

Research Articles: Behavioral/Cognitive

Higher heart rate variability is associated with vmPFC activity and increased resistance to temptation in dietary self-control challenges

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2 **Higher heart rate variability is associated with vmPFC activity and increased**
3 **resistance to temptation in dietary self-control challenges**

4

5 **Abbreviated title (50 char. max):**

6 HRV predicts dietary self-control

7

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34 **Abstract**

35 Higher levels of self-control in decision making have been linked to better
36 psychosocial and physical health. A similar link to health outcomes has been
37 reported for heart rate variability (HRV), a marker of physiological flexibility. Here,
38 we sought to link these two, largely separate, research domains by testing the
39 hypothesis that greater HRV would be associated with better dietary self-control in
40 humans. Specifically, we examined whether total HRV at sedentary rest (measured
41 as the standard deviation of normal-to-normal intervals, SDNN) can serve as a
42 biomarker for the neurophysiological adaptability that putatively underlies self-
43 controlled behavior. We found that HRV explained a significant portion of the
44 individual variability in dietary self-control, with individuals having higher HRV
45 being better able to down-regulate their cravings in the face of taste temptations.
46 Furthermore, HRV was associated with activity patterns in the ventromedial
47 prefrontal cortex (vmPFC), a key node in the brain's valuation and decision
48 circuitry. Specifically, individuals with higher HRV showed both higher overall
49 vmPFC BOLD activity and attenuated taste representations when presented with a
50 dietary self-control challenge. Lastly, the behavioral and neural associations with
51 HRV were consistent across both our stress induction and control experimental
52 conditions. The stability of this association across experimental conditions
53 suggests that HRV may serve as both a readily obtainable and robust biomarker for
54 self-control ability across environmental contexts.

55

56

57 **Significance statement**

58 Self-control is associated with better health, but behavioral and psychometric self-
59 control measures allow only indirect associations with health outcomes and may
60 be distorted by reporting bias. We tested whether resting heart rate variability
61 (HRV), a physiological indicator of psychological and physical health, can predict
62 individual differences in dietary self-control in humans. We found that higher HRV
63 was associated with better self-control and improved predictions of choice
64 behavior. Specifically, higher HRV was associated with more effective down-
65 regulation of taste temptations, and with a diminished neural representation of
66 taste temptations during self-control challenges. Our results suggest that HRV may
67 serve as an easily acquired, non-invasive and low-cost biomarker for self-control
68 ability.

69

70 **Introduction**

71 Self-regulation has been associated with a wide range of life outcomes, from
72 educational achievement and socio-economic status to mental and physical health
73 (Mischel et al., 1989; Duckworth, 2011; Moffitt et al., 2011). Therefore, accurate
74 predictors of individuals' self-regulatory abilities are important tools in both basic
75 scientific research as well as applied domains including education and medicine.
76 Self-regulation is generally assessed in specific domains by psychometric
77 questionnaires or laboratory tasks. Unfortunately, participants can potentially
78 distort these measurements by reporting socially desirable answers or behaving
79 according to the presumed goals of the experimenter. Therefore, measures based
80 on physiological readouts that are easy to obtain, domain independent and robust
81 to reporting biases could be an important tool in the assessment of self-control.

82 One such readout is heart rate variability (HRV). Measures of HRV have
83 been linked to self-regulatory capacities and performance in the domain of
84 emotion (Thayer and Lane, 2000, 2009), raising the question of whether they
85 might serve as more general predictors of self-control. Heart rate variability is a
86 well-established physiological characteristic of all vertebrates (Grossman and
87 Taylor, 2007): the timing between subsequent heartbeats oscillates on the order of
88 milliseconds and no two neighboring beat pairs (RR intervals) are of exactly the
89 same length (Camm et al., 1996). An animal's HRV is sensitive to both physical and
90 mental strain (Porges and Raskin, 1969), and differences in resting HRV can
91 distinguish between states of health and disease (Heni et al., 2014; Heni et al.,
92 2015). High resting HRV has been associated with good physical (Masi et al., 2007;
93 Brandle et al., 2015) and mental health (Thayer and Brosschot, 2005), while

94 chronic decreases in HRV indicated disease states and slow recovery from stress
95 (Weber et al., 2010; Stalder et al., 2011).

96 The Polyvagal (Porges, 1995, 2001) and Neurovisceral Integration (Thayer
97 and Lane, 2000, 2009) theories postulate a mechanistic link between HRV and self-
98 regulation. Both associate central nervous system regulation of the cardiovascular
99 system, which is necessary to prepare reactions to challenges in the environment,
100 with adaptive behavior at a higher cognitive level. However, we note that it
101 remains unclear to what degree the central versus peripheral nervous system
102 influences HRV. Despite the fact that we do not yet fully understand all of the
103 physiological and cognitive factors driving HRV (Heathers, 2014), we build on
104 previous proposals (Grossman and Taylor, 2007) and posit that HRV serves as a
105 readout of an individual's allostatic capacities to integrate behavioral strategies
106 and energy stores in response to demands in the environment.

107 Higher HRV has been linked to several cognitive processes that support
108 self-regulation including: (1) re-allocation of attention (e.g., disengaging from
109 stimuli that are not threatening in the current context), which may reduce
110 allostatic load (McEwen and Wingfield, 2003), (2) persistence (Reynard et al.,
111 2011), and (3) working memory (Gianaros et al., 2004; Hansen et al., 2004). In
112 contrast, low HRV has been associated with disinhibition and dysregulated social
113 conduct (Beauchaine, 2001; Beauchaine et al., 2007). Furthermore, Daly et al.
114 (2014) reported that higher trait self-control, measured using the self-report scale
115 developed by Tangney, Baumeister & Boone (2004), correlates with higher resting
116 HRV. However, the links between HRV and self-control at the neural level remain
117 unknown.

118 In this study, we investigated the relationship between dietary self-control
119 and resting HRV using fMRI. We hypothesized that better self-control should be
120 associated with higher heart rate variability, and that individual differences in HRV
121 would be associated with neural processing within a self-control network
122 including dlPFC and vmPFC (Hare et al., 2009; Maier et al., 2015). We indeed found
123 that higher resting HRV was associated with better dietary self-control.
124 Furthermore, we found that HRV positively correlated with activity in
125 ventromedial prefrontal cortex (vmPFC) when individuals faced self-control
126 challenges, and that high HRV individuals showed a decreased sensitivity to taste
127 attributes in vmPFC. These vmPFC findings suggest a neural mechanism for the
128 down-regulation of tempting taste attributes that may facilitate dietary self-
129 control.

130

131 **Materials and Methods**

132 **Participants.** Fifty-one men participated in this study. The sample is the same as
133 in Maier, Makwana & Hare (2015), where we reported the effects of stress on
134 behavioral and neural self-control processes, but no heart rate analyses. We
135 included only male participants to facilitate the collection and analysis of cortisol
136 responses to stress in our previous work. Baseline HR data for two participants
137 were lost due to recording failure. In the present report, we include the subset of
138 participants for whom we have both heart rate and fMRI data (22 control and 27
139 stress group participants). The Ethics Committee of the Canton of Zurich approved
140 this study and all participants provided written informed consent on the study day.
141 All participants were right-handed and had normal or corrected to normal vision.
142 None of them reported any history of somatic or psychiatric disease, nor did they

143 take any prescription medication. On average, participants in the sample had a
144 blood pressure in the (high) normal range for their age group (mean systolic blood
145 pressure: 130 ± 14 SD; mean diastolic blood pressure: 77 ± 9).

146 Participants were excluded during the recruitment stage if they suffered
147 from any allergies, food intolerances or eating disorders. We also excluded
148 individuals who followed a specific diet (e.g., eating vegetarian, vegan, gluten-
149 /lactose-free, etc.), or who did not report enjoying and regularly consuming snack
150 foods (regularly was defined as more than two occasions per week). A final
151 eligibility criterion was that participants had to report making an effort to
152 maintain a healthy lifestyle, including exercise and an overall balanced diet.
153 Together, these criteria ensured that participants would face a meaningful self-
154 control challenge in the dietary choice task.

155 To ensure a homogeneous reaction of the hypothalamic-pituitary-adrenal
156 (HPA) axis in response to stress induction, participants were asked to abstain from
157 drinking alcoholic or caffeinated beverages in the 18 hours before the study, to not
158 exercise in the 6 hours prior to the study, and come to the laboratory well rested.
159 We only recruited nonsmokers who had no history of drug abuse. We asked
160 participants to go to bed by 24:00 at the latest on the day before the study and to
161 get a good night's sleep. We instructed participants to not take any medication that
162 alters the blood flow (e.g., analgesics) in the 72 hours before their appointment. In
163 order to motivate the dietary choices, participants were instructed to eat a small
164 meal (sandwich or salad with approximately 450 kcal) 3 hours prior to the study
165 and consume nothing but water after that.

166 Allen, Chambers & Towers (2007) identified age, exercise habits and
167 obesity as potential confounding factors for heart rate analyses. Our sample was

168 relatively homogeneous with regard to these factors. The men were 21.2 ± 2 years
169 old, had a normal BMI (Mean: 22.7 ± 2.1 SD), trained on average 1.6 ± 1.4 SD times
170 per week for building strength and had completed an average of 1.9 ± 1.3 SD
171 cardio training sessions per week during the past four weeks before the study,
172 resulting in a combined mean of 3.6 ± 2.1 weekly training sessions per participant.
173 Other factors identified by Allen and colleagues including smoking, gender,
174 caffeine and alcohol intake and circadian rhythm were controlled for by our study
175 exclusion criteria and design.

176

177 **Procedure.** In the 30-40 minutes preceding the resting HRV measurement,
178 participants had rated 180 food items for health and taste in order to create
179 tempting dietary choice pairs. Subsequent to the heart beat interval measurement
180 a stress induction (Socially Evaluated Cold Pressor Test, SECPT) or control
181 procedure was administered. Assignment to the stress induction or control
182 conditions was unknown to both the participant and the experimenter at the time
183 of HRV measurement, however participants knew that they would be randomly
184 assigned to one treatment or the other based on the information provided with the
185 consent forms at the beginning of the study. The SECPT treatment elicited an acute
186 stress response, as indicated by higher cortisol values in the Stress group (mean
187 cortisol in nanomol / liter at maximum: Stress = 9.64 ± 1.09 SEM, Control = $6.6 \pm$
188 0.67 SEM), and higher reports of perceiving to be stressed than the Control group
189 (on a visual analog scale from 0, “not at all stressed” to 100, “extremely stressed”:
190 mean Stress = $33 \pm 4\%$ SEM, mean Control = $19 \pm 5\%$ SEM). Details of the stress
191 induction and behavioral task were reported in Maier et al. (2015). Here, we focus
192 on the relationship between the baseline HRV parameter and dietary self-control

193 success and its neural correlates. However, given that the stress treatment is
194 known to change dietary choices (Maier et al., 2015), we included it as a factor in
195 all regression models.

196 Immediately after the stress induction, participants were scanned with
197 BOLD fMRI while they made choices in a dietary self-control task. The screen
198 always depicted two food items, and participants had to choose whether they
199 wanted to eat the item on the right or on the left (Figure 1a). The binary food
200 choices fell into one of two categories. In the first, choosing the healthier item is
201 trivial because the healthier item was also tastier. We refer to this category as no
202 challenge trials because there is no self-control challenge. In the second choice
203 category, self-control challenges, the healthier item was the less tasty of the two
204 foods and thus presented a conflict between taste and health attributes. Self-
205 control challenges were presented on approximately half of the 210 trials for each
206 participant. To examine the variability of the challenge that different participants
207 faced, we normalized the ratings to fall between 0 and 100 points, and calculated
208 absolute taste and health differences between every pair of food items each
209 participant faced. On a scale from 0 to 100, the mean health difference was 34 ± 25
210 points (mean \pm standard deviation) and the mean taste difference was 29 ± 21
211 points.

212 The behavioral and fMRI analyses in this paper focus on the self-control
213 challenge cases. Before the task started, they were reminded to choose the
214 healthier item as often as they could, consistent with their healthy lifestyle goals.
215 Participants knew that one of their choices would be realized in the end, and they
216 would have to eat whatever they chose on the trial that was randomly drawn for
217 being paid out.

218

219 ***Psychometric inventories.*** German versions of the Spielberger State-Trait Anxiety
220 Inventory (Laux et al., 1981), Three Factor Eating Questionnaire (Pudel and
221 Westenhöfer, 1989), and Behavioral Inhibition and Activation Scales (Strobel et al.,
222 2001) were administered at the end of the study. Data for the trait anxiety scale of
223 the State-Trait Anxiety Inventory are missing for one participant, as he failed to
224 complete the second page of the questionnaire.

225

226 ***Statistical Analyses.*** All behavioral data were analyzed using either the Matlab
227 (Release 2014b, version 8.4.0.150421 (The MathWorks Inc., 2014),
228 RRID:SCR_001622) or R (Version 3.2.1 (“R Core Team,” 2015), RRID:SCR_001905)
229 statistical software packages. The fMRI results were depicted using the MRIcron
230 software package (<http://www.mccauslandcenter.sc.edu/mricro/mricron/>,
231 RRID:SCR_002403). All correlations reported in this paper were assessed with a
232 nonparametric bootstrap method. Two-tailed p-values for correlations were
233 obtained by testing the Pearson correlation coefficients (r) against a null
234 distribution generated from 5000 permutations of the data. The 95 % confidence
235 intervals for the correlations were computed from 5000 bootstrapped samples of
236 the data. The multiple regression model in equation 2 below was fit using the “lm”
237 function in R. In order to visualize the HRV by taste and health difference
238 interactions, we plot the estimated self-control success levels at specific
239 combinations of HRV and taste or health differences from this regression model
240 (Figure 2b and c).

241

242 **Heart rate data acquisition.** We measured baseline heart rate (HR) at rest with
243 the Polar RS 800 CX system (for a cross-validation of this method with ECG see
244 Quintana, Heathers & Kemp (2012)). All measurements were collected between
245 13.30 and 17.00 in the afternoon to control for circadian rhythms (Heathers,
246 2014). The baseline measurement was always taken in a single session before any
247 stress or control treatment was administered. Participants were seated in a quiet
248 room and instructed that upon mounting the Polar watch and pressing start, they
249 would need to sit upright and remain quiet and calm during the subsequent
250 baseline-recording interval. A baseline recording was taken for 6 minutes. The first
251 3 minutes of the recording were discarded from the analysis to yield a set of data
252 that were less affected by aspects such as initial motion while acclimatizing to the
253 recording environment (Quintana et al., 2016). We focused on baseline (i.e.
254 resting) heart rate measures in order to obtain a domain-general index of HRV.

255

256 **Heart rate data analyses.** HRV can be calculated in two different domains: time
257 and frequency. The full range of measures is discussed in the guidelines by the
258 Task Force on HRV (Camm et al., 1996). Time domain measures have the
259 advantage of being more robust than frequency measures. Two different time
260 domain measures are commonly used and both characterize the distribution of
261 inter-beat intervals, which are defined as the time between two subsequent heart
262 beats (i.e., the difference between two R peaks in the ECG (Guyton and Hall, 2006),
263 hence also called the “RR interval”; see Figure 1b). The standard deviation of all RR
264 (also “NN” for “normal-to-normal”) intervals, SDNN, describes the total heart rate
265 variability within a given period (see equation 1). The root mean square of
266 successive differences (RMSSD) calculated between adjacent RR intervals is more

267 sensitive to influences of short-term regulation of the heartbeat. Here we focus on
268 HRV at rest (i.e. in the absence of specific, discrete input stimuli), and thus take
269 SDNN as our primary measure of variability.

270 We chose total HRV (measured as standard deviation over all RR intervals,
271 SDNN) as our biomarker for two reasons: First, SDNN is deemed to be the most
272 robust measure of HRV. Among all commonly computed HRV measures it has been
273 reported to be least compromised by different data preprocessing pipelines,
274 especially the application of artifact correction (Salo et al., 2001). Second, the
275 process of dietary choice is a complex behavioral outcome that may not only
276 depend on a capacity for effective cognitive regulation that helps to achieve self-
277 control goals, but may also be influenced by peripheral factors (e.g., endocrine
278 status, metabolism and energy expenditure) that are indicative of the current state
279 of the organism. SDNN reflects all influences on the RR interval series, while it is
280 known to correlate highly, although not perfectly, with measures that putatively
281 reflect phasic vagal control of cardiac variability in measures taken under
282 sedentary resting conditions (Allen et al., 2007).

283 The complete recording of RR intervals for each participant was extracted
284 using the Polar software, without any transformations of the data. Three-minute
285 intervals of the raw data were then pre-processed with the Artifact toolbox
286 (Version 2.08, 64-bit, Kaufmann et al. (2011)), which has a better artifact detection
287 rate and shows less false detections than the commonly used Kubios HRV toolbox.
288 The Artifact toolbox implements the algorithm of Berntson & Stowell (1998) for
289 identifying artifacts, which aims to exclude any potential artifacts before
290 computing the criterion for identifying true artifacts. Based on the report of Salo
291 and colleagues (2001), who compared editing procedures for correcting single RR

292 artifacts, the identified artifacts were deleted from the RR sequence to obtain the
293 cleanest estimate for SDNN. On average, we corrected 2.1 ± 3.1 SD % of the RR
294 intervals in each sample. Apart from two datasets that had a high number of
295 artifacts requiring correction (12.6 % and 10.5 % RR intervals removed), all other
296 datasets had between 0 and 6% artifacts corrected (21 datasets were diagnosed as
297 being completely artifact free). As a high number of corrected artifacts might be a
298 concern for interpreting our findings, we checked all models for robustness with
299 regard to the number of corrected artifacts.

300

301 SDNN was calculated as

302 (1)

$$SDNN = \sqrt{\frac{1}{N-1} \sum_{j=1}^N (RR_j - \overline{RR})^2}$$

303

304

305 Heart rate variability was calculated with the Artifact software suite, using Fast
306 Fourier Transforms (Berntson and Stowell, 1998; Kaufmann et al., 2011) with an
307 interpolation rate of 4 Hz (spline interpolation) and a Hanning window width that
308 matched the total length of the edited recording (max. 180 seconds or slightly less
309 in case of deletion correction). Frequency bands were bounded between 0.003 and
310 0.04 Hz for the very low frequency band, 0.04 and 0.15 Hz for the low frequency
311 band, and 0.15 and 0.4 Hz for the high frequency band.

312 **fMRI data acquisition.** Images were acquired using a Philips Achieva 3 T whole-
313 body scanner with an eight-channel sensitivity-encoding head coil (Philips Medical

314 Systems) at the Laboratory for Social and Neural Systems Research, University
315 Hospital Zurich. Stimulus presentation was controlled with the Psychophysics
316 Toolbox Software (Psychtoolbox 3.0, Brainard (1997), RRID:SCR_002881); the
317 paradigm was presented via a back-projection system to a mirror that was
318 mounted on the head-coil.

319 We acquired gradient echo T2*-weighted echo-planar images (EPIs) with
320 blood-oxygen-level-dependent (BOLD) contrast (41 slices per volume, Field of
321 View 200 x 126.5 x 200 mm, slice thickness 2.5 mm, 0.6 mm gap, in-plane
322 resolution 2.5*2.5 mm, matrix 80*80, repetition time 2460 ms, echo time 30 ms,
323 flip angle 77°) and a SENSE reduction (i.e. acceleration) factor of 2. Volumes were
324 acquired in axial orientation at a +15° tilt to the anterior commissure-posterior
325 commissure line. We collected 161 volumes in ascending order during each of the
326 three experimental runs, together with five “dummy” volumes at the start and end
327 of each run. A T1-weighted turbo field echo structural image was acquired in
328 sagittal orientation for each participant at the end of the scanning session with the
329 same angulation that applied to the functional scans (181 slices, Field of View 256
330 x 256 x 181 mm, slice thickness 1 mm, no gap, in-plane resolution 1*1 mm, matrix
331 256*256, repetition time 8.4 ms, echo time 3.89 ms, flip angle 8°). To measure the
332 homogeneity of the magnetic field we collected B0/B1 maps before the first and
333 second run and before acquiring the structural scan (short echo time = 4.29 ms,
334 long echo time = 7.4 ms). We measured breathing frequency and took an
335 electrocardiogram with the in-built system of the scanner in order to correct for
336 physiological noise.

337 **fMRI Preprocessing.** Functional data were spatially realigned and unwarped with
338 statistical parametric mapping software (SPM8, Update Rev. Nr. 5236; Functional

339 Imaging Laboratory, University College London, RRID:SCR_007037), segmented
340 according to the participant's T1-weighted high resolution structural image and
341 normalized to the individual mean EPI template before smoothing with an
342 isometric Gaussian kernel (4 mm full width at half maximum). As a last step in
343 preprocessing, we used RETROICOR, as implemented in the PhysIO toolbox, to
344 model respiration and heartbeat (Glover et al., 2000) in order to account for
345 fluctuations in the BOLD signal due to physiological noise. The PhysIO Toolbox by
346 Kasper (2009) is distributed as open source code as part of the TAPAS software
347 collection: www.translationalneuromodeling.org/tapas/. Following Harvey et al.
348 (2008), its algorithm uses Fourier expansions of different order to estimate the
349 phases of cardiac pulsation (3rd order), respiration (4th order) and cardio-
350 respiratory interactions (1st order). For two participants, the scanner could not
351 save physiological data due to a technical problem. For these participants, only the
352 standard motion correction procedure was applied.

353

354 *fMRI analyses*

355 *General linear models.* In all fMRI analyses, regressors in the models were defined
356 as boxcar functions with durations equal to the reaction time on each trial. All
357 three fMRI models also included regressors for head motion, respiratory and
358 cardiac effects on each trial to account for variance in the BOLD signal associated
359 with these sources of noise.

360 Our primary general linear model (GLM-CH) tested for regions that
361 correlated with HRV during self-control challenges (CH). The regression modeled
362 as events of interest all trials that contained 1) a challenge, 2) no challenge, while
363 controlling for 3) healthier experimenter recommendations and 4) less healthy

364 experimenter recommendations. Note that the experimenter recommendations
365 were included in the choice task to test a separate hypothesis unrelated to the
366 current report and are not discussed here. Self-control challenge and no challenge
367 trials included parametric modulators for relative health and taste differences. We
368 computed a first-level contrast for Challenge > No Challenge trials. At the second
369 (group) level, we examined whether increases in BOLD activity on challenge trials
370 were correlated with HRV levels using non-parametric permutation tests ($n =$
371 5000 permutations) and included threshold-free cluster enhancement (TFCE) as
372 implemented in the function “Randomise” in the fMRIB Software library (FSL 5,
373 FMRIB, Winkler, Ridgway, Webster, Smith & Nichols (2014), RRID:SCR_002823).
374 We used FSL for the group level analyses because the TFCE and permutation
375 algorithms are more fully documented and run considerably faster in FSL
376 compared to their implementation in SPM12.

377 A second, separate GLM (GLM-SV) was computed to determine if BOLD
378 activity was related to the integrated value of the chosen food. This GLM included
379 parametric regressors for the integrated subjective value of the chosen and non-
380 chosen food items on every choice onset. Once again, additional regressors
381 controlling for the impact of the experimenter recommendations were included in
382 the model with separate regressors for events in which participants chose based
383 on the recommendation, and in which they did not follow the recommendation. We
384 modeled each participant’s subjective value of food items on every trial by
385 combining the weighted values for the taste and health of each food. The weights
386 were derived from individual logistic regressions on the participant’s choices
387 (identical to Maier et al. (2015)). Briefly, for each participant, a logistic regression
388 estimating the probability of choosing the left item as a function of the taste and

389 health of the left and right item, with all ratings z-scored within participant before
390 entering them in the model. Two additional binary regressors indicated whether
391 the left or right item had been recommended. These regressors for left and right
392 item recommendations took the value of 1 when the item was recommended, and
393 0 when it was not recommended. When no recommendation was given on a trial,
394 both regressors had a value of zero. Note that the spatial presentation of the items
395 was completely randomized, so that the left item was equally likely to be the
396 healthier, or the tastier of both options. We took the mean of the taste betas for the
397 left and right item obtained for each participant, averaging them into a common
398 taste weight for this individual. The same was done for health. These averaged
399 taste and health weights were then used to multiply the z-scored taste and health
400 values of each item presented in the choice paradigm. To obtain the subjective
401 value for each food, the weighted taste and health values were added up to a
402 weighted subjective value separately for the left and right food items.

403 We computed a first-level contrast for the chosen food value for each
404 participant and extracted betas from this contrast within our functional ROI of the
405 ventromedial prefrontal cortex (vmPFC).

406 To examine the impact of health and taste attributes on the BOLD signal, we
407 used a third GLM that modeled five events: 1) all choices, 2) trials on which the
408 healthier food was recommended and chosen, 3) trials on which the healthier food
409 was recommended and not chosen, 4) trials on which the less healthy food was
410 recommended and chosen, and 5) trials on which the less healthy food was
411 recommended and not chosen. Note that the 30 baseline trials did not contain any
412 recommendation, and therefore, the sum of regressors 2-5 does not equal
413 regressor 1. The first regressor for all choices included four parametric

414 modulators: 1) health of the chosen item (Hc), 2) taste of the chosen item (Tc), 3)
415 health of the non-chosen item (Hnc), and 4) taste of non-chosen item (Tnc). These
416 parametric regressors were not orthogonalized with respect to one another. We
417 computed first-level contrasts for Tc-Tnc and Hc-Hnc. We then extracted the betas
418 for these contrasts from our functional vmPFC ROI. The significance of the
419 correlations between BOLD sensitivity to taste and health differences in vmPFC
420 and HRV were determined from 5000 permutations of the data.

421 *Anatomical masks.* The combined anatomical mask for the vmPFC was
422 constructed from a conjunction of the bilateral frontal pole, frontal medial,
423 paracingulate and subcallosal cortex areas that exceeded 20% probability of
424 belonging to the respective structure in the Harvard-Oxford Cortical Atlas (HOA;
425 Desikan et al. (2006)). In order to limit the mask to our region of interest along the
426 medial wall, the HOA-derived anatomical mask was intersected with a rectangular
427 box around the midline (coordinates in mm : $x = [-22, 21]$, $y = [-110, 73]$, $z = [-35,$
428 $9]$).

429 The anatomical mask of the left dlPFC was constructed from a conjunction
430 of the left inferior frontal gyrus (pars opercularis and reticularis) and left superior
431 frontal gyrus areas that exceeded 20% probability of belonging to these structures
432 according to the HOA.

433 Because we tested two separate regions of interest (vmPFC and dlPFC), we
434 used a critical value of $p < 0.025$ (i.e. $0.05 / 2$) for small volume correction at the
435 voxel-level.

436

437 ***Health, taste, and appetitiveness ratings.*** Participants rated health, taste, and
438 how appetizing they found the depicted foods on a continuous rating scale with

439 anchor points from -5 for “very untasty / unhealthy” to +5 for “very tasty /
440 healthy”, or vice versa, to counterbalance order effects. Taste and health ratings
441 were not correlated: the median correlation was -0.09 ± 0.31 MAD in the Stress
442 group, and -0.06 ± 0.20 MAD in the Control group. Neither health ($r = -0.12$, $p =$
443 0.40), nor taste ($r = 0.09$, $p = 0.56$), nor appetitiveness ratings ($r = 0.13$, $p = 0.37$)
444 were correlated with hunger levels.

445

446 **Results**

447 **HRV.** The mean duration of RR intervals across all participants was 929.3 ± 136.3
448 ms (sample median of the median duration of RR intervals: 947 ± 115 ms),
449 resulting in a mean heart rate of 66 ± 10 beats per minute in our sample (values
450 are derived after deletion of artifacts). Our participants expressed a median total
451 HRV (measured as standard deviation over all RR intervals, SDNN) of 98.7 ± 30.1
452 ms median absolute deviation (MAD) within our 3-minute baseline measurement.
453 Consistent with previous reports (Tsuji et al., 1996), HRV was inversely related to
454 average heart rate ($\beta = -1.17 \pm 0.47$, $T = -2.48$, $p = 0.017$; see Table 2).
455 However, total HRV did not differ between participants later assigned to the Stress
456 (S) or Control (C) groups (S: 98.7 ± 29.6 ms; C: 97.7 ± 30.9 ms, $p = 0.93$, $Z = 0.09$,
457 Wilcoxon rank sum test). Regarding biological and psychological markers of the
458 stress reaction, baseline SDNN and cortisol reactions (area under the curve with
459 respect to ground (Pruessner et al., 2003)) were not significantly correlated ($r =$
460 -0.19 , $p = 0.18$), nor were baseline SDNN and perceived stress ($r = -0.10$, $p = 0.49$).
461 Visual inspection of a scatter plot revealed one outlier in the SDNN measure: The
462 value for this participant fell between two and three standard deviations from the

463 sample mean. Therefore, we checked our results for robustness with and without
464 this participant's data and found that all results remained significant in both cases.
465 One concern in the evaluation of heart rate variability is that applying artifact
466 correction might inflate indices of HRV (Heathers, 2014; Quintana and Heathers,
467 2014) and as little as one edited artifact in the RR interval series may do so
468 (Berntson and Stowell, 1998). Indeed, we observed a significant positive
469 correlation between the number of artifacts that we corrected per dataset and the
470 SDNN ($r = 0.44$, $p = 0.003$, CI [0.26, 0.61]). Thus, we included the number of
471 corrected artifacts and mean heart rate as additional covariates in our regression
472 model to test whether HRV would be predictive beyond these influences.

473

474 ***HRV and self-control behavior.*** We originally defined self-control success as
475 choosing the healthier, but less tasty of two food items in challenging trials in
476 which health and taste conflicted, meaning that the participant had to overcome
477 his own taste preferences in order to choose the healthier option. We initially
478 tested the relationship between total HRV (i.e. SDNN) and self-control success in a
479 bivariate correlation analysis. Total HRV was associated with the frequency of self-
480 control success in the dietary choice task over all participants (Pearson $r = 0.36$, p
481 $= 0.01$, CI = [0.07, 0.59]; all p values are derived from 5000 permutations of the
482 data; excluding the HRV outlier: $r = 0.33$, $p = 0.02$, CI = [0.03, 0.58]). For
483 comparison, the correlation between self-control success and the cognitive
484 restraint in eating score (RE) obtained from the Three Factor Eating Questionnaire
485 (Pudel and Westenhöfer, 1989) was $r = 0.35$ ($p = 0.01$, CI = [0.11, 0.55]). This
486 restraint score captures the degree to which individuals use cognitive strategies to
487 limit calorie intake, for example by counting calories, deliberately picking small

488 portions of food, or consuming foods with lower calorie content. Thus, as a
489 biomarker of dietary self-control, HRV explains roughly the same amount of
490 individual variance in choice behavior as an established psychometric index of
491 eating behavior. Restrained eating scores were not significantly associated with
492 HRV ($r = 0.14$, $p = 0.35$, $CI = [-0.28, 0.42]$), suggesting that the two measures could
493 be readily combined to explain additional variation in self-control behavior.

494 Therefore, we modeled self-control success (i.e., choosing a healthier, less
495 tasty item; SCS) in a multiple regression that included both HRV and RE together
496 (see Eq. 2). Beyond testing whether or not HRV and RE could be combined to
497 explain additional variance in self-control, we included RE in the model because it
498 is a widely used, validated measure for dietary self-control success (Laessle et al.,
499 1989; Allison et al., 1992; Williamson et al., 2007). As such, it serves as a
500 benchmark for judging the utility of HRV as a biomarker for dietary self-control.
501 When including both RE and HRV into the same model, we can assess whether
502 HRV is predictive beyond a known trait characteristic of dietary self-control
503 success.

504

$$505 \quad (2) \text{ SCS} = (\text{Stress} + \text{HRV} + \text{RE}) * (\text{Hdiff} + \text{Tdiff}) + \text{error}$$

506

507 This regression allowed us to examine potential interactions between the
508 individual characteristics of HRV and RE and task features such as the stress
509 manipulation (Stress) as well as the average health (Hdiff) and taste differences
510 (Tdiff) a participant faced within the food choice task. Note that although all
511 participants faced self-control challenges in the food choice task, the degree of the

512 challenges depended on each individual's opinions on the taste and healthiness of
513 the various foods.

514 Higher HRV and RE characteristics reduced the influence of taste
515 temptations in self-control dilemmas. All results from the regression in equation 2
516 are listed in Table 1. Higher HRV levels increased the degree to which high taste
517 temptations (i.e. taste differences) were overcome, leading to greater self-control
518 success (Figure 2b). Moreover, unlike low HRV participants, those with high HRV
519 successfully employed self-control regardless of the average health difference
520 between the two options suggesting that they engaged self-control even when the
521 benefit of doing so (i.e. the increase in healthiness) was relatively small (Fig. 2c). A
522 similar interaction was observed between RE and taste differences. As previously
523 reported (Maier et al., 2015), acute stress reduced the use of self-control in dietary
524 choice. To determine if HRV could act as a buffer against acute stress, we computed
525 an extended version of the model in Eq. 2 that also included interactions between
526 stress and HRV and RE. However, we did not observe significant interactions
527 between Stress and HRV or RE indicating that the relationship between HRV and
528 dietary self-control persisted in both in the Stress and Control groups, but that
529 HRV was not associated with resilience to acute stress. For simplicity and ease of
530 interpretation we report the reduced model without interaction terms in Table 1.

531 As a robustness check, we controlled for the influences of the HRV outlier
532 and several other factors that might relate to HRV. We estimated the basic model
533 (equation (2)) without the HRV outlier, and adding: age, the combined number of
534 cardio and strength exercise sessions per week, BMI, hunger level, trait anxiety
535 score, mean heart rate, and number of corrected artifacts in the recording as
536 nuisance regressors. The results were qualitatively unchanged and we still

537 observed a significant relationship between taste and HRV as described above ($T =$
538 4.77 , $p = 4.85e-05$). Note that we included trait anxiety in this robustness check
539 because previous work has shown that trait anxiety is also correlated with HRV
540 (Gaburro et al., 2011; Verkuil et al., 2014), and therefore we tested for this
541 relationship in our data as well. We used the trait scale of the Spielberger State-
542 Trait Anxiety Inventory as our measure of anxiety (Median score for our sample:
543 34.5 ± 5.9 out of possible score ranging from 20-80). Consistent with previous
544 reports, we observed a negative correlation between HRV and trait anxiety scores
545 (permutation $r = -0.28$, $p = 0.0488$, CI $[-0.48, -0.06]$). Trait anxiety scores were also
546 positively correlated with mean resting heart rates across participants ($r = 0.39$, p
547 $= 0.01$, CI $[0.11, 0.60]$).

548 In order to assess the predictive qualities of RE and HRV with regard to self-
549 control in a more robust way, we predicted self-control levels out-of-sample using
550 the leave-one-subject-out (LOSO) method. After taking one participant's data out
551 of the sample, we fit the model in equation (2) to explain the variance in self-
552 control levels of the remaining participants. Using the beta coefficients from the
553 training set, we then predicted the self-control level of the left-out participant.
554 Squaring the obtained correlation coefficient for the true and predicted self-
555 control levels in the full model ($r = 0.88$, $p < 0.0001$, CI $[0.81, 0.92]$) yielded the
556 coefficient of determination for the model with combined predictors of RE and
557 HRV, $R^2 = 0.77$ (Figure 2a). For comparison, fitting the model without the
558 predictors for HRV and its interactions yielded a lower correlation between true
559 and predicted self-control levels ($r = 0.81$, $p < 0.0001$, CI $[0.63, 0.88]$), leading to
560 an observed $R^2 = 0.65$. That is, by combining RE and HRV, we were able to
561 significantly explain an extra 12% of the variation in out-of-sample self-control

562 rates. Using a “split half” instead of a LOSO procedure (i.e. randomly sampling half
563 the dataset for model fitting and using the remaining half for predicting out of
564 sample) yielded a similar benefit (16%) for including HRV in the predictive model
565 (full model: $r = 0.81$, $p < 0.0001$, $CI = [0.55, 0.92]$, $R^2 = 0.66$; model without HRV: $r =$
566 0.71 , $p = 0.0004$, $CI = [0.26, 0.89]$, $R^2 = 0.50$).

567 During the initial review of this manuscript an anonymous reviewer made
568 the insightful suggestion that we could also test the relationship between HRV and
569 another form of self-control in our dataset. Our food choice paradigm included
570 recommendations about which food to choose, and in some cases these
571 recommendations were in favor of the unhealthy food (Participants were told that
572 recommendations were usually, but not always in favor of the healthier item). This
573 feature allows us to test whether HRV is associated with the fraction of trials in
574 which participants overrode this unhealthy recommendation and still chose the
575 healthier food. We found that there was also a positive correlation between HRV
576 and this alternative measure of control ($r = 0.31$; $p = 0.01$, $CI: [0.01, 0.56]$).
577 Although these two measures of self-control are not independent because both are
578 based, in part, on the incorporation of health attributes into the choice process
579 (correlation between self-control measures: $r = 0.77$, $p < 0.0001$, $CI: [0.62, 0.87]$),
580 this post-hoc finding is consistent with the idea that HRV is a domain general
581 marker of self-regulatory ability or efficiency as outlined in the introduction
582 section.

583

584 ***HRV and BOLD activity during self-control.*** To investigate whether HRV could
585 serve as a biomarker of changes in the brain’s decision circuitry in the food self-
586 control paradigm, we analyzed blood oxygenation level-dependent (BOLD) activity

587 measured during the choice task. Our primary general linear model (GLM-CH)
588 tested for regions that correlated with HRV during self-control challenges (CH).

589 Heart rate variability positively correlated with self-control at the level of
590 observed choices, and therefore, we hypothesized that HRV would be associated
591 with BOLD activity in regions known to be involved in the value computation
592 process during self-controlled choices, namely the vmPFC and dlPFC. We tested
593 this hypothesis in anatomical masks of the vmPFC and dlPFC based on the
594 Harvard-Oxford Cortical Atlas (Desikan et al., 2006). The vmPFC mask comprised
595 the bilateral ventromedial prefrontal cortex that is part of the brain's valuation
596 system (Bartra et al., 2013; Clithero and Rangel, 2014; Abitbol et al., 2015;
597 Pessiglione and Delgado, 2015) and has been shown to integrate taste and health
598 values in the dietary self-control paradigm (Hare et al., 2009; Hare et al., 2011;
599 Hare et al., 2014; Foerde et al., 2015; Maier et al., 2015) as well as the separate
600 characteristics of multi-attribute choices in other, non-food domains (Kahnt et al.,
601 2010; Rudolf and Hare, 2014). Our second anatomical mask included the region of
602 left dlPFC that has been presumed to modulate activity in the vmPFC during self-
603 control choices (Hare et al., 2009; Hare et al., 2011; Hare et al., 2014). We found
604 that BOLD activity in portions of the vmPFC increased as a function of baseline
605 HRV in Challenge > No Challenge trials (MNI peak: [1 46 0] in the paracingulate /
606 cingulate gyrus, small-volume-corrected (SVC) $p = 0.004$, $T = 4.8$, and a separate,
607 more dorsal cluster in the cingulate gyrus at [21 41 9], SVC $p = 0.038$, $T = 3.86$; see
608 Figure 3a). However, we found no association between HRV and BOLD activity in
609 the left dlPFC for the Challenge > No Challenge trials that survived small-volume
610 correction within the anatomical region of left dlPFC. Exploratory whole-brain
611 analyses yielded no other regions that survived correcting for multiple

612 comparisons. The results of these exploratory analyses can be accessed in a
613 Neurovault repository under the following link:
614 <http://www.neurovault.org/collections/DNXFVQPJ/>.

615 To establish that activity in this vmPFC region (the larger cluster with a
616 peak at xyz = 1 46 0) was relevant to the participants' choices, we tested whether
617 the chosen food values were represented in the functional ROI correlating with
618 HRV. An integrated value of the chosen food was calculated in a separate GLM
619 (GLM-SV) and we extracted the betas for this chosen food value in the vmPFC ROI.
620 We found that activity in this ROI encoded the integrated value of the chosen food
621 ($T_{46} = 3.52$; $p < 0.001$).

622 Given our behavioral data linking HRV to the relative influence of taste on
623 dietary choices, we tested whether HRV was also correlated with the degree to
624 which BOLD activity in the vmPFC ROI represented taste attributes (Taste chosen
625 - nonchosen from GLM-HT). We found that HRV was negatively correlated with
626 the relative taste value representation (Pearson $r = -0.42$, $p = 0.002$, CI = [-0.60,
627 -0.19]; see Figure 3b), but not correlated with the relative health value ($r = -0.12$,
628 $p = 0.42$, CI = [-0.43, 0.21], Figure 3c). Excluding the HRV outlier did not change the
629 results (taste $r = -0.43$, $p = 0.004$, CI = [-0.63, -0.17]; health $r = -0.09$, $p = 0.56$, CI =
630 [-0.43, 0.23]).

631

632 Discussion

633 We found that higher HRV is associated with better self-control in the face of
634 dietary challenges. More specifically, our results show that the choices of
635 individuals with higher HRV are less affected by tempting taste attributes than
636 choices of participants with lower HRV. In parallel, at the neural level, higher HRV

637 correlated with a decreased representation of taste attributes in vmPFC, a brain
638 region that has been associated with both regulating autonomic responses
639 (Benarroch, 1993) and calculating subjective values of choice options (Bartra et al.,
640 2013; Clithero and Rangel, 2014; Abitbol et al., 2015; Pessiglione and Delgado,
641 2015). Heart rate variability is a measure of physiological fitness that relates to the
642 integrated functioning of the nervous and cardiac systems. Similarly, successful
643 self-control (SC) relies on the integration, and potentially modified evaluation, of
644 actions in the context of higher order goal attainment. Our data indicate a
645 significant association between these integration processes at the basic
646 physiological (i.e. HRV) and cognitive (i.e. SC) levels, suggesting that HRV measures
647 may serve as a useful and readily obtainable biomarker for self-control abilities.

648 Resting HRV measured over a few minutes with relatively inexpensive and
649 commercially available equipment predicted subsequent self-control in a dietary
650 choice task as well as a validated psychometric index of dietary behavior
651 (restrained eating scale of the Three Factor Eating Questionnaire, RE). Moreover,
652 as a physiological measure that is presumably outside the domain of conscious
653 control, HRV also has the advantage of being immune to socially desirable
654 reporting (Logan et al., 2008; DeVlyder and Hilimire, 2015) or memory errors that
655 can affect the accuracy of self-reports. However, when entered into a joint model,
656 both HRV and RE were significantly related to dietary self-control suggesting that
657 they explained separate components of the variance in dietary choice. Thus, it is
658 possible to combine biomarkers such as HRV with behavioral and self-report
659 measures (e.g. the Three Factor Eating Questionnaire) to predict future self-
660 control more accurately.

661 The fact that biomarkers such as HRV can be easily acquired and readily
662 combined with other survey or task-based measures of self-control is important
663 because, taken in isolation, any single measure is likely to reveal only a partial
664 picture of self-control abilities or proclivities. In a recent meta-analysis by
665 Duckworth and Kern (2011), informant-report and self-report questionnaires,
666 behavioral readouts of executive function and delay of gratification measures
667 showed only moderate convergent validity. In other words, self-control assessed in
668 one fashion was only moderately related to self-control measured in another
669 manner. In agreement with those authors, we believe that self-control is a
670 multidimensional construct that is best assessed, and potentially forecasted, by
671 combining measures taken across multiple domains including behavior, self and
672 informant report, and both neural and more general physiological markers such as
673 HRV.

674 Heart rate variability can explain individual differences in self-control that
675 are robust to changes in environmental context. We have previously shown that
676 experiencing an acute stressor results in diminished self-control in the 45-minute
677 period following stressor onset (Maier et al., 2015). In the same sample, we find
678 that resting HRV before stressor onset predicts the level of self-control following
679 stress as well as it predicts choice in the control (i.e. not stressed) participants.
680 Thus, the association between HRV and self-controlled behavior is maintained
681 under the influence of acute stress, suggesting that the association between HRV
682 and self-control may be context independent.

683 Our current findings linking resting HRV to subsequent self-control
684 performance extend previous work reporting correlations between HRV and
685 neural activity measured simultaneously during affective and cognitive tasks. In a

686 study using Positron Emission Tomography and an emotion task, Lane et al.
687 (2009) measured regional cerebral blood flow (rCBF) when participants immersed
688 themselves during 1 minute-blocks into positive, negative, and neutral emotions
689 (evoked by film clips and vignettes of personal emotional memories) while parallel
690 PET and HRV were recorded. During the presentation of emotional (versus
691 neutral) stimuli, HRV correlated with rCBF in the caudate, midbrain, left insula,
692 and medial prefrontal cortex. When excluding all emotion-specific activation, HRV
693 correlated with rCBF in the right dorsolateral prefrontal cortex (dlPFC), bilateral
694 parietal cortex, and the left rostral anterior cingulate cortex (ACC) with high-
695 frequency (parasympathetic) components of HRV. Similarly, Gianaros et al. (2004)
696 used PET to correlate HRV with changes in rCBF in medial orbitofrontal cortex
697 (OFC), insula, ACC, amygdala, hippocampus and cerebellum as a function of task
698 demand in a working memory paradigm. A study by Nugent, Bain, Thayer, Sollers
699 & Drevets (2011) found HRV to be correlated with rCBF in lateral and medial OFC
700 when participants had to achieve different levels of strength in a handgrip task.

701 In contrast to Lane and colleagues' (2009) emotion task results and our *a*
702 *priori* predictions, we did not observe any significant correlations between HRV
703 and activity in the dlPFC during dietary choices. However, the differences in HRV
704 indices and measurement times (resting vs. task) preclude direct comparisons
705 between the previous emotion regulation and current dietary self-control results.
706 It is possible that HRV measures collected during the self-control task would tie in
707 more closely with regulation processes in dlPFC. However, our goal in the current
708 study was to test whether simple, task-independent measures of HRV are
709 associated with dietary self-control. What is consistent across studies is that
710 individual differences in HRV are correlated with activity in neural regions linked

711 to task performance across several domains (e.g. emotion regulation, working
712 memory, physical effort and dietary self-control). Together these results indicate
713 that efforts to link cognition with central and peripheral neurophysiology may
714 promote a better understanding of the nature of individual differences in health
715 and cognitive behaviors, and provide opportunities for prediction and early
716 intervention against dysfunctions (see for example Sokol-Hessner et al. (2009) and
717 Raio et al. (2013)).

718 Our study represents an important initial step in linking total HRV to self-
719 control ability. This result suggests total HRV should be considered when
720 investigating links between self-control and allostatic capacity in addition to more
721 direct indices of phasic vagal cardiac control of HRV, such as RMSSD and high-
722 frequency HRV. One rationale for doing so in the domain of dietary self-control is
723 that frequency components outside the high-frequency spectrum may include
724 information on metabolic and endocrine processes that are directly relevant to
725 dietary decisions. These components contribute to the total HRV, but oscillate on a
726 slower time scale (Berntson et al., 1997).

727 Further progress could be made by addressing this question with causal
728 manipulations, for example by inducing endocrine signals of hunger and satiety
729 and investigating whether the association between total HRV and self-control
730 success varies during these states. Another interesting avenue to pursue is
731 whether plasticity-induced changes that enable better regulation, for example
732 through transcranial electrical or magnetic stimulation of the dlPFC, might also
733 lead to an increase in HRV. A study in autistic children suggests this might be the
734 case: Wang et al. (2015) found that weekly treatment with low-frequency
735 repetitive transcranial magnetic stimulation (rTMS) for 3 months both improved

736 chronic autonomic imbalance (i.e., higher low frequency and lower high-frequency
737 contributions to total HRV, putatively reflecting a tonically high arousal level due
738 to activation of the sympathetic nervous system) and reduced the tonically
739 elevated skin conductance levels commonly seen in autism. This change was
740 accompanied by decreased irritability, hyperactivity, and less stereotyped and
741 compulsive behavior in the autistic children. Future work could therefore address
742 this regulatory mechanism in a healthy population with a similar causal
743 manipulation by stimulation techniques to further explore the nature of the link
744 between neural correlates of self-regulation and physiological markers of allostatic
745 capacity.

746 In conclusion, heart rate variability is a marker of cardiovascular and
747 mental health. Our results indicate that heart rate variability also explains
748 significant variation in self-control during dietary choice. Moreover, both HRV and
749 a standard psychometric scale of restrained eating contributed independently to
750 explaining variance in our behavioral model of self-control and could be used in
751 combination to better predict dietary self-control levels.

752

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757

758 **Conflict of interest**

759 The authors declare no competing financial interests.

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960 **Figure Legends**

961 **Figure 1.** Behavioral and physiological measurements. **(a)** In the dietary self-
962 control task, participants made a series of choices between two items on the
963 screen, that represented items they would eat at the end of the study. In the
964 challenge trials that are the focus of this paper, choosing the healthier food
965 required forgoing the tastier option. **(b)** This stylized sketch highlights the R peaks
966 of the ECG curve. The RR interval describes the distance between two subsequent
967 R peaks. In the healthy heart, the length of subsequent RR intervals consistently
968 differs on the order of milliseconds, which allows calculating heart rate variability
969 characteristics.

970

971 **Figure 2.** Combining behavioral and heart-rate variability measures to predict
972 self-control success rates. HRV and restrained eating trait (RE) were uncorrelated
973 and predicted independent and significant portions of the variation in self-control
974 behavior in our combined behavioral model (see Table 1). **(a)** This scatter plot
975 shows the association between predicted and observed self-control (SC) success
976 rates. We used the model listed in equation 2 together with a “Leave One Subject
977 Out” (LOSO) procedure to predict self-control success. Including the predictors for
978 baseline HRV and its interactions with taste and health aspects yielded a
979 coefficient of determination $R^2 = 0.77$. Moreover, omitting HRV from the predictive
980 model resulted in a 12% decrease in explained variance. The error bar plots in
981 panels b and c are intended to convey the nature of the HRV by taste and health
982 interactions listed in Table 1. **(b)** The HRV endophenotype interacted with the
983 level of taste temptation faced during self-control challenges. To visualize this
984 result, the plot shows the response patterns from participants falling into the

985 highest (black square) and lowest (gray diamond) quartiles of total HRV. The x-
986 axis represents the average taste difference level (i.e. SC difficulty) a participant
987 faced during the dietary choice task. The estimated self-control success on the y-
988 axis represents the model fit for discrete levels of the HRV by taste temptation
989 interaction. Participants with higher HRV overcame even the largest taste
990 temptations, whereas participants with low HRV who faced large taste temptations
991 frequently failed to use self-control. Panel **(c)** analogously shows the interaction
992 with the average difference in health: the higher the health difference between the
993 two foods, the more health benefit could be gained by refusing the tastier item. The
994 x-axis represents the average health difference level (i.e. potential SC benefit) a
995 participant faced during the dietary choice task. The estimated self-control success
996 on the y-axis represents the model fit for discrete levels of the HRV by health gain
997 interaction. Participants with the lowest HRV rarely used self-control if potential
998 health gains were small, whereas participants with the highest HRV engaged self-
999 control at a relatively high level regardless of how much health benefit could be
1000 gained.

1001

1002 **Figure 3.** Heart-rate variability (HRV) is correlated with BOLD signal in the
1003 ventromedial prefrontal cortex (vmPFC). Panel **(a)**: Baseline HRV positively
1004 correlated with higher activity in Self-Control Challenge > No Challenge trials in
1005 the vmPFC ($p < 0.05$, small-volume corrected). The color bar represents small-
1006 volume corrected p-values. **(b)** Within this functional ROI, the relative taste
1007 representation (taste of the chosen minus taste of the non-chosen food) correlated
1008 negatively with individual HRV ($r = -0.42$, $p = 0.002$). **(c)** There was no significant
1009 correlation between HRV and the relative health value ($r = -0.12$, $p = 0.42$).

1010 **Tables**1011 **Table 1.** Predictors of self-control success.

1012

Fixed effects	Beta estimate	Standard Error of the Mean	T	p
Intercept	0.45483	0.04434	10.258	2.28e-12
Stress	-0.07869	0.06450	-1.220	0.23021
Tdiff	-0.02450	0.11721	-0.209	0.83555
Hdiff	0.35598	0.10108	3.522	0.00116
HRV	0.01239	0.03785	0.327	0.74524
RE	0.02995	0.03951	0.758	0.45326
Stress x Tdiff	-0.38367	0.11756	-3.264	0.00237
Stress x Hdiff	0.33003	0.11868	2.781	0.00848
HRV x Tdiff	0.30100	0.06253	4.814	2.51e-05
HRV x Hdiff	-0.20929	0.06429	-3.255	0.00242
RE x Tdiff	0.23935	0.07978	3.000	0.00481
RE x Hdiff	-0.17495	0.08761	-1.997	0.05323

1013

1014 Results from a general linear model of self-control success. Self-control success
1015 was computed as the mean number of trials in which participants chose the
1016 healthier, less tasty item in trials in which health and taste were not aligned
1017 (challenge trials). Resting heart-rate-variability (HRV) was defined as the standard
1018 deviation of all RR intervals over a three-minute period. The cognitive restraint in
1019 eating score (RE) was obtained from the Three Factor Eating Questionnaire (Pudel
1020 and Westenhöfer, 1989). The regressor, Stress, is a binary factor indicating that the
1021 participant underwent the stress manipulation. The average health (Hdiff) and
1022 taste difference (Tdiff) regressors represent the mean taste temptation and health
1023 gain that participants were faced with during the dietary choice task. All estimates
1024 are reported with their standard error of the mean (SEM).

1025 **Table 2.** General linear model predicting total HRV (GLM-HRV).

Regressor	Beta estimate	Standard Error of the Mean	t	p
Intercept	189.41	31.17	6.08	< .001
# of Artifacts	5.07	1.49	3.41	0.0014
Mean Heart Rate	-1.17	0.47	-2.48	0.017
Trait Anxiety	-0.57	0.63	-0.91	0.37

1026

1027 Results from a general linear model with possible determinants of HRV
1028 (represented as untransformed values of SDNN in milliseconds): the number of
1029 artifacts corrected in the dataset and mean heart rate (after artifact correction by
1030 deletion). In order to assess whether trait anxiety explains additional variance
1031 beyond an increase in mean heart rate, we added a regressor with the trait anxiety
1032 score as measured by the Spielberger State-Trait-Anxiety Inventory, so that mean
1033 heart rate and trait anxiety compete for variance in the same model. When doing
1034 so, mean heart rate accounts for a decrease in HRV, but trait anxiety does not
1035 explain further variance. The results above hold when excluding the HRV outlier
1036 from this model.





