuracy data were subjected to a 2 (HRV level: high, low) \times 3 (spatial frequency: broad, high, low) \times 2 (emotion: fearful, neutral) mixed factorial ANOVA.⁴ All variables were within subjects, except for HRV level. There was a main effect of spatial frequency, $F(2, 68) = 34.40$, $p < .01$, $\eta_p^2 = .42$. Participants were more accurate for BSF ($M = 92\%$, $SD = 10.50$) and HSF ($M = 92\%$, $SD = 9.78$) faces than for LSF faces ($M = 87\%$, $SD = 11.52$). Replicating previous research (Park et al., 2012a), participants were more accurate for neutral faces ($M = 96\%$, $SD = 4.20$) than for fearful faces ($M = 85\%$, $SD = 19.62$), $F(1, 34) = 11.35$, $p < .01$, $\eta_p^2 = .25$. An interaction between spatial frequency and emotion was significant, $F(2, 68) = 4.27$, $p < .02$, $\eta_p^2 = .11$ (see Table 2). To decompose the interaction, we examined effects of emotion for BSF, HSF, and LSF, separately. There were significant main effects of emotion, $F(1, 35) = 7.21$, $p < .02$, $\eta_p^2 = .17$ for BSF; $F(1, 35) = 8.84$, $p < .01$, $\eta_p^2 = .20$ for HSF; and $F(1, 35) = 15.71$, $p < .01$, $\eta_p^2 = .31$ for LSF. Participants were significantly more accurate for neutral faces at BSF ($M = 97\%$, $SD = 4.26$), HSF ($M = 97\%$, $SD = 3.60$), and LSF ($M = 94\%$, $SD = 8.16$), as compared with fearful faces at BSF ($M =$

³ There were a relatively large number of incorrect responses because some participants made subjective responses to each face, instead of making objective discrimination of the emotion of each face. That is, they chose fearful if they felt fearful in response to a stimulus. We ensured that participants made objective judgments afterward.

⁴ There was no significant three-way interaction in RTs ($p > .85$; see Table 2). On the basis of a suggestion from a previous study (see Park et al., 2012a), we focused on accuracy data.

Table 2 Means and standard deviations of percentages of response accuracy and reaction times (in milliseconds), as a function of types of spatial frequency and emotion in the emotion discrimination task (with standard deviations in parentheses)

			Mean
BSF	Fearful	Accuracy	87.6 (19.8)
		RTs	596.6 (131.8)
	Neutral	Accuracy	96.6 (4.2)
		RTs	572.5 (103.5)
HSF	Fearful	Accuracy	87.7 (18.8)
		RTs	588.8 (116.3)
	Neutral	Accuracy	97.1 (3.3)
		RTs	552.7 (101.9)
LSF	Fearful	Accuracy	80.6 (20.2)
		RTs	573.9 (113.2)
	Neutral	Accuracy	94.3 (8.0)
		RTs	557.7 (100.5)

88%, $SD = 20.22$), HSF ($M = 88\%$, $SD = 19.20$), and LSF ($M = 81\%$, $SD = 20.52$).

Although a previous study (Park et al., 2012a) showed that higher HRV was correlated with better task performance on discriminating HSF fearful faces, there was no interaction with HRV in the present study ($p > .97$). The difference may be potentially due to the longer duration at which stimuli were presented in the present study (i.e., 500 ms), as compared with the previous study (i.e., 200 ms; Park et al., 2012a). Participants with low resting HRV might have taken advantage of the longer presentation duration and performed better in the present study. Furthermore, previous studies recommended that the same identity should not be presented in both BSF and filtered images to a given participant, because the BSF image would influence the ratings of the filtered images (Neta & Whalen, 2010; Vuilleumier et al., 2003). However, in the present study, we presented the same identity in BSF and filtered (HSF and LSF) images due to the insufficient number of stimuli, which might explain the different result.

ERP data

P100 component at occipito-temporal locations (70–140 ms): ANOVA We hypothesized that (1) LSF fearful faces would elicit greater P100 activity than would LSF neutral faces and (2) participants with low resting HRV would show greater P100 activity to LSF fearful and LSF neutral faces than would participants with high resting HRV. There was a significant main effect of electrode site, $F(3, 102) = 6.02$, $p < .01$, $\eta_p^2 = .15$, with greater activity at PO7 ($M = 3.09$, $SD = 2.40$) or at PO8 ($M = 3.04$, $SD = 3.06$) than at P7 ($M = 1.72$, $SD = 1.92$) or at P8 ($M = 1.94$, $SD = 2.64$). A main effect of spatial

frequency was also significant, $F(2, 68) = 17.29$, $p < .01$, $\eta_p^2 = .34$, with greater activities for HSF ($M = 3.03$, $SD = 2.16$) than for BSF ($M = 1.84$, $SD = 2.16$) or LSF ($M = 2.47$, $SD = 2.16$). These main effects were qualified by an interaction between electrode site, spatial frequency, and emotion, $F(6, 204) = 2.25$, $p = .04$, $\eta_p^2 = .06$. However, when a Greenhouse–Geisser correction was inspected, the four-way interaction dropped to nonsignificant ($p = .08$). Thus, contrary to our predictions, LSF fearful faces did not elicit greater P100 activity, as compared with LSF neutral faces. Also, participants with low resting HRV did not show greater P100 activity to LSF faces than did participants with high resting HRV.

N170 component at occipito-temporal locations (140–200 ms): ANOVA We hypothesized that (1) LSF fearful faces would elicit greater N170 activity than would LSF neutral faces and (2) participants with low resting HRV would show greater N170 activity to LSF fearful and LSF neutral faces than would participants with high resting HRV. There was a main effect of electrode site, $F(3, 102) = 5.93$, $p < .01$, $\eta_p^2 = .15$. Also, a main effect of spatial frequency was significant, $F(2, 68) = 20.46$, $p < .01$, $\eta_p^2 = .38$, such that N170 activity was greater for LSF ($M = -.66$, $SD = .48$) than for HSF ($M = 0.20$, $SD = 0.50$) or BSF ($M = 0.37$, $SD = 0.50$). A main effect of emotion was significant, $F(1, 34) = 6.97$, $p < .02$, $\eta_p^2 = .17$, such that N170 activity was greater for fearful faces ($M = -0.32$, $SD = 2.76$) than for neutral faces ($M = 0.25$, $SD = 2.76$). These main effects were qualified by a three-way interaction between electrode site, spatial frequency, and emotion, $F(6, 204) = 2.44$, $p < .03$, $\eta_p^2 = .07$. To break down the interaction, we examined the data for different electrode sites separately. There was a significant two-way interaction between spatial frequency and emotion at P8, $F(2, 70) = 5.17$, $p < .01$, $\eta_p^2 = .13$, and at PO8, $F(2, 70) = 4.95$, $p = .01$, $\eta_p^2 = .12$.

To investigate whether LSF fearful faces elicited greater N170 activity than did LSF neutral faces, we examined the data for BSF, HSF, and LSF ranges separately. Significant main effects of emotion were observed for LSF at P8, $F(1, 35) = 12.89$, $p < .01$, $\eta_p^2 = .27$, and at PO8, $F(1, 35) = 12.68$, $p < .01$, $\eta_p^2 = .27$. Replicating a previous finding (Vlamings et al., 2009), LSF fearful faces elicited greater N170 activity at P8 ($M = -2.45$, $SD = 4.32$) and at PO8 ($M = -0.59$, $SD = 3.90$), as compared with LSF neutral faces at P8 ($M = -1.07$, $SD = 3.90$) and at PO8 ($M = .56$, $SD = 3.42$) (see Fig. 2 for P8 and PO8). Also, significant main effects of emotion were observed for BSF at P8, $F(1, 35) = 7.31$, $p < .02$, $\eta_p^2 = .17$, and at PO8, $F(1, 35) = 5.76$, $p < .03$, $\eta_p^2 = .14$. BSF fearful faces elicited greater N170 activity at P8 ($M = -0.78$, $SD = 2.16$) and at PO8 ($M = 0.38$, $SD = 3.18$), as compared with BSF neutral faces at P8 ($M = 0.04$, $SD = 3.24$) and at PO8 ($M = 1.21$, $SD = 3.12$). There was a marginally significant four-way interaction between electrode site, spatial frequency, emotion, and HRV, F

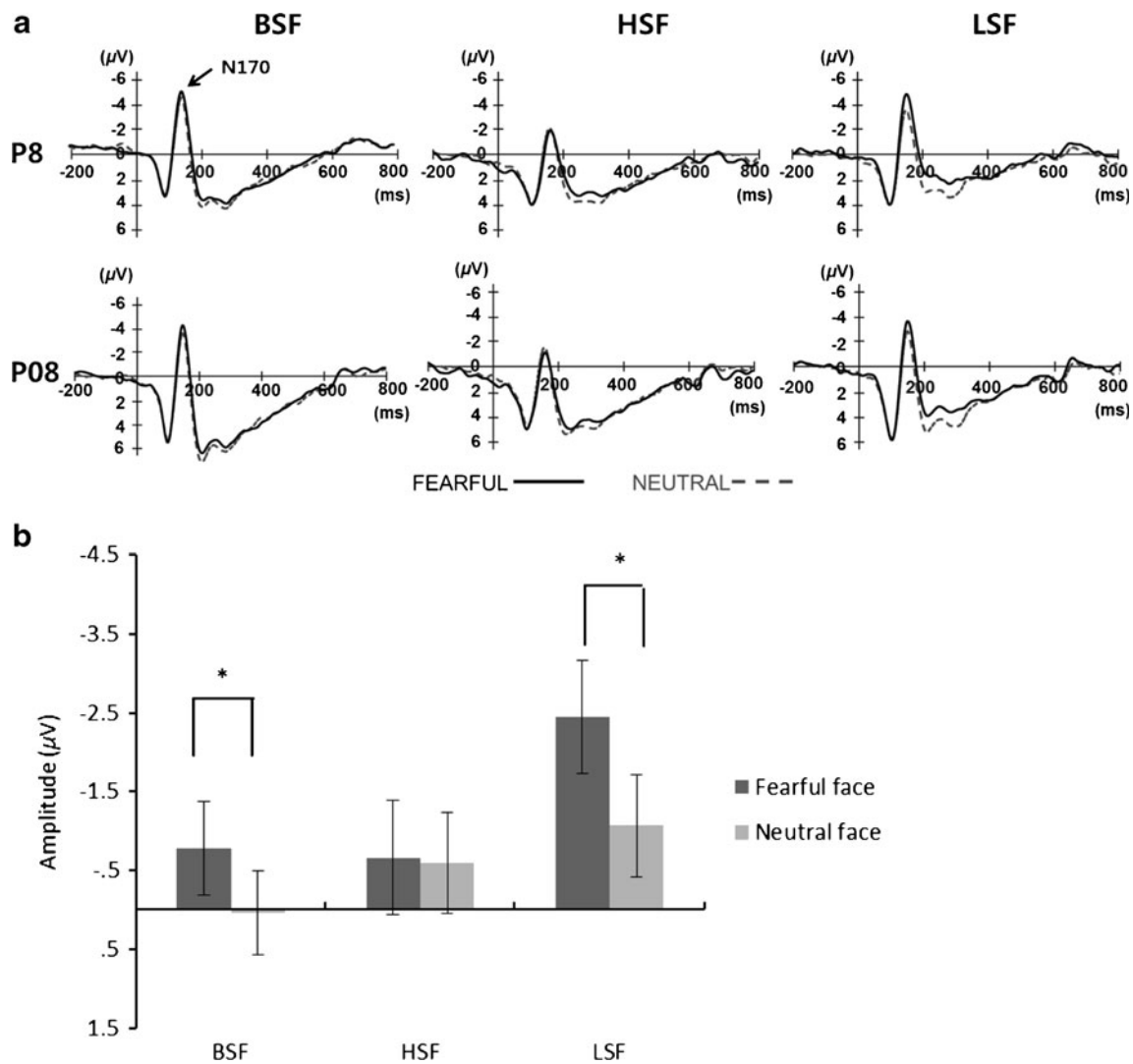


Fig. 2 a Grand-averaged ERP waveforms of the N170 component elicited at the electrodes P8 and PO8 in response to fearful (solid lines) or neutral (dashed lines) faces, shown separately for broadband (BSF), high spatial frequency (HSF), and low spatial frequency (LSF) stimuli.

b Mean activity and standard errors of the N170 at P8 as a function of spatial frequency and emotion. BSF and LSF fearful faces elicited greater N170 activity at P8 than did BSF and LSF neutral faces

(6, 204) = 2.05, $p = .06$, $\eta_p^2 = .06$. When Greenhouse–Geisser correction was inspected, the four-way interaction dropped to nonsignificant ($p = .08$). Thus, contrary to our prediction, HRV was not associated with N170 activity. To sum up, consistent with our prediction, greater N170 activity was observed in response to LSF fearful faces, as compared with LSF neutral faces. Although we did not expect it, there was greater N170 activity elicited in response to BSF fearful faces, as compared with BSF neutral faces. However, contrary to our prediction, participants with low resting HRV did not show greater N170 activity in response to LSF faces, as compared with participants with high resting HRV.

N200 component at central-frontal locations (200–300 ms): ANOVA We hypothesized that participants with low resting

HRV would show greater N200 activity to fearful and neutral faces at HSFs and LSFs, as compared with participants with high resting HRV. There were significant main effects of electrode site, $F(2, 68) = 34.10$, $p < .01$, $\eta_p^2 = .50$, spatial frequency, $F(2, 68) = 12.62$, $p < .01$, $\eta_p^2 = .27$, and emotion, $F(1, 34) = 7.13$, $p < .01$, $\eta_p^2 = .17$. These main effects were qualified by electrode site \times spatial frequency, $F(4, 136) = 5.76$, $p < .01$, $\eta_p^2 = .15$, and electrode site \times emotion, $F(2, 68) = 5.44$, $p < .01$, $\eta_p^2 = .14$, interactions. More important, there was a significant three-way interaction between HRV level, spatial frequency, and emotion, $F(2, 68) = 7.87$, $p < .01$, $\eta_p^2 = .19$, which was qualified by a four-way interaction between electrode site, HRV level, spatial frequency, and emotion, $F(4, 136) = 2.78$, $p < .03$, $\eta_p^2 = .08$ (with the Greenhouse–Geisser correction, $p = .06$). When each electrode was examined

separately, the three-way interaction between HRV level, spatial frequency, and emotion emerged at Fz, $F(2, 68) = 5.52, p < .01, \eta_p^2 = .14$, and at Cz, $F(2, 68) = 8.64, p < .01, \eta_p^2 = .20$, but not at Pz ($p = .86$).

To directly examine the hypothesis that participants with low resting HRV would show greater N200 activity for HSF and LSF faces than would participants with high resting HRV, we examined the data for BSF, HSF, and LSF ranges separately. At BSF and HSF ranges, two-way mixed ANOVAs yielded no significant main effect or interaction in all three electrode sites. However, at LSF, a significant interaction between HRV level and emotion emerged at Fz, $F(1, 34) = 5.01, p < .04, \eta_p^2 = .13$, and at Cz, $F(1, 34) = 6.87, p < .02, \eta_p^2 = .17$ (see Fig. 3). As was expected, planned comparisons indicated that participants with low resting HRV showed significantly increased N200 activity, as compared with participants with high resting HRV, at Cz in response to LSF fearful faces, $F(1, 34) = 8.00, p < .01, d = 0.98$ (see Fig. 4). However, contrary to our predictions, participants with low resting HRV did not show greater N200 activity to HSF fearful, HSF neutral, or LSF neutral faces, as compared with participants with high resting HRV.

N200 component: regression analyses We also reexamined the result using regressions informed by the ANOVAs above. Findings from the ANOVAs suggested that the interaction between HRV and N200 activity was maximal at electrode Cz. To examine HRV as a continuous variable, we conducted the regression analysis in which HRV was the predictor and N200 activity in response to LSF fearful faces at Cz was the dependent variable (Dennis & Chen, 2007). The regression analysis showed that rMSSD significantly predicted N200 activity at Cz in response to LSF fearful faces, $R^2 = .34, F(1, 34) = 4.50, p < .05, B = .04, \beta = .34$ (see Fig. 5).⁵ As HRV decreased, N200 activity for LSF fearful faces increased.

LPP component at central-frontal locations (300–600 ms): ANOVA We hypothesized that low HRV participants would show greater LPP activity to HSF fearful and/or HSF neutral faces, as compared with high HRV participants. There was a significant main effect of electrode site, $F(2, 68) = 52.73, p < .01, \eta_p^2 = .61$. Also, an interaction between spatial frequency and HRV level was significant, $F(2, 68) = 6.06, p < .01, \eta_p^2 = .15$. The interaction was qualified by a three-way interaction between HRV level, spatial frequency, and emotion, $F(2, 68) = 5.50, p < .01, \eta_p^2 = .14$, and a four-way interaction between electrode site, HRV level, spatial

frequency, and emotion, $F(4, 136) = 3.87, p < .01, \eta_p^2 = .10$ (with the Greenhouse–Geisser correction, $p < .02$). When each electrode was examined separately, the three-way interaction between HRV level, spatial frequency, and emotion emerged at Fz, $F(2, 68) = 5.42, p < .01, \eta_p^2 = .14$, and at Cz, $F(2, 68) = 7.60, p < .01, \eta_p^2 = .16$, but not at Pz ($ps > .54$). This is consistent with previous research showing that greater LPP activity was observed in a central electrode site (e.g., Cz) when participants were asked to identify the emotion of stimuli (Hajcak, Moser, & Simons, 2006).

To examine the hypothesis that participants with low resting HRV would be associated with greater LPP activity in response to HSF faces, as compared with participants with high resting HRV, we examined the data for BSFs, HSFs, and LSFs separately at Fz and at Cz. At Cz, two-way mixed ANOVAs yielded no significant main effect or interaction for BSF and LSF ($ps > .09$). However, there was a significant interaction between HRV level and emotion for HSF at Cz, $F(1, 34) = 6.25, p < .02, \eta_p^2 = .16$. Participants with low resting HRV showed greater LPP activity for HSF neutral faces than did participants with high resting HRV, $t(34) = -2.59, p < .02, d = 0.89$ (see Fig. 6). At Fz, two-way mixed ANOVAs yielded no significant main effect or interaction for BSF and HSF ($ps > .14$). There was a significant interaction between HRV level and emotion for LSF at Fz, $F(1, 34) = 7.46, p = .01, \eta_p^2 = .18$. However, further analyses showed that there was no significant difference between participants with high and low resting HRV ($ps > .13$). Therefore, the result partially supported our prediction, such that participants with low resting HRV showed greater LPP activity to HSF neutral faces, but not to HSF fearful faces, as compared with participants with high resting HRV.

LPP component: regression analyses We reexamined the result obtained by the ANOVAs using regressions. To examine HRV as a continuous variable, we conducted the regression analysis in which HRV was the predictor and LPP activity in response to HSF neutral faces at Cz was the dependent variable. The regression analyses showed that rMSSD significantly predicted LPP activity at Cz in response to HSF neutral faces, $R^2 = .45, F(1, 34) = 8.77, p < .01, B = .03, \beta = .45$.⁶ As HRV decreased, LPP activity for HSF neutral faces increased (see Fig. 7).

⁵ In addition, we analyzed N200 activity using a regression analysis on log-transformed HFP, another measure of vagally mediated HRV. The regression analyses showed that log-transformed HSF significantly predicted N200 activity at Cz in response to LSF fearful faces, $R^2 = .41, F(1, 34) = 6.80, p < .05, B = 1.05, \beta = .41$, which was consistent with the result from rMSSD.

⁶ We also analyzed LPP activity using a regression analysis on log-transformed HFP. The regression analyses showed that log-transformed HSF significantly predicted LPP activity at Cz in response to HSF neutral faces, $R^2 = .43, F(1, 34) = 7.81, p < .01, B = .70, \beta = .43$, which was consistent with the result from rMSSD.

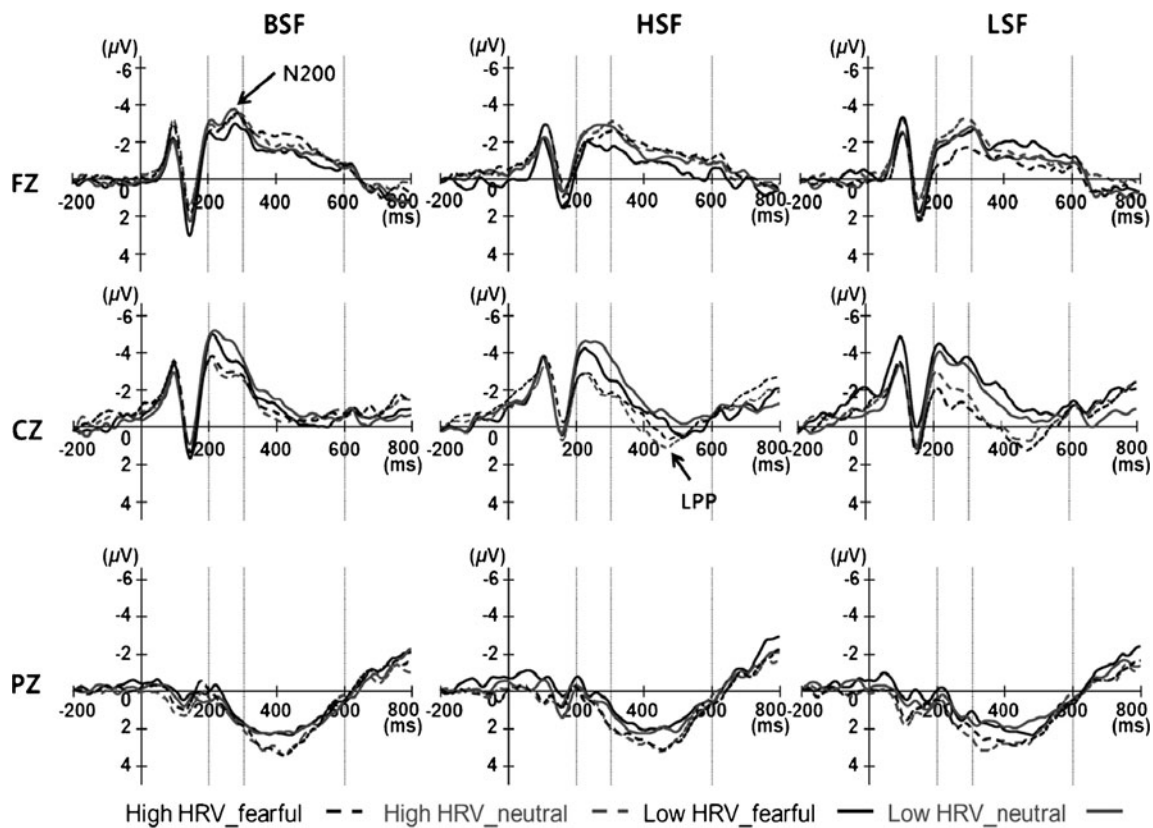


Fig. 3 Grand-averaged ERP waveforms of the N200 and LPP components elicited at electrodes Fz, Cz, and Pz for high (solid lines) versus low (dashed lines) resting HRV groups in response to fearful or neutral

faces, shown separately for broadband (BSF), high spatial frequency (HSF), and low spatial frequency (LSF) stimuli

sLORETA results As compared with participants with high resting HRV, participants with low resting HRV showed greater P100 source activity for LSF fearful faces in areas associated with visual perception, such as the middle occipital gyrus (BA 18, 19) and the cuneus (BA 17), and for HSF fearful faces in the cuneus (BA 17; see Table 3 and Fig. 8). In addition, as compared with participants with high resting HRV,

participants with low resting HRV showed significantly greater N170 source activity for LSF fearful faces in the cuneus (BA 6). Furthermore, as compared with participants with high resting HRV, participants with low resting HRV showed greater N200 source activity for BSF, HSF, and LSF neutral faces and LSF fearful faces in the middle occipital gyrus (BA 18, 19; $p < .05$; see Table 3 and Fig. 9).

Fig. 4 Mean activity of N200 and standard errors at Cz as a function of HRV level, spatial frequency, and emotion. Participants with low resting HRV showed significantly greater N200 activity in response to LSF fearful faces than did participants with high resting HRV

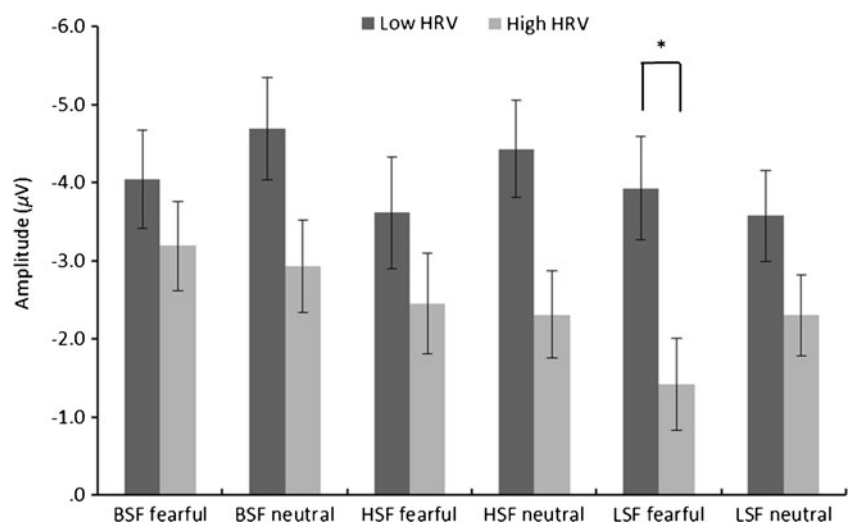
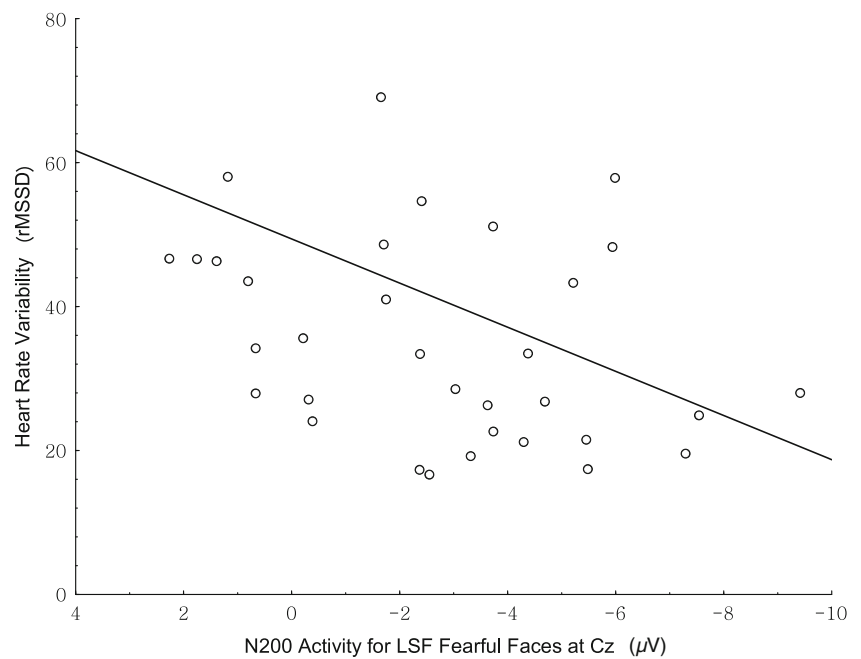


Fig. 5 A scatterplot indicating the negative correlation between HRV (*y*-axis) and N200 activity in response to LSF fearful faces at Cz (*x*-axis). $r = .34, p < .05$



Discussion

The present research shows that individual differences in resting HRV, an index of autonomic, cognitive, and emotional self-regulation, are associated with differential neural responses to fearful and neutral faces at different spatial frequencies. Contrary to our prediction, participants with low resting HRV did not show enhanced P100 activity but showed heightened P100 source activities for LSF and HSF fearful faces in areas associated with visual processing, such as the middle occipital gyrus and the cuneus. Consistent with previous studies, BSF and LSF fearful faces evoked

greater N170 activity, as compared with BSF and LSF neutral faces, respectively. Although participants with low resting HRV did not show increased N170 activity, they showed increased N170 source activity in the cuneus for LSF fearful faces. As was predicted, participants with low resting HRV showed enhanced N200 activity in response to LSF fearful faces, which was confirmed using the regression analysis. Participants with low resting HRV showed greater N200 source activities for BSF, HSF, and LSF neutral faces and LSF fearful faces in the middle occipital areas. In addition, participants with low resting HRV showed increased LPP activity in response to HSF neutral faces,

Fig. 6 Mean activity of LPP and standard errors at Cz as a function of HRV level, spatial frequency, and emotion. Participants with low resting HRV showed significantly greater LPP activity in response to HSF neutral faces than did participants with high resting HRV

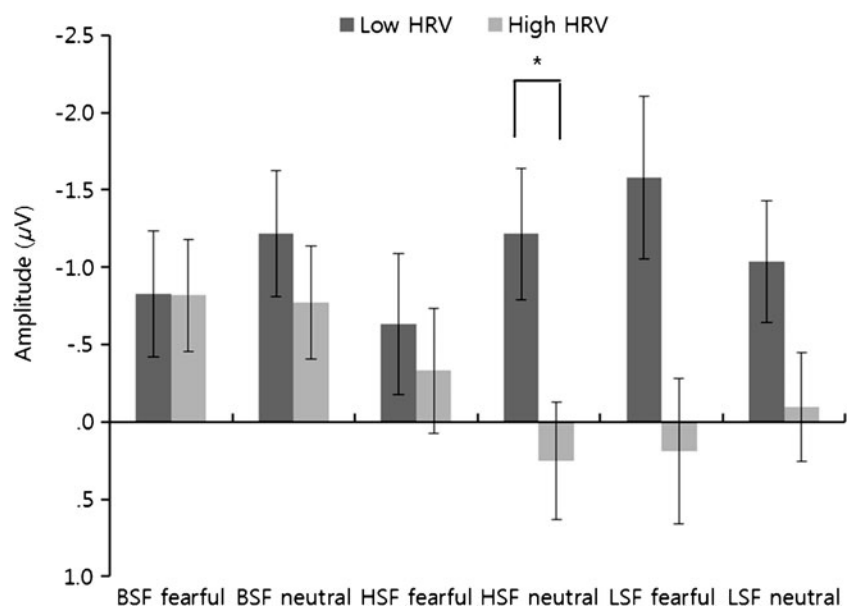
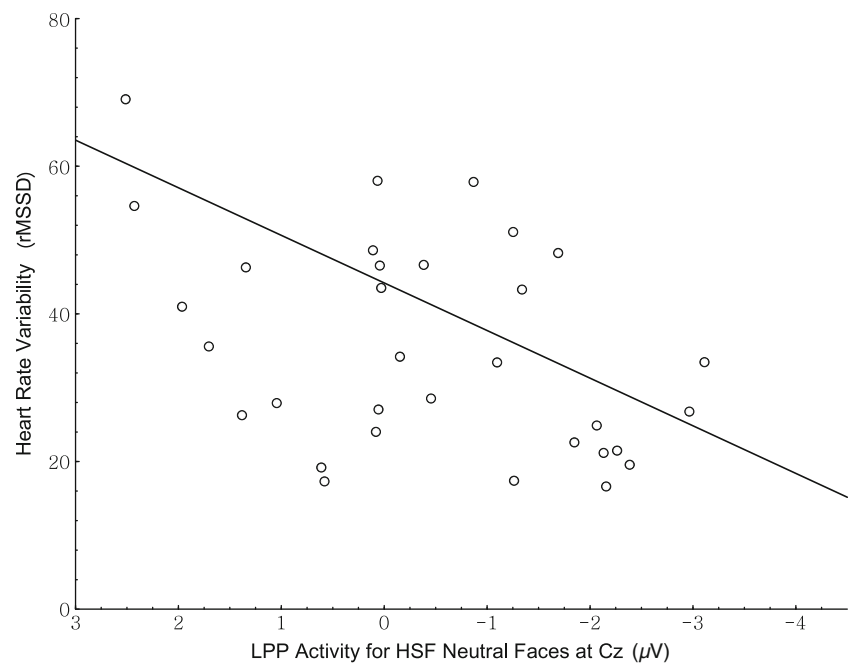


Fig. 7 A scatterplot indicating the negative correlation between HRV (y -axis) and LPP activity in response to HSF neutral faces at Cz (x -axis). $r = .34$, $p < .05$



which was confirmed using the regression analysis. Contrary to our prediction, HRV was not associated with LPP source activity.

Although previous studies reported that LSF fearful faces elicited enhanced P100 responses (Pourtois et al., 2005; Vlamings et al., 2009), the present study did not replicate the effect. However, Holmes et al. (2005) did not find enhanced P100 activity for LSF fearful faces, suggesting that P100 responses to LSF fearful faces may not be so robust. Participants with high and low resting HRV did not

show different P100 activity in response to LSF faces. However, participants with low resting HRV showed increased P100 source activity for LSF fearful faces in the areas associated with visual processing, such as the cuneus and the middle occipital gyrus. Although we did not expect that HSF information would influence the early component, source analyses seemed to show that low HRV participants had increased P100 source activity in the cuneus to HSF fearful faces. The cuneus is primarily involved in basic visual perception and emotional processing (Seiferth et al.,

Table 3 Brain regions showing significant differences in P100, N170, and N200 source activity between high and low resting HRV participants in response to BSF, HSF, and LSF fearful and neutral faces

	Brain Lobe & Region	BA	MNI coordinates			Talairach coordinates			t scores
			X	Y	Z	X	Y	Z	
P100 for HSF fearful faces	Occipital lobe Cuneus	17	20	-85	5	20	-82	9	-2.89
P100 for LSF fearful faces	Occipital lobe	19	30	-95	10	30	-92	14	-3.70
	Middle occipital gyurs Cuneus	17	20	-95	5	20	-82	9	-3.68
N170 for LSF fearful faces	Occipital lobe	17	20	-85	10	20	-82	13	-4.01
	Cuneus								
N200 for BSF neutral faces	Occipital lobe	19	30	-95	10	30	-92	14	-2.38
	Middle occipital gyrus								
N200 for HSF neutral faces	Occipital lobe	19	30	-95	15	30	-95	18	-3.52
	Middle occipital gyrus								
N200 for LSF fearful faces	Occipital lobe	19	30	-90	15	30	-87	18	-4.60
	Middle occipital gyrus								
N200 for LSF neutral faces	Occipital lobe	19	30	-90	15	30	-87	18	-4.96
	Middle occipital gyrus								

Note. All brain regions were thresholded at $p < .05$. BA, Brodmann's area; MNI, Montréal Neurological Institute

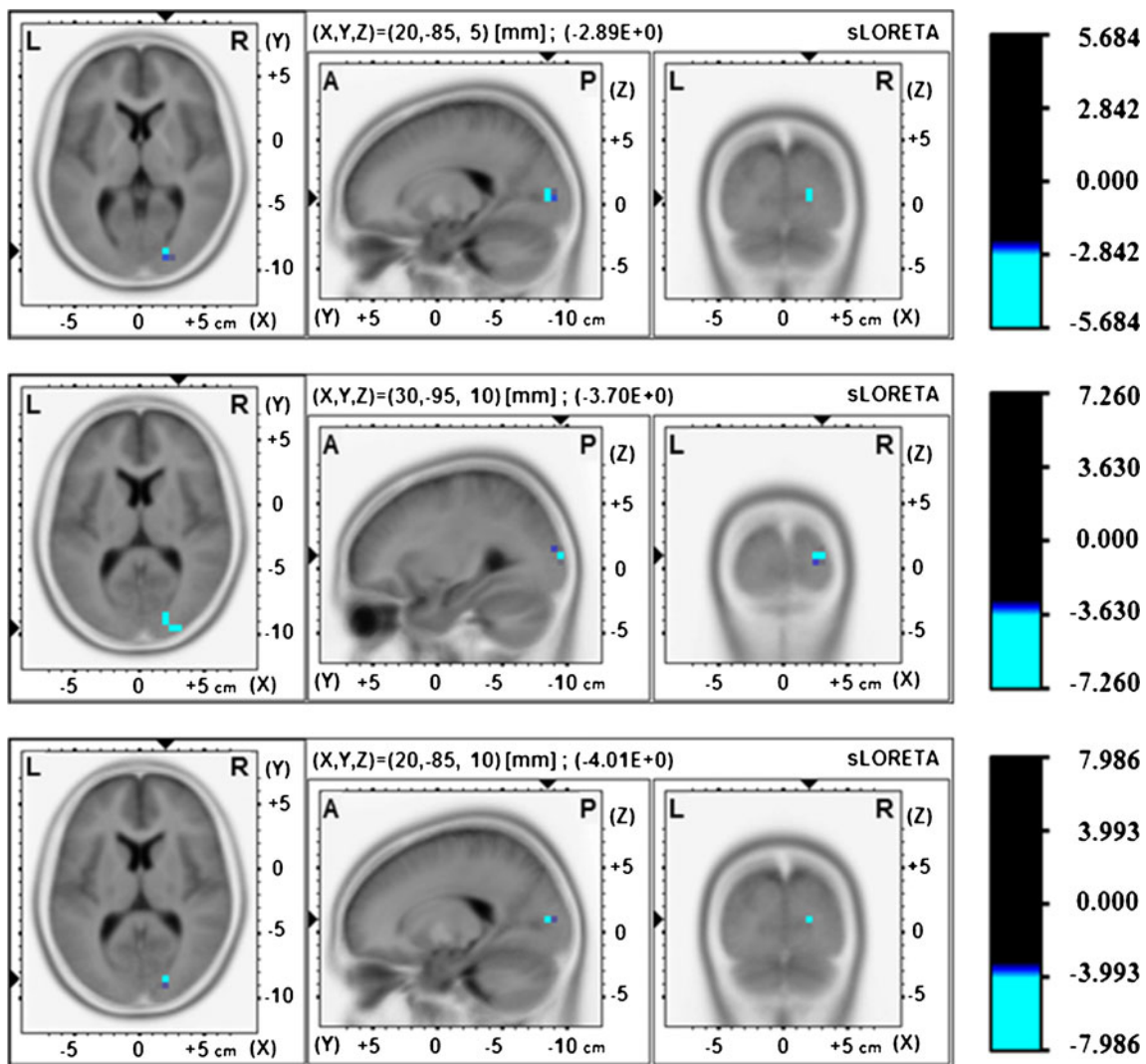


Fig. 8 Source localization results, based on sLORETA. Participants with low resting HRV showed greater P100 source activity in response to HSF fearful faces in the cuneus (Brodmann area 17; top row), greater P100 source activity in response to LSF fearful faces in the

middle occipital gyrus (Brodmann area 18, 19; middle row), and cuneus (Brodmann area 17; middle row), and greater N170 source activity in response to LSF fearful faces in the cuneus (Brodmann area 17; bottom row), as compared with participants with high resting HRV

2009). A previous study revealed that young schizophrenic patients showed increased activations in the cuneus in response to fearful faces (Seiferth et al., 2009). Similarly, participants with low resting HRV showed heightened activity in the cuneus in response to HSF as well as LSF fearful faces. Thus, it appears that participants with low resting HRV show hyperactivity in brain regions involved in visual perception in response to fearful faces at HSF and LSF ranges.

The present study found that BSF and LSF fearful faces elicited greater N170 activity, as compared with BSF and LSF neutral faces, respectively. The result is consistent with a previous study reporting greater N170 activity in response to emotional faces, including LSF fearful faces (Vlamings et al., 2009). Contrary to our prediction, participants with low resting HRV did not show increased N170 activity, as

compared with participants with high resting HRV. However, participants with low resting HRV showed increased N170 source activity for LSF fearful faces in the cuneus, as compared with participants with high resting HRV.

Participants with low resting HRV showed greater N200 activity in response to LSF fearful faces than did participants with high resting HRV. Extensive evidence has suggested that the N200 component is associated with cognitive and emotional self-regulation, such as inhibitory control and conflict monitoring (Bartholow et al., 2005; Dennis & Chen, 2007; van Veen & Carter, 2002). Our result suggests that the N200 activity may reflect self-regulatory capacity of people with high and low resting HRV. Greater N200 activity evoked by LSF fearful faces in participants with low resting HRV

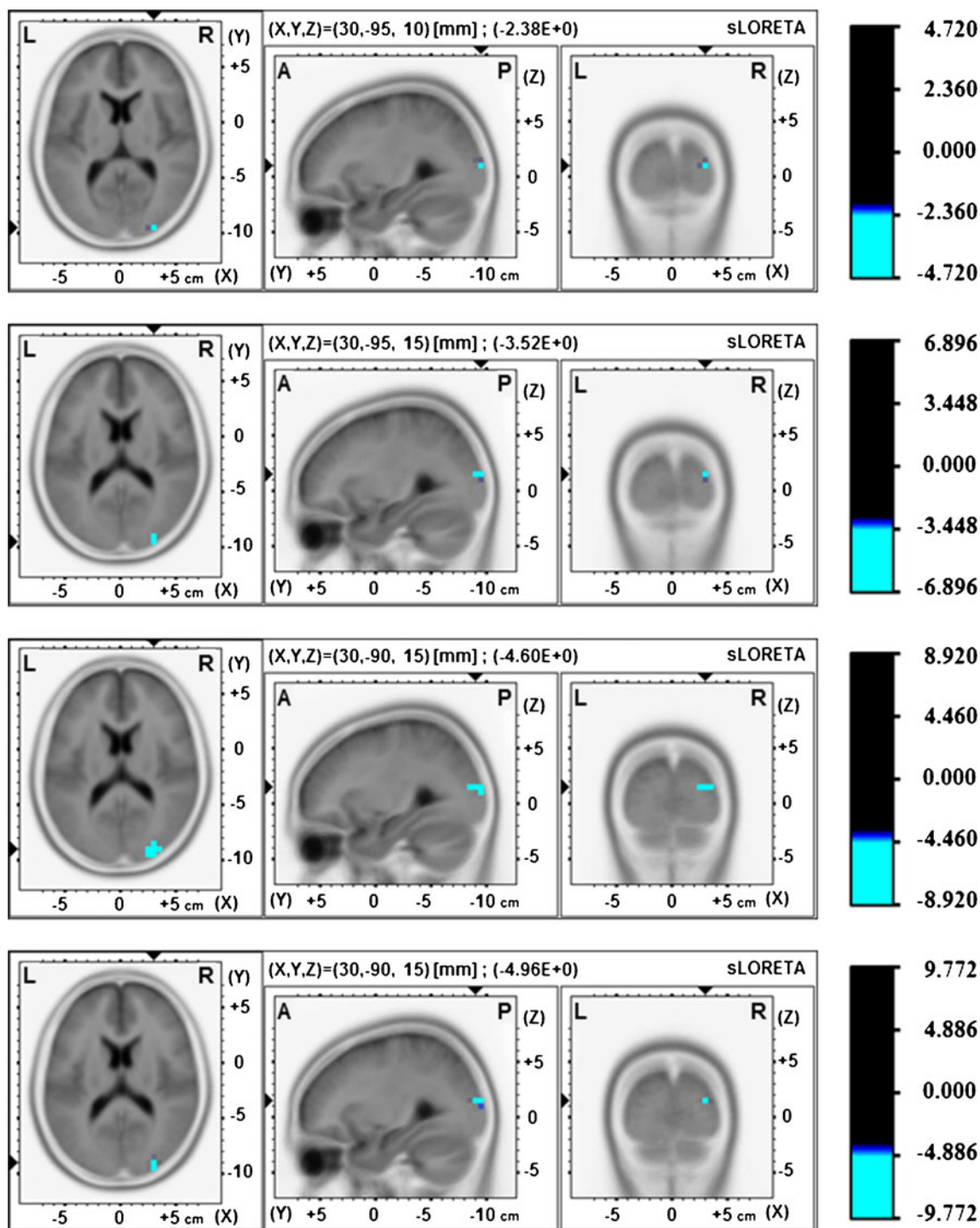


Fig. 9 Source localization results, based on sLORETA. Participants with low resting HRV showed greater N200 source activity in response to BSF neutral faces in the middle occipital gyrus (Brodmann area 19; the first row), to HSF neutral faces in the middle occipital gyrus

(Brodmann area 19; the second row), to LSF neutral faces in the middle occipital gyrus (Brodmann area 18, 19; the third row), and to LSF fearful faces in the middle occipital gyrus (Brodmann area 19; the fourth row), as compared with participants with high resting HRV

suggests that they may have trouble exerting executive function and making regulatory emotional responses to LSF fearful faces that trigger the emotional processing via subcortical mechanisms.

Source analyses seem to show that participants with low resting HRV in this study are associated with heightened N200 source activities in the middle occipital gyrus and the cuneus for BSF, HSF, LSF neutral faces and LSF fearful

faces. The middle occipital gyrus was typically involved in basic visual processing, such as detecting light intensity, color recognition, and the visual patterns (Claeys et al., 2004; Schluppeck & Engel, 2002). Therefore, people with high and low resting HRV appear to show different activations in brain areas associated with the visual processing for neutral and fearful faces. A recent neuroimaging study showed that people with high risk of psychosis showed greater activations in the middle occipital gyrus and the cuneus in response to neutral stimuli during the emotion discrimination task, which was also observed in schizophrenic patients (Seifert et al., 2008). The present study indicates that people with low resting HRV show heightened activities in similar brain areas for neutral face stimuli. There is extensive evidence suggesting that reduced HRV was associated with serious psychiatric illness, such as bipolar disorder and schizophrenia (Bär et al., 2009; Castro et al., 2008). Severity of psychotic symptoms of schizophrenia was associated with cardiac autonomic disturbance (Bär et al., 2008). Taken together, low HRV may be a predisposing factor that leads to dysfunctional neural processing of visual stimuli, which may eventually lead to the development of psychiatric illness, such as schizophrenia (Park et al., 2012b; Thayer & Lane, 2009).

In the present study, source analyses did not find source activities of the N200 components in the ventral prefrontal cortex and/or the dorsal anterior cingulate cortex, which were found to be significant source areas in previous studies (Pliszka et al., 2000; van Veen & Carter, 2002). The discrepant result could be explained by the fact that we used a simple perceptual discrimination task, whereas those studies that linked the N200 component with activity of the ventral PFC and/or the dorsal ACC used more complex tasks that required extensive inhibitory attention and executive function.

Participants with low resting HRV showed enhanced LPP activity in response to HSF neutral faces. A number of studies have reported that enhanced LPP activity was elicited by highly arousing unpleasant (e.g., mutilations) and pleasant (e.g., erotic) pictures (Schupp et al., 2000; Schupp et al., 2004). Underlying source activity of the LPP component has been traced to occipito-temporal areas caused by heightened amygdala activity to affectively significant stimuli (Hajcak et al., 2010; Sabatinelli et al., 2007). In the present study, participants with low resting HRV showed enhanced LPP to HSF neutral faces, suggesting that low HRV may be associated with hypervigilant neural responses to neutral faces in later stages of processing. This result is consistent with previous research showing that low HRV was associated with hypervigilant physiological responses to neutral stimuli (e.g., startle reflex; Ruiz-Padial et al., 2003; Thayer et al., 2000).

Conclusion

The present research provides initial evidence that individual differences in HRV are associated with differential neural activity to fearful and neutral faces at different spatial frequencies. Specifically, participants with low resting HRV show enhanced N200 activity in response to LSF fearful faces and enhanced LPP activity in response to HSF neutral faces, as compared with participants with high resting HRV. Furthermore, source analyses using sLORETA revealed that participants with low HRV tend to exhibit greater activation of brain areas implicated in the visual and emotional processing. The dysfunctional neural activity associated with low HRV may be associated with emotional dysregulation, which may eventually lead to serious pathological conditions (Thayer & Lane, 2009).

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References

- Ahern, G. L., Sollers, J. J., Lane, R. D., Labiner, D. M., Herring, A. M., Weinand, M. E., et al. (2001). Heart rate and heart rate variability changes in the intracarotid sodium amobarbital (ISA) test. *Epilepsia*, *42*, 912–921.
- Ashley, V., Vuilleumier, P., & Swick, D. (2004). Time course and specificity of event-related potentials to emotional expressions. *Neuroreport*, *15*, 211–216.
- Bär, K.-J., Berger, S., Metzner, M., Boettger, M. K., Schulz, S. C., Ramachandriaiah, C. T., & Sauer, H. (2009). Autonomic dysfunction in unaffected first-degree relatives of patients suffering from schizophrenia. *Schizophrenia Bulletin*, *36*, 1050–1058.
- Bär, K.-J., Wernich, K., Boettger, S., Cordes, J., Boettger, M. K., Löffler, S., et al. (2008). Relationship between cardiovagal modulation and psychotic state in patients with paranoid schizophrenia. *Psychiatry Research*, *157*, 255–257.
- Bartholow, B. D., Pearson, M. A., Dickter, C. L., Sher, K. J., Fabiani, M., & Gratton, G. (2005). Strategic control and medial frontal negativity: Beyond errors and response conflict. *Psychophysiology*, *42*, 33–42.
- Batty, M., & Taylor, M. J. (2003). Early processing of the six basic facial emotional expressions. *Cognitive Brain Research*, *17*, 613–620.
- Berntson, G. G., Bigger, J. T., Eckberg, D. L., Grossman, P., Kaufmann, P. G., Malik, M., et al. (1997). Heart rate variability: Origins, methods, and interpretive caveats. *Psychophysiology*, *34*, 623–648.
- Campanella, S., Gaspard, C., Debatisse, D., Bruyer, R., Crommelinck, M., & Guerit, J. M. (2002). Discrimination of emotional facial expressions in a visual oddball task: An ERP study. *Biological Psychology*, *59*, 171–186.
- Carretié, L., Hinojosam, J. A., López-Martín, S., & Tapia, M. (2007). An electrophysiological study on the interaction between emotional content and spatial frequency of visual stimuli. *Neuropsychologia*, *45*, 1187–1195.

- Castro, M. N., Vigo, D. E., Weidema, H., Fahrner, R. D., Chu, E. M., Achaval, D., et al. (2008). Heart rate variability response to mental arithmetic stress in patients with schizophrenia: Autonomic response to stress in schizophrenia. *Schizophrenia Research*, *99*, 294–303.
- Claeys, K. G., Dupont, P., Cornette, L., Sunaert, S., Van Hecke, P., De Schutter, E., & Orban, G. A. (2004). Color discrimination involves ventral and dorsal stream visual areas. *Cerebral Cortex*, *14*, 802–822.
- Couture, S. M., Penn, D. L., & Roberts, D. L. (2006). The functional significance of social cognition in schizophrenia: A review. *Schizophrenia Bulletin*, *32*, S44–S63.
- Dennis, T. A., & Chen, C.-C. (2007). Neurophysiological mechanisms in the emotional modulation of attention: The balance between threat sensitivity and attentional control. *Biological Psychology*, *76*, 1–10.
- Ellis, R. J., & Thayer, J. F. (2010). Music and autonomic nervous system (dys)function. *Music Perception*, *27*, 317–326.
- Fallgatter, A. J., Bartsch, A. J., Zielasek, J., & Herrmann, M. J. (2003). Brain electrical dysfunction of the anterior cingulate in schizophrenic patients. *Psychiatry Research*, *124*, 37–48.
- Friedman, B. H. (2007). An autonomic flexibility-neurovisceral integration model of anxiety and cardiac vagal tone. *Biological Psychology*, *74*, 185–199.
- Fuchs, M., Kastner, J., Wagner, M., Hawes, S., & Ebersole, J. S. (2002). A standardized boundary element method volume conductor model. *Clinical Neurophysiology*, *5*, 702–712.
- Goffaux, V., Hault, B., Michel, C., Vuong, Q. C., & Rossion, B. (2005). The respective role of low and high spatial frequencies in supporting configural and featural processing of faces. *Perception*, *34*, 77–86.
- Goffaux, V., & Rossion, B. (2006). Faces are “spatial” – Holistic face perception is supported by low spatial frequencies. *Journal of Experimental Psychology: Human Perception and Performance*, *32*, 1023–1039.
- Hajcak, G., MacNamara, A., & Olvet, D. M. (2010). Event-related potentials, emotion, and emotional regulation: An integrative Review. *Developmental Neuropsychology*, *35*, 129–155.
- Hajcak, G., Moser, J. S., & Simons, R. F. (2006). Attending to affect: Appraisal strategies modulate the electrocortical response to arousing pictures. *Emotion*, *6*, 517–522.
- Hansen, A. L., Johnsen, B. H., & Thayer, J. F. (2003). Vagal influence on working memory and attention. *International Journal of Psychophysiology*, *48*, 263–274.
- Heisz, J. J., Watter, S., & Shedden, J. M. (2006). Automatic face identity encoding at the N170. *Vision Research*, *46*, 4604–4614.
- Holmes, A., Winston, J. S., & Eimer, M. (2005). The processing of emotional facial expression is gated by spatial attention: Evidence from event-related brain potentials. *Cognitive Brain Research*, *16*, 174–184.
- Jacques, C., & Rossion, B. (2006). The speed of individual face categorization. *Psychological Science*, *17*, 485–492.
- Lamm, C., & Lewis, M. D. (2010). Developmental change in the neurophysiological correlates of self-regulation in high- and low-emotion conditions. *Developmental Neuropsychology*, *35*, 152–176.
- Lee, S. H., Kim, E. Y., Kim, S., & Bae, S. M. (2010). Event-related potential patterns and gender effects underlying facial affect processing in schizophrenia patients. *Neuroscience Reserach*, *67*, 172–180.
- Lee, T.-H., Lee, K., Lee, K.-Y., Choi, J.-S., & Kim, H.-T. (2006). *Korea University Facial Expression Collection: KUEFC*. Lab of Behavioral Neuroscience, Department of Psychology, Korea University.
- Lewis, M. D., Lamm, C., Segalowitz, S. J., Stieben, S., & Zelazo, P. D. (2006). Neurophysiological correlates of emotion regulation in children and adolescents. *Journal of Cognitive Neuroscience*, *8*, 430–443.
- Liddell, B. J., Williams, L. M., Rathjen, J., Shevrin, H., & Gordon, E. (2006). A temporal dissociation of subliminal versus supraliminal fear perception: An event-related potential study. *Journal of Cognitive Neuroscience*, *16*, 479–486.
- Livingstone, M., & Hubel, D. (1988). Segregation of form, color, movement, and depth: Anatomy, physiology, and perception. *Science*, *240*, 740–749.
- Mazziotta, J., Toga, A., Evans, A., Fox, P., Lancaster, J., Zilles, K., et al. (2001). A probabilistic atlas and reference system for the human brain: International Consortium for Brain Mapping (ICBM). *Philosophical Transactions of the Royal Society B Biological Science*, *356*, 1293–1322.
- Merigan, W. H., & Maunsell, J. H. R. (1993). How parallel are the primate visual pathways. *Annual Review of Neuroscience*, *16*, 369–402.
- Morrison, D. J., & Schyns, P. G. (2001). Usage of spatial scales for the categorization of faces, objects, and scenes. *Psychonomic Bulletin & Review*, *8*, 454–469.
- Neta, M., & Whalen, P. J. (2010). The primacy of negative interpretations when resolving the valence of ambiguous facial expression. *Psychological Science*, *21*, 901–907.
- Nieuwenhuis, S., Jepma, M., Fors, S. L., & Olivers, C. N. L. (2008). The role of the magnocellular and parvocellular pathways in the attentional blink. *Brain and Cognition*, *68*, 42–48.
- Nunan, D., Donovan, G., Jakovljevic, D., Hodges, L., Sandercock, G., & Brodie, D. (2009). Validity and reliability of short-term heart-rate variability from the Polar S810. *Medicine & Science in Sports & Exercise*, *41*, 243–250.
- Park, G., Van Bavel, J. J., Egan, E., Vasey, M. W., & Thayer, J. F. (2012a). From the heart to the mind's eye: Cardiac vagal tone is related to visual perception of fearful faces at high spatial frequency. *Biological Psychology*, *90*, 171–178.
- Park, G., Van Bavel, J. J., Vasey, M. W., & Thayer, J. F. (2012b). Cardiac vagal tone predicts inhibited attention to fearful faces. *Emotion*.
- Pascual-Marqui, R. D. (2002). Standardized low resolution brain electro-magnetic tomography (sLORETA): Technical details. *Methods and Findings in Experimental and Clinical Pharmacology*, *24*, 5–12.
- Pascual-Marqui, R. D., Lehmann, D., Koenig, T., Kochi, K., Merlo, M. C. G., Hell, D., & Koukkou, M. (1999). Low resolution brain electromagnetic tomography (loreta) functional imaging in acute, neuroleptic-naïve, first-break, productive schizophrenics. *Psychiatry Research*, *90*, 169–179.
- Pliszka, S. R., Liotti, M., & Woldorff, M. G. (2000). Inhibitory control in children with attention-deficit/hyperactivity disorder: Event-related potentials identify the processing component and timing of an impaired right-frontal response-inhibition mechanism. *Biological Psychiatry*, *48*, 238–246.
- Pourtois, G., Dan, E. S., Grandjean, D., Sander, D., & Vuilleumier, P. (2005). Enhanced extrastriate visual response to bandpass spatial frequency filtered fearful faces: Time course and topographic evoked-potentials mapping. *Human Brain Mapping*, *26*, 65–79.
- Ruiz-Padial, E., Sollers, J. J., Vila, J., & Thayer, J. F. (2003). The rhythm of the heart in the blink of an eye: Emotion-modulated startle magnitude covaries with heart rate variability. *Psychophysiology*, *40*, 306–313.
- Sabatinelli, D., Lang, P. J., Keil, A., & Bradley, M. M. (2007). Emotional perception: Correlation of functional MRI and event-related potentials. *Cerebral Cortex*, *17*, 1085–1091.
- Scharmüller, W., Leutgeb, V., Schäfer, A., Kächele, A., & Schienle, A. (2011). Source localization of late electrocortical positivity during symptom provocation in spider phobia: An sLORETA study. *Brain Research*, *1397*, 10–18.

- Schluppeck, D., & Engel, S. A. (2002). Color opponent neurons in V1: A review and model reconciling results from imaging and single-unit recording. *Journal of Vision*, *2*, 480–492.
- Schupp, H. T., Cuthbert, B. N., Bradley, M. M., Cacioppo, J. T., Ito, T., & Lang, P. J. (2000). Affective picture processing: The late positive potential is modulated by motivational relevance. *Psychophysiology*, *39*, 257–261.
- Schupp, H. T., Junghöfer, M., Weike, A. I., & Hamm, A. O. (2003). Attention and emotion: An ERP analysis of facilitated emotional stimulus processing. *Neuroreport*, *14*, 1107–1110.
- Schupp, H. T., Ohman, A., Junghöfer, M., Weike, A. I., Stockburger, J., & Hamm, A. O. (2004). The facilitated processing of threatening faces: An ERP analysis. *Emotion*, *4*, 189–200.
- Seiferth, N. Y., Pauly, K., Habel, U., Kellermann, T., Shah, N. J., Ruhrmann, S., et al. (2008). Increased neural response related to neutral faces in individuals at risk for psychosis. *NeuroImage*, *40*, 289–297.
- Seiferth, N. Y., Pauly, K., Kellermann, T., Shah, N. J., Ott, G., Herpertz-Dahlmann, B., et al. (2009). Neural correlates of facial emotion discrimination in early onset schizophrenia. *Neuropsychopharmacology*, *34*, 477–487.
- Semlitsch, H. V., Anderer, P., Schuster, P., & Presslich, O. (1986). A solution for reliable and valid reduction of ocular artifacts, applied to the P300 ERP. *Psychophysiology*, *23*, 695–703.
- Spielberger, C. D., & Diaz-Guerrero, R. (Eds.). (1983). *Cross-cultural anxiety (Vol. 2)*. Washington, D C: Hemisphere.
- Task Force of the European Society of Cardiology and the North American Society of Pacing and Electrophysiology. (1996). Heart rate variability: Standards of measurement, physiology interpretation, and clinical use. *Circulation*, *93*, 1043–1065.
- Thayer, J. F., & Friedman, B. H. (2004). A neurovisceral integration model of health disparities in aging. In N. B. Anderson, R. A. Bulatao, & B. Cohen (Eds.), *Critical perspective on racial and ethnic differences in health in late life*. Washington D.C: The National Academies.
- Thayer, J. F., Friedman, B. H., Borkovec, T. D., Johnsen, B. H., & Molina, S. (2000). Phasic heart period reactions to cued threat and non-threat stimuli in generalized anxiety disorder. *Psychophysiology*, *37*, 361–368.
- Thayer, J. F., Hansen, A. L., Saus-Rose, E., & Johnsen, B. H. (2009). Heart rate variability, prefrontal neural function and cognitive performance: The neurovisceral integration perspective on self-regulation, adaptation, and health. *Annals of Behavioral Medicine*, *37*, 141–153.
- Thayer, J. F., & Lane, R. D. (2000). A model of neurovisceral integration in emotion regulation and dysregulation. *Journal of Affective Disorders*, *61*, 201–216.
- 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 Review*, *33*, 81–88.
- Thayer, J. F., & Siegle, G. J. (2002). Neurovisceral integration in cardiac and emotional regulation. *IEEE Engineering in Medicine and Biology*, *21*, 24–28.
- Turetsky, B. I., Kohler, C. G., Indersmitten, T., Bhati, M. T., Charbonnier, D., & Gur, R. C. (2007). Facial emotion recognition in schizophrenia: When and why does it go awry? *Schizophrenia Research*, *94*, 253–263.
- van Veen, V., & Carter, C. S. (2002). The timing of action-monitoring processes in the anterior cingulate cortex. *Journal of Cognitive Neuroscience*, *14*, 593–602.
- Vanderlei, L., Silva, R., Pastre, C., Azevedo, F., & Godoy, M. (2008). Comparison of the Polar S810i monitor and the ECG for the analysis of heart rate variability in the time and frequency domains. *Brazilian Journal of Medical and Biological Research*, *41*, 854–859.
- Vlamings, P. H. J. M., Goffaux, V., & Kemner, C. (2009). Is the early modulation of brain activity by fearful facial expressions primarily mediated by coarse low spatial frequency information? *Journal of Vision*, *9*, 1–13.
- Vuilleumier, P. (2005). How brains beware: Neutral mechanisms of emotional attention. *Trends in Cognitive Sciences*, *9*, 585–594.
- Vuilleumier, P., Armony, J. L., Driver, J., & Dolan, R. J. (2003). Distinct spatial frequency sensitivities for processing faces and emotional expressions. *Nature Neuroscience*, *6*, 624–631.
- Williams, L. M., Liddell, B. J., Rathjen, J., Brown, K. J., Gray, J., Phillips, M., et al. (2004). Mapping the time course of nonconscious and conscious perception of fear: An integration of central and peripheral measures. *Human Brain Mapping*, *21*, 64–74.