

# Linking brain-heart interactions to emotional arousal in immersive virtual reality

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## Data availability

We did not obtain participants' consent to release their individual data. Since our analyses focus on the single-subject level, we have only limited data which are sufficiently anonymized (e.g., summarized or averaged) to be publicly shared. Wherever possible, we provide "source data" to reproduce the manuscript's tables and figures. All code used for all analyses and plots are publicly available on GitHub at <https://github.com/afourcade/evrbhi>.

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## Author contributions

F.K., S.M.H., A.M. and M.G. conceived the original experiment, performed data acquisition and provided data. M.G. and A.F. developed the analyses. V.N. and A.V. advised analyses. A.F. wrote the analysis code, analyzed the data and wrote the first draft of the manuscript. All authors edited the manuscript.

## Competing interests

The authors declare no competing interests.

# 1 Abstract

2 The subjective experience of emotions is rooted in the contextualized perception of changes in  
3 bodily (e.g., heart) activity. Increased emotional arousal (EA) has been related to lower high-  
4 frequency heart rate variability (HF-HRV), lower EEG parieto-occipital alpha power, and higher  
5 heartbeat-evoked potential (HEP) amplitudes. We studied EA-related brain-heart interactions  
6 (BHIs) using immersive virtual reality (VR) for naturalistic yet controlled emotion induction. 29  
7 healthy adults (13 women, age:  $26\pm 3$ ) completed a VR experience that included rollercoasters  
8 while EEG and ECG were recorded. Continuous EA ratings were collected during a video replay  
9 immediately after. We analyzed EA-related changes in HF-HRV as well as in BHIs using HEPs  
10 and directional functional BHI modeling.

11 Higher EA was associated with lower HEP amplitudes in a left fronto-central electrode cluster.  
12 While parasympathetic modulation of the heart (HF-HRV) and parieto-occipital EEG alpha power  
13 were reduced during higher EA, there was no evidence for the hypothesized EA-related changes  
14 in bidirectional information flow between them. Whole-brain exploratory analyses in additional  
15 EEG (delta, theta, alpha, beta and gamma) and HRV (low-frequency, LF, and HF) frequency bands  
16 indicated a temporo-occipital cluster, in which higher EA was linked to decreased brain-to-heart  
17 ( $\text{gamma} \rightarrow \text{HF-HRV}$ ) and increased heart-to-brain ( $\text{LF-HRV} \rightarrow \text{gamma}$ ) information flow. Our  
18 results confirm previous findings from less naturalistic experiments and suggest EA-related BHI  
19 changes in temporo-occipital gamma power.

## 20 **Introduction**

21 Emotions result from internal or external events that are appraised as relevant to an organism's  
22 well-being (Gross, 1998; Rottenberg & Gross, 2003). Emotions have subjective and physiological  
23 components (Mauss & Robinson, 2009), among others (e.g., expressive; Sander et al., 2005). We  
24 aimed to link subjective emotional experience to physiological activity not only in the brain but  
25 also in the heart and their interaction under naturalistic stimulation using immersive virtual reality.

26 The subjective component of emotions or - more generally - of affect is a basic property of human  
27 experience (Wundt, 1897) or consciousness (Barrett, 2016), and it is rooted in the contextualized  
28 perception of bodily changes (James, 1884; Lange, 1885). That is, interoceptive information (e.g.,  
29 autonomic, visceral) about the physiological state of the internal body (Craig, 2002; Barrett, 2016)  
30 is combined with exteroceptive information (e.g., auditory, visual) about the physical state of the  
31 external world. The subjective experience of affect is often described using the two continuous  
32 dimensions or “core affects” of valence and *emotional* arousal (EA; Russell, 2003): Valence refers  
33 to how pleasant or unpleasant, and EA refers to how intense the experience is (Barrett & Russell,  
34 1999).

35 Sweaty palms, increased heart rate, and the throat tightening at the sight of a snake are examples  
36 of physiological responses connected to emotions. These peripheral physiological responses are  
37 regulated by the autonomic nervous system (ANS), with activity of the parasympathetic branch of  
38 the ANS being linked to rest and digestion and activity of the sympathetic branch to the “flight-  
39 or-fight” response (McCorry, 2007). Focusing on the cardiovascular response, the two branches  
40 can modulate the activity of the sinoatrial node in the heart and change the heart rate (Levy, 1971).  
41 These influences have different temporal dynamics, with sympathetic regulation being relatively

42 slow (at the order of seconds) and parasympathetic regulation being relatively fast (at the order of  
43 milliseconds; Warner & Cox, 1962; Levy & Martin, 1984). While isolating the sympathetic  
44 influence on the heart has been difficult (Goldstein et al., 2011; Reyes del Paso et al., 2013; Shaffer  
45 et al., 2014), the parasympathetic influence, or vagal cardioregulation, can be quantified by high-  
46 frequency heart rate variability (HF-HRV; Task Force, 1996). HRV refers to the fluctuations of  
47 the time between heartbeats (i.e., the interbeat interval, IBI), and its HF component (typically  
48 between 0.15 and 0.4 Hz) captures the rapid IBI changes caused by changes in parasympathetic  
49 activity - whereas its low frequency component (LF-HRV; typically between 0.04 and 0.15 Hz)  
50 reflects both sympathetic and parasympathetic influence on the heart. Autonomic and heart activity  
51 have been linked to emotion, but specific patterns that are exclusively associated with particular  
52 emotion categories could not be identified (Kreibig, 2010; Siegel et al., 2018). For the dimensional  
53 core affects of EA and valence, changes in autonomic or heart activity appear more consistently  
54 in the literature; unpleasant (i.e., negatively valenced) stimuli (e.g., movie, music) were associated  
55 with a decrease in heart rate (Palomba et al., 2000; Sammler et al., 2007) and higher EA was linked  
56 to decreased HF-HRV (Valenza et al., 2012; Luft & Bhattacharya, 2015; Hildebrandt et al., 2016),  
57 suggesting a decreased parasympathetic influence on the heart during higher EA.

58 The integration of external (exteroceptive) and internal (interoceptive) signals (e.g., from the  
59 heart), which gives rise to emotional experiences, takes place in the brain (Craig, 2009; Seth,  
60 2013). The two autonomic branches transmit sensory signals from the heart (e.g., via the vagus  
61 nerve, through the dorsal root and stellate ganglia; Dusi & Ardell, 2020) to the brainstem, where  
62 they are relayed to the cerebrum and cerebellum. Reversely, preganglionic autonomic motor  
63 neurons are also controlled by the brain; in particular by the central autonomic network (CAN),  
64 which includes the hypothalamus, amygdala, anterior cingulate, insula and medial prefrontal

65 cortex (Benarroch, 1993; Thayer & Lane, 2000, 2009). These brain regions are also consistently  
66 reported in neuroimaging studies of emotions (Dagleish, 2004; Lindquist et al., 2012). Recent  
67 causal evidence from rodents suggests that insula and brainstem circuits in particular integrate  
68 cardiac activity into information processing, influencing perception and behavior (Gehrlach et al.,  
69 2019; Hsueh et al., 2023; Klein et al., 2021; Signoret-Genest et al., 2023).

70 The activation in the heart and the brain can be electrophysiologically recorded using ECG and  
71 EEG, respectively. Both signals contain oscillatory and aperiodic components (heart: Babloyantz  
72 & Destexhe, 1988; brain: Buzsáki et al., 2013; He, 2014). In the ECG signal, oscillations in HRV  
73 are typically decomposed into LF- and HF-HRV, while in the EEG signal, five frequency bands  
74 are commonly defined: delta ( $\delta$ ; 0.3–4 Hz), theta ( $\theta$ ; 4–8 Hz), alpha ( $\alpha$ ; 8–13 Hz), beta ( $\beta$ ; 13–30  
75 Hz) and gamma ( $\gamma$ ; 30–45 Hz). Various functions, from more fundamental sensory and motor to  
76 higher cognitive processes, have been ascribed to different types of regionally distributed neural  
77 oscillations (Buzsaki, 2006). In particular, the parieto-occipital alpha rhythm is the dominant EEG  
78 rhythm in awake adults with eyes closed (Berger, 1929), where it varies with vigilance (Olbrich et  
79 al., 2009). Its physiological bases are large-scale synchronization of neuronal activity (Buzsaki,  
80 2006) and metabolic deactivation (Moosmann et al., 2003). Psychophysically, parieto-  
81 occipital alpha power is correlated to EA (Koelstra et al., 2012; Luft & Bhattacharya, 2015;  
82 Hofmann, Klotzsche, Mariola et al., 2021), as well as to attentional processes (Klimesch, 2012;  
83 van Diepen et al., 2019) which help prioritize and select sensory inputs (Treisman, 1969; Driver,  
84 2001). Particularly bottom-up or stimulus-driven attention is assumed to direct perception towards  
85 a subset of salient external stimuli (Egeth & Yantis, 1997).

86 Besides sharing an electrophysiological pattern, affect and attention have been psychologically  
87 linked. On the one hand, emotional stimuli capture attentional focus (Nummenmaa et al., 2006,

88 2009) and their processing is prioritized over non-emotional stimuli (Okon-Singer et al., 2013).  
89 On the other hand, changes in affective states (and particularly the level of EA) alter attention-  
90 related changes in salience also for non-emotional stimuli (Sutherland & Mather, 2018). As a side  
91 node, the CAN overlaps with the salience network (SN; Menon, 2015; Seeley, 2019), which is  
92 involved in directing attention towards (e.g., emotionally) relevant stimuli (Vuilleumier, 2005;  
93 Menon & Uddin, 2010).

94 In sum, as activity in the heart and the brain separately play important roles for affective  
95 experiences, their multimodal or joint analysis promises to capture the physiology of human  
96 experience more comprehensively than the analysis of either of the modalities alone (e.g.,  
97 Raimondo et al., 2017). Emotion-related brain-heart interactions (BHIs), typically measured  
98 through electrophysiological recordings, have been investigated using different methodologies: for  
99 instance, by means of event-related (e.g., heartbeat-evoked potentials [HEP]; Luft & Bhattacharya,  
100 2015) and oscillatory analyses (e.g., directional functional BHI: Candia-Rivera et al., 2022).

101 The HEP is an event-related potential (ERP) component that can be observed when the EEG signal  
102 is time-locked to the R-peaks in the ECG (Schandry et al., 1986). The HEP is taken to reflect the  
103 cortical processing of the heartbeat (Park & Blanke, 2019) and its amplitude is modulated by  
104 interoceptive (Pollatos et al., 2016) and emotional processing. For example, Luft and Bhattacharya  
105 (2015) manipulated EA through videos and music (NB: without assessing subjective experience)  
106 and found higher HEP amplitudes during blocks of higher (HA) compared to lower EA (LA) -  
107 particularly over right parietal electrodes (P6 and P8) from 0.38 to 0.46 s after the R-peak. Higher  
108 HEP amplitude has been interpreted as reflecting a shift of attentional focus from external stimuli  
109 to internal bodily states (García-Cordero et al., 2017; Villena-González et al., 2017; Petzschner et  
110 al., 2019; Zaccaro et al., 2022).

111 Directional functional BHI can be computed by jointly analyzing oscillations in EEG and ECG  
112 data, for example with the synthetic data generation (SDG) model (Catrambone et al., 2019). Based  
113 on the assumption of a bidirectional communication loop in which ongoing HRV (as a proxy for  
114 ANS activity) modulates EEG activity and, in turn, ongoing EEG activity modulates HRV, the  
115 SDG combines generative models for the EEG and the heartbeat. Using this approach, Candia-  
116 Rivera and colleagues (2022) recently found that the ascending information flow from the vagal  
117 cardiorespiration (i.e., HF-HRV) to the EEG oscillations in the delta, theta, and gamma bands  
118 correlated with EA ratings, particularly in frontal and parieto-occipital electrodes. Furthermore,  
119 higher ascending heart-to-brain information flow preceded lower descending brain-to-heart  
120 information flow and these EA-related changes in BHI were associated with HF-HRV but not LF-  
121 HRV (Candia-Rivera et al., 2022).

122 Besides advances in the multimodal analysis of physiological signals, affective neuroscience is  
123 currently experiencing advances in emotion elicitation. Past research has extensively used static  
124 images repeatedly presented in trial-based designs, often creating an artificial and discontinuous  
125 experience (Bridwell et al., 2018; Huk et al., 2018). However, affective phenomena, along with  
126 their associated physiological responses, are varying on different continuous time scales; for  
127 example, EA can fluctuate on the order of minutes (Kuppens et al., 2010) or seconds (Mikutta et  
128 al., 2012). Dynamic stimuli that capture such naturalistic fluctuations in affective experience could  
129 be videos (Samide et al., 2020) or even emotional stimuli in everyday life (Grosse Rueschkamp et  
130 al., 2019). While the former remain relatively artificial (e.g., non-interactive), the latter are difficult  
131 to experimentally control (e.g., comprehensively measure). Immersive Virtual Reality (VR;  
132 wherein the user is surrounded by the virtual environment) presents a trade-off between naturalism  
133 and experimental control (Bohil et al., 2011) and offers several advantages: It enables (1) the

134 creation and presentation of computer-generated scenarios that are contextually rich and engaging  
135 (Diemer et al., 2015), (2) naturalistic elicitation of specific psychological states (which may be  
136 particularly relevant for affective states; Baumgartner et al., 2006; Riva et al., 2007; Dores et al.,  
137 2014; Meuleman & Rudrauf, 2021), and (3) the recording of multimodal measurements (e.g.,  
138 subjective ratings, movements, heart and brain signals) - with more experimental control (and less  
139 noise) than in real-life assessments (Meuleman & Rudrauf, 2021).

140 Recently, we used an emotionally arousing VR experience (including two rollercoasters with a  
141 break in-between) while EEG and ECG were recorded and EA was continuously rated (Hofmann,  
142 Klotzsche, Mariola et al., 2021). Using spatial filtering and non-linear machine learning for the  
143 analysis of the EEG data, we could decode subjective EA from parieto-occipital alpha power.  
144 Given the importance of cardiac activity and the heart-brain axis for affective experience and EA,  
145 we now included the ECG into the analysis. We thereby expected the joint analysis to offer insights  
146 about the physiology of EA that are not accessible when investigating EEG signals alone. In  
147 particular, we investigated the role of vagal cardioregulation for the EEG alpha power reduction  
148 during HA compared to LA, and our hypotheses were:

- 149 1. Cardiac activity and vagal cardioregulation (indexed by IBIs and HF-HRV, respectively)  
150 differ between states of HA and LA.
- 151 2. HEP amplitudes differ between states of HA and LA, particularly around 400 ms after a  
152 heartbeat and in right temporo-parietal electrodes (based on Luft & Bhattacharya, 2015).
- 153 3. EA-related changes in parieto-occipital alpha oscillations (Hofmann, Klotzsche, Mariola  
154 et al., 2021) are related to changes in heart activity (i.e., HF-HRV).



## 155 **Methods**

### 156 1. Participants

157 Participants were recruited via the participant database at the Berlin School of Mind and Brain (an  
158 adaptation of ORSEE; Greiner, 2015). Inclusion criteria were right-handedness, normal or  
159 corrected-to-normal vision, proficiency in German, no (self-reported) psychiatric, or neurological  
160 diagnoses in the past 10 years, and less than 3 hr of experience with VR. Participants were  
161 requested not to drink coffee or other stimulants 1 hr before coming to the lab. The experiment  
162 took ~2.5 hr, and participants were reimbursed with 9 € per hour. They signed informed consent  
163 before their participation, and the study was approved by the Ethics Committee of the Department  
164 of Psychology at the Humboldt-Universität zu Berlin. Forty-five healthy young adults (22 men,  
165 mean age:  $23 \pm 4$ , range: 20-32 years) came to the lab. Data from eleven participants needed to be  
166 discarded due to technical problems ( $n = 5$ ), electrode malfunctioning (EEG:  $n = 1$ , ECG:  $n = 3$ ),  
167 discontinuation of the experiment ( $n = 1$ ) or violation of inclusion criteria ( $n = 1$ ), so that data from  
168 34 participants were processed. After EEG quality assurance (details below), data from 29  
169 participants (16 men, mean age:  $26 \pm 3$ , range: 20-31 years) entered the analyses.

### 170 2. Materials

171 *EEG* (sampled at 500 Hz, hardware-based low-pass filter at 131 Hz) was recorded with 30 active  
172 Ag/AgCl electrodes attached according to the international 10-20 system (actiCap and LiveAmp,  
173 Brain Products GmbH, Germany) and referenced to electrode FCz. Two additional electrodes  
174 captured eye movements (electrooculography) and were placed below and next to the right eye.

175 ECG was synchronously recorded (sampled at 500 Hz) with additional electrodes in a bipolar Lead  
176 I configuration. A grounding electrode was placed on the right clavicle and two passive lead  
177 electrodes were positioned bilaterally on the participant's torso (lower rib cage). In addition, skin  
178 conductance was recorded at the index and annular fingers of the left hand (data not considered  
179 here).

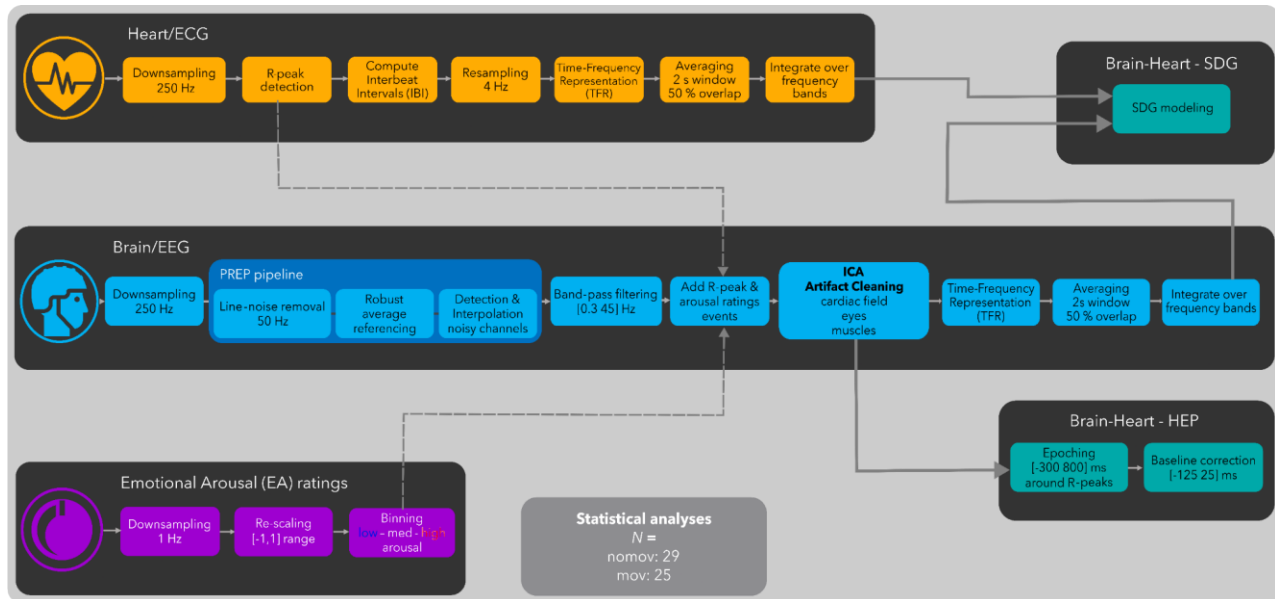
180 *VR setup:* A HTC Vive HMD (HTC, Taiwan) with headphones was attached on top of the EEG  
181 cap using cushions to avoid pressure artifacts. The VR experience was commercially available on  
182 Steam ("Russian VR Coasters" by Funny Twins Games, 2016).

### 183 3. Design and Procedure

184 Participants had a 280-s VR experience, which included two rollercoasters (153 s, 97 s) and a 30-  
185 s intermediate break, twice: once keeping their head straight to avoid movement-related artifacts  
186 in the EEG data (*nomov* condition) and once freely moving their head (*mov* condition). The order  
187 was randomized across participants (in the 29 analyzed, *nomov-mov*:  $n = 13$ ; *mov-nomov*:  $n = 16$ ).  
188 In the subsequent rating phase (following immediately after the VR experience for each movement  
189 condition), the participants saw a 2D recording of their experience on a virtual screen. While  
190 viewing the video, the participants recalled their EA and continuously reported it using a dial  
191 (Griffin PowerMate USB; sampling frequency: 50 Hz), with which they manipulated a vertical  
192 rating bar next to the video, ranging from low (0) to high (50) EA (McCall et al., 2015). For further  
193 details of the experimental setup and data acquisition procedures, please refer to Hofmann,  
194 Klotzsche, Mariola et al. (2021).

## 195 4. Preprocessing

196 An overview of the preprocessing steps is presented in Figure 1. The preprocessing steps were  
197 applied separately for data recorded during the *nomov* and *mov* conditions (i.e., without and with  
198 head movement, respectively).



200 **Figure 1.** Flowchart of the preprocessing pipeline. Emotional arousal (EA) ratings (in purple),  
201 Heart/ECG (in orange), Brain/EEG (in blue), Brain-Heart (in turquoise): Heart-evoked potentials  
202 (HEP) and synthetic data generation (SDG) modeling; Please note that TFR computation and  
203 SDG modeling was preceded by symmetric padding. Further details of the preprocessing steps  
204 can be found in the corresponding sections.

### 205 4.1. Data Cropping

206 EEG data, ECG data, and retrospective arousal ratings were cropped by 10 s (2.5 s at beginning  
207 and 2.5 s at end of each rollercoaster) to avoid outliers related to the onset and offset of the virtual  
208 rollercoaster rides. This resulted in two time series (*nomov*, *mov*) of 270 s per participant.

## 209 4.2. Emotional Arousal (EA) Ratings

210 Subjective reports were downsampled to 1 Hz by averaging non-overlapping sliding windows and  
211 rescaled to a [-1 1] range. The ratings were then divided by a tertile split into three distinct bins of  
212 arousal ratings (low, medium, high) per participant. The medium arousal ratings were discarded,  
213 resulting in 180 samples per subject (90 for low, 90 for high EA).

## 214 4.3. Heart/ECG

215 ECG recordings were downsampled to 250 Hz. Automatic R-peak detection and manual  
216 inspection/correction was performed with the EEGLAB extension HEPLAB (version 1.0.1;  
217 Perakakis, 2019) in MATLAB (version R2022a).

218 IBI time series were computed, resampled to 4 Hz (cubic-spline interpolation) and their time-  
219 frequency representation (TFR) performed using Continuous Wavelet Transform (CWT, mother  
220 wavelet: Morlet,  $\omega_0 = 6$ ), using the neurokit2 package (version 0.2.3; Makowski et al., 2021) in  
221 Python (version 3.10). To this end, to minimize artifacts due to semi-continuity (i.e., transition  
222 effects at the beginning and end of the break), the first R-peak after the beginning and end of the  
223 break were removed before resampling. To minimize edge artifacts at the beginning and end of  
224 the time-series, a symmetric padding (70 s of inverted data, concatenated at the beginning and end  
225 of time-series) was added to the IBI time-series before computing CWT.

226 The TFRs were downsampled to 1 Hz by averaging within a sliding window of 2 s and 50 %  
227 overlap. High and low heart rate variability spectral-power time series were derived by integrating  
228 TFRs within the frequency ranges 0.04–0.15 Hz (LF-HRV) and 0.15–0.4 Hz (HF-HRV). Finally,  
229 the symmetric padding was partially removed from the IBI and HRV time-series, keeping 35 s of  
230 symmetric padding in order to initialize the SDG models (see below).

#### 231 4.4. Brain/EEG

232 EEG data were preprocessed and analyzed with custom MATLAB and Python scripts building on  
233 the EEGLAB toolbox (version 2023.0; Delorme & Makeig, 2004) and MNE (version 1.1.0;  
234 Gramfort et al., 2013; Larson et al., 2022). Continuous data were downsampled to 250 Hz and  
235 PREP pipeline (v.0.56.0; Bigdely-Shamlo et al., 2015) procedures were applied for line-noise  
236 removal (line frequency: 50 Hz), robust referencing to average, and detection as well as spherical  
237 interpolation of noisy channels. On average, 2.08 and 2.47 channels per subject were interpolated  
238 in the *nomov* and *mov* condition, respectively. Data were then bandpass filtered (0.3–45 Hz;  
239 Hamming windowed sinc FIR filter). Retrospective arousal ratings and R-peak timings were added  
240 as event markers to the data sets.

241 ICA (Extended infomax; Lee et al., 1999) decomposition was used to identify and remove EEG  
242 artifacts caused by eye movements, blinks, cardiac field artifacts (CFA) and muscular activity. To  
243 facilitate the decomposition, ICA projection matrices were calculated on a copy of the data, high-  
244 pass filtered at 1 Hz (instead of 0.3 Hz; Winkler et al., 2015) and from which the noisiest parts had  
245 been removed. To this end, a copy of the continuous data was split into 270 epochs of 1 s length.  
246 Epochs containing absolute voltage values  $> 100 \mu\text{V}$  in at least one channel (excluding channels  
247 that reflected eye movements, i.e., EOG channels, Fp1, Fp2, F7, F8) were deleted. Extended  
248 infomax (Lee et al., 1999) ICA decomposition was calculated on the remaining parts of the data  
249 (after correcting for rank deficiency with a principal component analysis). Subjects with  $> 90$  to-  
250 be-deleted epochs (33 % of the data) were discarded from further analyses (*nomov*:  $n = 5$ ; *mov*:  $n$   
251  $= 9$ ). Artefactual ICA components were semi-automatically selected using the SASICA extension  
252 (version 1.3.8; Chaumon et al., 2015) of EEGLAB and visual inspection. On average, 10.51  
253 (*nomov*; eye: 2.97, muscle: 4.79, CFA: 1.21, other: 1.45) and 13.40 (*mov*; eye: 3.36, muscle: 5.84,

254 CFA: 1.01, other: 2.92) components per subject were discarded. The remaining ICA weights were  
255 back-projected onto the continuous time-series.  
256 TFRs were calculated using Continuous Wavelet Transform (CWT; mother wavelet: Morlet,  
257 number of cycles = 7). To minimize edge artifacts and transition effects, CWT was computed on  
258 each section separately (roller coaster 1, break, roller coaster 2) with a symmetric padding and then  
259 re-concatenated together.  
260 The resulting TFRs were downsampled to 1 Hz by averaging within a moving window of 2 s and  
261 50 % overlap. The EEG spectral power time-series at each electrode were derived by integrating  
262 the TFRs within the five classical frequency bands: delta ( $\delta$ ; 0.3–4 Hz), theta ( $\theta$ ; 4–8 Hz), alpha  
263 ( $\alpha$ ; 8–13 Hz), beta ( $\beta$ ; 13–30 Hz) and gamma ( $\gamma$ ; 30–45 Hz). Thirty-five seconds of symmetric  
264 padding at the beginning of the time-series was kept to initialize the SDG models (see below).

#### 265 4.5. Brain-Heart

266 In addition to the preprocessing steps described above, additional processing steps were applied  
267 for the joint analysis of heart and brain signals:

##### 268 4.5.1. Heartbeat-Evoked Potentials (HEP)

269 In the time domain, the preprocessed EEG data were epoched, from 300 ms before each R-peak to  
270 800 ms after. Epochs were then baseline corrected by subtracting for each epoch the mean voltage  
271 in the time-window [-125 -25] ms.

##### 272 4.5.2. Synthetic Data Generation (SDG)

273 IBI, LF-HRV, HF-HRV, and alpha spectral power time-series for each subject and head movement  
274 condition were used as inputs for the SDG model (Catrambone et al., 2019).

275 In this approach, the ECG R-peaks are modeled (based on integral pulse frequency modulation;  
276 Brennan et al., 2002) as a sequence of Dirac delta functions, which are generated by integrating  
277 the activity of two oscillators (one for each HRV frequency band: LF and HF) representing the  
278 autonomic regulation of the heart activity. Crucially, the amplitudes of the oscillators depend on  
279 an additional brain-to-heart coupling coefficient. This coefficient quantifies the strength of the  
280 information flow from a specific EEG frequency band to a specific HRV frequency band. The  
281 EEG signal, in turn, is modeled (based on adaptive Markov process amplitude; Al-Nashash et al.,  
282 2004) as multiple oscillators (one for each frequency band: delta, theta, alpha, beta, gamma),  
283 whose amplitudes depend on an additional heart-to-brain coupling coefficient. This coefficient  
284 quantifies the strength of the information flow from a specific HRV frequency range to a specific  
285 EEG frequency range. Therefore, both EEG and HRV time-series are mutually dependent, and  
286 their interaction is modulated by the introduced coupling coefficients. Finally, by means of inverse  
287 modeling, both brain-to-heart and heart-to-brain coupling coefficients can be derived.

288 As model parameters, a 15 s long time window with a 1 s step was used to estimate the coefficients,  
289 and the central frequencies used were  $\omega_s = 2\pi \cdot 0.1 \text{ rad/s}$  (LF band central frequency = 0.1 Hz)  
290 and  $\omega_p = 2\pi \cdot 0.25 \text{ rad/s}$  (HF band central frequency = 0.25 Hz). The output of the model was  
291 the time courses of the coupling coefficients, in both direction (i.e., brain-to-heart and heart-to-  
292 brain), for all combinations of brain oscillations (delta, theta, alpha, beta, and gamma) and HRV  
293 components (LF and HF).

294 Please note that with these parameters, the SDG model needed 30 s to initialize. To avoid missing  
295 data for the first 30 s of the VR experience, all the inputs had 35 s of symmetric padding added at  
296 the beginning and end. This symmetric padding was kept from the previous preprocessing steps  
297 (TFR computation).

298

## 299 5. Statistical Analysis

### 300 5.1. Selection of Region of Interest (ROI)

301 Based on previous findings (Hofmann, Klotzsche, Mariola et al., 2021; Candia-Rivera et al., 2022),  
302 we focused on the interaction between alpha power and HF-HRV, in all parieto-occipital  
303 electrodes. We therefore defined a ROI including the following EEG electrodes: Pz, P3, P4, P7,  
304 P8, O1, O2, and Oz.

### 305 5.2. Heart/ECG

306 From the IBI and HRV time-series, time-points corresponding to low and high arousal ratings were  
307 selected and entered into linear mixed models (LMM; lme4 [version 1.1-29] and lmerTest [version  
308 3.1-3] packages in R [version 4.1.0]; Bates et al., 2014; Kuznetsova et al., 2017), with two factors:  
309 (emotional) arousal (two levels: high, low); and (head) movement (two levels: nomov, mov). HRV  
310 values were log-transformed in order to approximate a normal distribution.

311 Each factor and their interaction were entered both as fixed and random effect (i.e., full model;  
312 Barr et al., 2013), as follows:

313  $IBI \text{ or } \log(HRV) \sim 1 + \text{arousal} + \text{movement} + \text{arousal} * \text{movement}$

314  $+ (1 + \text{arousal} + \text{movement} + \text{arousal} * \text{movement} | ID)$

315 In the fixed effects, an intercept and slopes for the two factors and their interaction were estimated.

316 In the random effects, an intercept and slopes for the two factors and their interaction were  
317 estimated within participants.



318 *P*-values for *F*- and *t*-tests were calculated using the lmerTest ANOVA (type 3) function using  
319 Satterthwaite's method. Estimated marginal means (with 95% confidence intervals) and post hoc  
320 pairwise comparisons (with Tukey correction for *p*-values) were computed using the emmeans  
321 package (version 1.7.3; Lenth, n.d.).

### 322 5.3. Brain/EEG

323 For each participant and each head movement condition, alpha spectral power was averaged over  
324 the electrode ROI. From the alpha spectral power time-series, time-points corresponding to low  
325 and high arousal ratings were selected and entered into the same LMM as for the Heart/ECG  
326 analysis, with two factors: (emotional) arousal (two levels: high, low); and (head) movement (two  
327 levels: nomov, mov). Alpha power values were log-transformed in order to approximate a normal  
328 distribution.

329 Each factor and their interaction were entered both as fixed and random effect, as follows:

330  $\log(\alpha) \sim 1 + \text{arousal} + \text{movement} + \text{arousal} * \text{movement}$

331  $+ (1 + \text{arousal} + \text{movement} + \text{arousal} * \text{movement} | \text{ID})$

### 332 5.4. Brain-Heart

#### 333 5.4.1. HEP

334 In a whole-head analysis, non-parametric cluster-based permutation *t*-tests were used to compare  
335 HEP amplitudes between HA and LA between 250 ms and 450 ms after R-peaks, by pooling the  
336 data from both head movement conditions. Previous studies (e.g., Schandry et al., 1986; Al et al.,  
337 2020) typically reported HEPs between 250 and 400 ms; we extended this time-window to 450 ms  
338 to include Luft and Battacharya (2015) findings. A cluster threshold of  $p = .05$  (for clustering data

339 points temporally and spatially adjacent) and 10,000 random permutations (to create the null  
340 distribution) were used. Clusters with  $p < .05$  (two-tailed) in the permutation test were considered  
341 significant.

#### 342 5.4.2. SDG

343 For each participant and each head movement condition, heart-to-brain and brain-to-heart  
344 couplings (model outputs  $\text{HF-HRV} \rightarrow \alpha$  and  $\alpha \rightarrow \text{HF-HRV}$ , respectively) were averaged over the  
345 electrode ROI. Time-points corresponding to low and high arousal ratings were selected and  
346 entered into the same LMM as for the Heart/EEG and Brain/EEG analyses, with two factors:  
347 (emotional) arousal (two levels: high, low); and (head) movement (two levels: nomov, mov).  
348 Coupling values were log-transformed in order to approximate a normal distribution.

349 Each factor and their interaction were entered both as fixed and random effect, as follows:

350  $\log(\text{HF-HRV} \rightarrow \alpha)$  or  $\log(\alpha \rightarrow \text{HF-HRV}) \sim 1 + \text{arousal} + \text{movement} + \text{arousal} * \text{movement}$

351  $+ (1 + \text{arousal} + \text{movement} + \text{arousal} * \text{movement} | \text{ID})$

## 352 6. HEP Source Localization

353 Exact low-resolution tomography analysis (eLORETA, RRID:SCR\_007077; Pascual-Marqui,  
354 2007) was used to localize the sources corresponding to HEP differences between HA and LA.  
355 Our pipeline was based on the work of Idaji et al., 2020, who customized the eLORETA  
356 implementation of the M/EEG Toolbox of Hamburg (<https://www.nitrc.org/projects/meth/>). Our  
357 forward model was constructed via the New York Head model (Haufe et al., 2014; Huang et al.,  
358 2016; Haufe & Ewald, 2019) with approximately 2000 voxels and by using 28 out of 30 scalp  
359 electrodes (TP9 and TP10 were removed because they are not contained in the model). Crucially,

360 we constrained our sources to be perpendicular to the cortical surface. Individual HA vs. LA scalp  
361 activations were taken as the averaged topography of the difference of HEPs between HA and LA  
362 within the time-window of observed EA-related HEP differences at the group level (328 to 360  
363 ms after R-peak, based on the cluster-based permutation testing). Inverse modeling was computed  
364 separately per participant and the L2-normalized source activations were then averaged across all  
365 subjects.

## 366 7. Control and Exploratory Analyses

367 To test the robustness of our methods and the specificity of our results, we conducted several  
368 control analyses.

### 369 7.1. ECG Waveform

370 To control for potential confounds in our HEP results, we tested for possible differences in the  
371 ECG waveforms between HA and LA. We compared the ECG signal time-locked to the R-peak  
372 of HA vs. LA within participants, using two-tailed paired t-tests at all time-points within the time-  
373 window of observed EA related HEP differences. The *p*-value was corrected for multiple  
374 comparisons with False Discovery Rate (FDR; Benjamini & Yekutieli, 2001).

### 375 7.2. Other frequency bands

376 To evaluate the specificity of the effects in the alpha band and explore arousal-related changes in  
377 (A) brain activity and (B) BHI (Candia-Rivera et al., 2022), we performed a whole-scalp analysis  
378 for (A) all the EEG frequency bands: delta ( $\delta$ ; 0.3–4 Hz), theta ( $\theta$ ; 4–8 Hz), alpha ( $\alpha$ ; 8–13 Hz),  
379 beta ( $\beta$ ; 13–30 Hz) and gamma ( $\gamma$ ; 30–45 Hz), and (B) their integration in SDG (LF-HRV  $\rightarrow$   $\delta$ ,  $\delta$   
380  $\rightarrow$  LF-HRV, HF-HRV  $\rightarrow$   $\delta$ ,  $\delta$   $\rightarrow$  HF-HRV; LF-HRV  $\rightarrow$   $\theta$ ,  $\theta$   $\rightarrow$  LF-HRV, HF-HRV  $\rightarrow$   $\theta$ ,  $\theta$   $\rightarrow$

381 HF-HRV; LF-HRV  $\rightarrow \alpha$ ,  $\alpha \rightarrow$  LF-HRV, HF-HRV  $\rightarrow \alpha$ ,  $\alpha \rightarrow$  HF-HRV; LF-HRV  $\rightarrow \beta$ ,  $\beta \rightarrow$  LF-  
382 HRV, HF-HRV  $\rightarrow \beta$ ,  $\beta \rightarrow$  HF-HRV; LF-HRV  $\rightarrow \gamma$ ,  $\gamma \rightarrow$  LF-HRV, HF-HRV  $\rightarrow \gamma$ ,  $\gamma \rightarrow$  HF-  
383 HRV). To this end, at each electrode, we averaged the different metrics over the head movement  
384 conditions, and performed paired t-tests between the mean during HA and the mean during LA  
385 for each participant.

## 386 Results

### 387 1. Participants

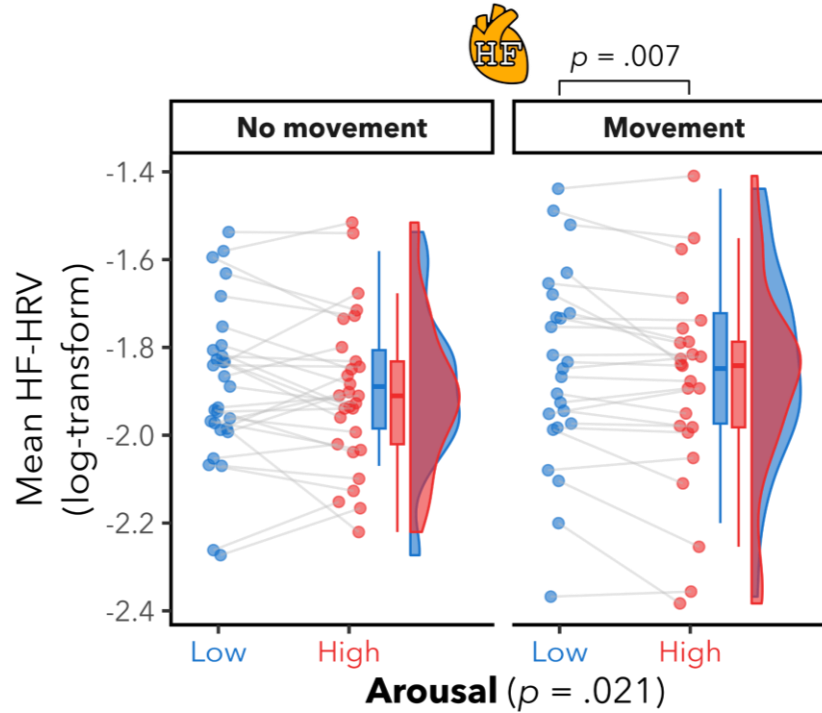
388 After the EEG quality assurance during preprocessing, the data from 29 participants (16 men, mean  
389 age:  $26 \pm 3$ , range: 20-31 years) entered the subsequent analyses. More specifically, after excluding  
390 5 (*nomov*) and 9 (*mov*) participants, results were based on :  $N_{nomov} = 29$  and  $N_{mov} = 25$ .

### 391 2. Heart/ECG

392 There was a significant main effect of arousal ( $F(1, 28.6) = 5.9, p = .021$ ) on HF-HRV (see Figure  
393 2). No evidence for a main effect of head movement ( $F(1, 24.6) = 1.6, p = .218$ ), nor the interaction  
394 ( $F(28.1) = 1.4, p = .245$ ) was found. Post-hoc pairwise comparisons of the estimated marginal  
395 means revealed significantly lower HF-HRV for HA compared to LA in the free head movement  
396 condition (*mov*;  $t(24.7) = -3.0, p = .007$ ), but not in the condition without head movement (*nomov*;  
397  $t(28.0) = -1.1, p = .285$ ).

398 We observed the same patterns for LF-HRV, that is, a significant main effect of arousal  $F(1,$   
399  $26.9) = 9.5, p = .005$ ; see Figure S1 in Supplements), no significant main effect of movement  
400 ( $F(1, 25.5) = 2.2, p = .152$ ), and no significant arousal-by-movement interaction ( $F(1, 26.0) =$   
401  $0.5, p = .492$ ). Post-hoc pairwise comparisons of the estimated marginal means revealed  
402 significantly lower LF-HRV during higher arousal in the *mov* ( $t(25.1) = -3.2, p = .004$ ), but not  
403 in the *nomov* ( $t(28.0) = -1.6, p = .124$ ) condition.

404 No significant effects were observed on heart rate (i.e., IBI; all  $p > .05$ ; see Figure S1 in  
405 Supplements).

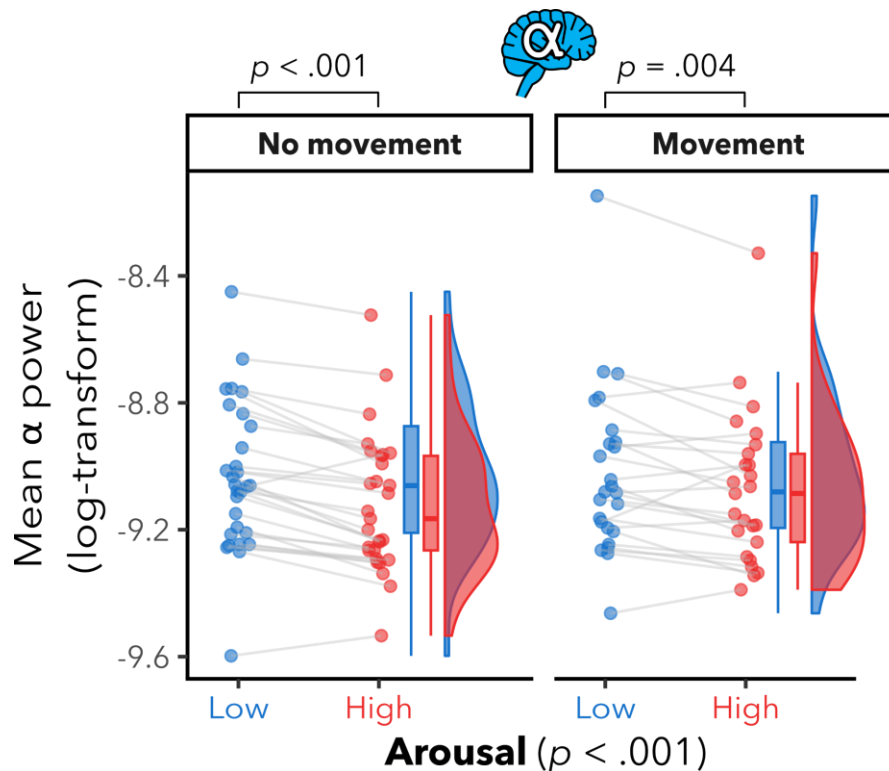


406

407 **Figure 2.** Significant high-frequency heart rate variability (HF-HRV) differences between high  
408 and low emotional arousal, in the free head movement condition. Mean HF-HRV per participant  
409 for low (blue color) and high (red color) arousal and for runs without and with free head  
410 movement. Box plots (horizontal bar: mean; whiskers: 1.5 interquartile range); individual dots  
411 represent individual participants. There was a significant effect of arousal, but not of head  
412 movement nor the interaction. Post-hoc pairwise comparisons showed lower HF-HRV during  
413 higher arousal in the free head movement condition, but not in the without head movement  
414 condition. There was no evidence for any significant effects of arousal, movement nor interaction  
415 on interbeat intervals (IBI) (see Figure S1 in Supplements). There was also a significant effect of  
416 arousal on LF-HRV (see Figure S1 in Supplements), but no significant effects of movement nor  
417 interaction.

418 3. Brain/EEG

419 We found a significant effect of arousal ( $F(1, 27.7) = 30.7, p < .001$ ) on participants' alpha power  
420 in parieto-occipital regions (see Figure 3). There were no significant head movement ( $F(1, 24.1)$   
421  $= 2.5, p = .128$ ) nor interaction effects ( $F(1, 24.1) = 2.9, p = .101$ ). Post-hoc pairwise comparisons  
422 of the estimated marginal means revealed significantly lower alpha power in parieto-occipital  
423 regions for HA compared to LA in both the free (*mov*;  $t(25.9) = -3.2, p = .004$ ) and without (*nomov*;  
424  $t(28.0) = -6.6, p < .001$ ) head movement conditions.



425  
426 **Figure 3.** Lower parieto-occipital alpha power in high vs. low arousal. Mean log  $\alpha$  power within  
427 the region of interest (ROI: electrodes Pz, P3, P4, P7, P8, O1, O2, and Oz) per participant for low  
428 (blue color) and high (red color) arousal and for runs with and without free head movement. Box  
429 plots (horizontal bar: mean; whiskers: 1.5 interquartile range); individual dots represent  
430 individual participants. There were significant effects of arousal, but not of head movement nor

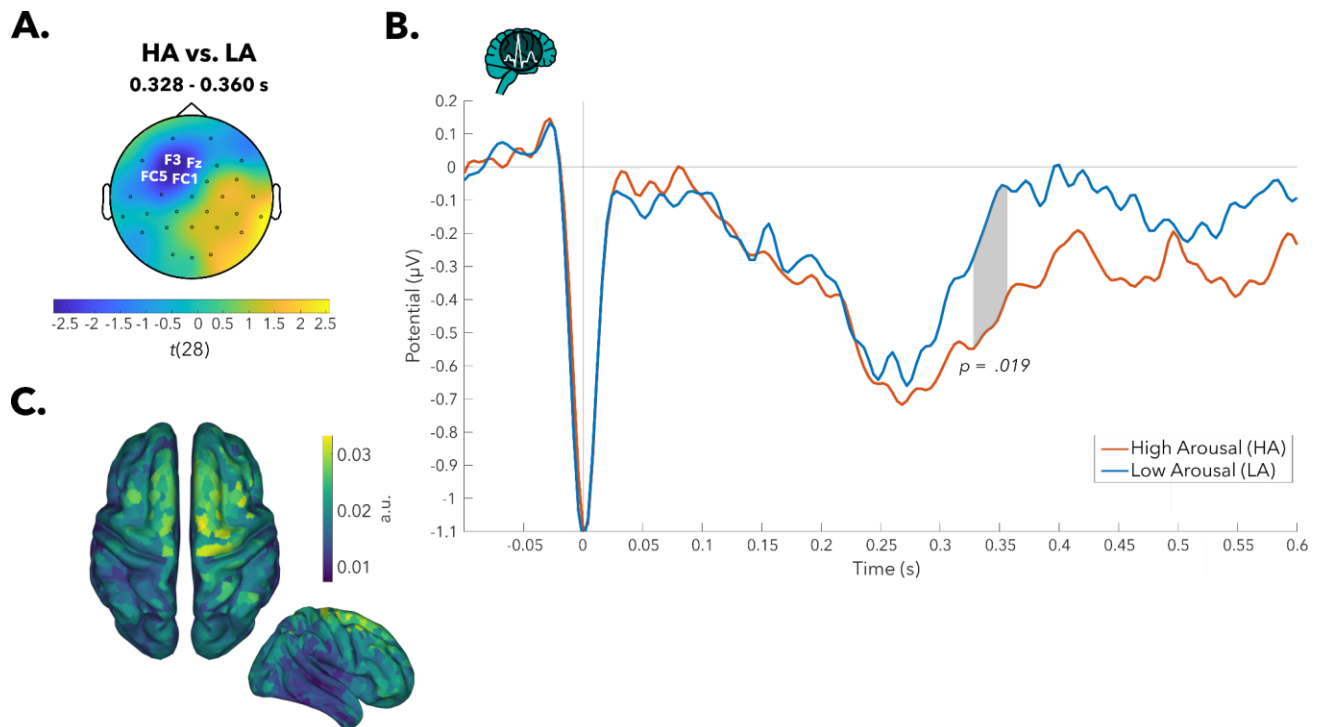
431 *interaction. Post-hoc pairwise comparisons showed significantly lower alpha power in parieto-*  
432 *occipital regions for HA compared to LA in both the free and without head movement conditions.*

#### 433 4. Brain-Heart

##### 434 4.1. HEP

435 The cluster-based permutation tests revealed a significant HEP difference between HA and LA,  
436 indicated by a cluster at the left fronto-central regions (C3, FC1, FC5, Fz, F3 electrodes; Monte  
437 Carlo  $p = .019$ ; see Figure 4A) from 328 to 360 ms after R-peak, with lower (i.e., more negative)  
438 HEP amplitude for HA than for LA (see Figure 4B).

439 The source localization (via eLORETA) yielded a distribution of sources where the strongest  
440 values were located close to and inside the central sulcus, in premotor, sensorimotor and  
441 supplementary motor areas (see Figure 4C).



442

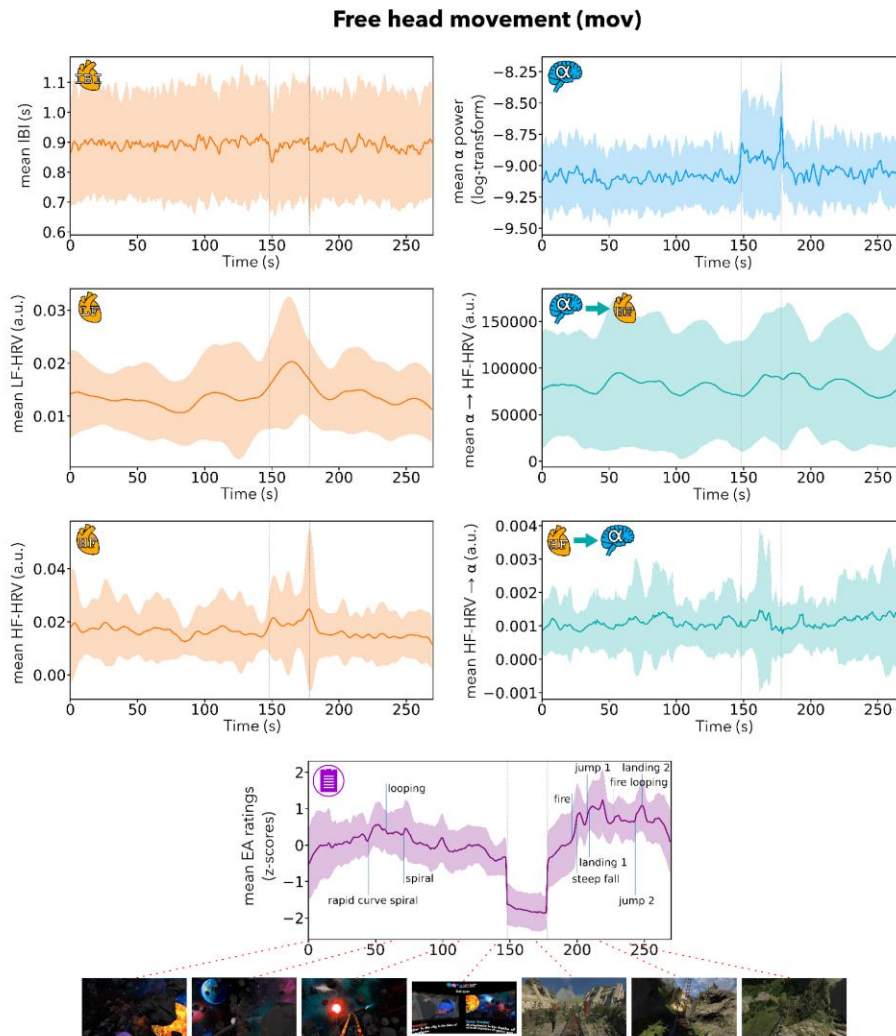


443 **Figure 4.** Heartbeat-evoked potential (HEP) amplitudes significantly differed between high (HA)  
444 and low arousal (LA) over left fronto-central electrodes. **A.** Topographical map of *t*-values for  
445 HEP differences between HA and LA: Grand average across 29 participants (pooled data across  
446 both head movement conditions) in the 328- to 360-ms time window, where a significant difference  
447 ( $HA > LA$ ) was observed in the cluster of highlighted electrodes. **B.** HEP time courses (HA in red,  
448 LA in blue) averaged across the cluster. **C.** Source localization (exact low resolution tomography  
449 analysis [eLORETA]) of HEP differences between HA and LA. The projection in source space  
450 suggests a distribution of sources with strongest values in premotor, sensorimotor, supplementary  
451 motor areas, around the central sulcus. Colors represent the inversely modeled contribution of the  
452 cortical voxels to the spatial pattern yielded by the HA vs. LA contrast.

453 We also observed another cluster over right temporo-parietal electrodes (P8, TP10, T8 electrodes,  
454 from 352 to 356 ms after R-peak), with higher HEP amplitudes for HA compared to LA. This  
455 cluster, however, did not survive cluster-correction for multiple comparisons (Monte Carlo  $p =$   
456 .310).

#### 457 4.2. SDG

458 For an overview, the mean time-series over all participants of heart, brain and brain-heart metrics  
459 of interest, for the condition with free head movement (*mov*), are presented in Figure 5. The time-  
460 series for the condition without head movement (*nomov*) are available in the Supplements (see  
461 Figure S2).

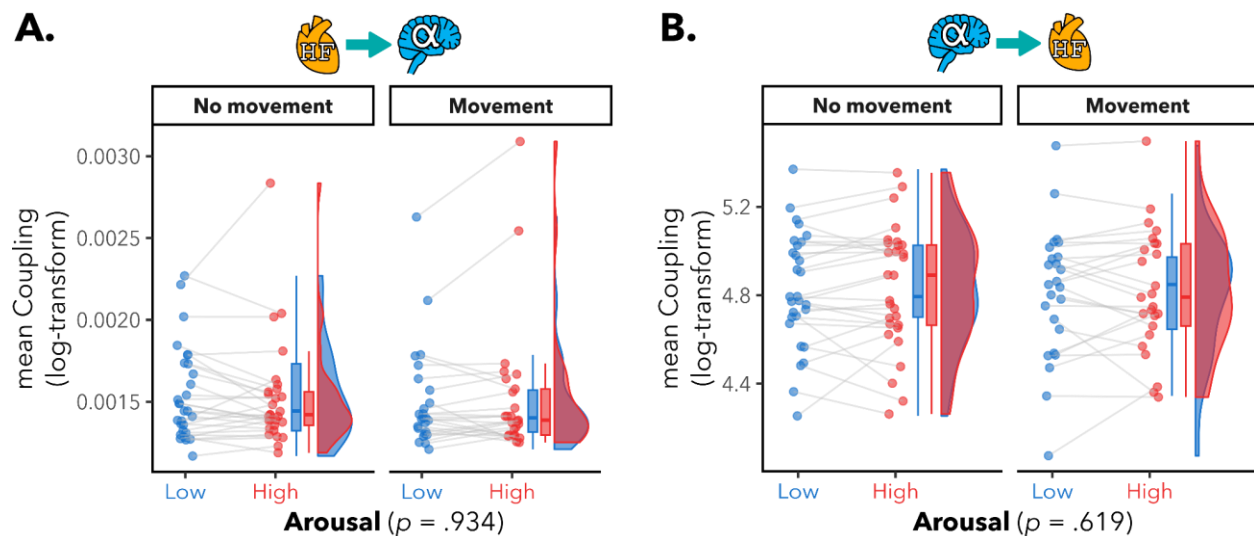


462

463 **Figure 5.** Mean time-series across participants of interbeat intervals (IBI), low-frequency heart  
 464 rate variability (LF-HRV), high-frequency heart rate variability (HF-HRV), log  $\alpha$  power averaged  
 465 across the region of interest (ROI: electrodes Pz, P3, P4, P7, P8, O1, O2, and Oz), brain-to-heart  
 466 coupling coefficient ( $\alpha \rightarrow$  HF-HRV; averaged across ROI), heart-to-brain coupling coefficient  
 467 (HF-HRV  $\rightarrow$   $\alpha$ ; averaged across ROI) and emotional arousal ratings, for the condition with free  
 468 head movement (mov). The shaded areas represent  $\pm 1$  SD. Coloured lines: mean across  
 469 participants; vertical lines (light grey): beginning and end of the break; vertical lines (blue):  
 470 manually labeled salient events (for illustration). Bottom row: exemplary screenshots of the virtual

471 reality (VR) experience. The time-series for the condition without head movement (nomov) are  
 472 shown in the Supplements (see Figure S2).

473 There was no significant main effect of arousal (HF-HRV  $\rightarrow$   $\alpha$ :  $F(1, 27.1) = 0.01, p = .934$ ;  $\alpha \rightarrow$   
 474 HF-HRV:  $F(1, 22.3) = 0.3, p = .619$ ) on the BHI coupling coefficients in both directions (see  
 475 Figure 6). There was also no evidence for a main effect of movement (HF-HRV  $\rightarrow$   $\alpha$ :  $F(1, 24.3)$   
 476  $= 0.8, p = .371$ ;  $\alpha \rightarrow$  HF-HRV:  $F(1, 23.5) = 1.0, p = .339$ ) nor an arousal-by-movement interaction  
 477 (HF-HRV  $\rightarrow$   $\alpha$ :  $F(1, 25.2) = 1.6, p = .217$ ;  $\alpha \rightarrow$  HF-HRV:  $F(1, 22.7) = 0.01, p = .930$ ).



478 **Figure 6.** No significant Brain-Heart Interaction (BHI) differences between high and low  
 479 emotional arousal. Mean directional BHI coupling coefficients per participant, for low (blue  
 480 color) and high (red color) arousal, and for runs with and without free head movement. The BHI  
 481 coupling coefficients were computed using a Synthetic Data Generation (SDG) model  
 482 (Catrambone et al., 2019); Heart related input: high-frequency heart rate variability (HF-HRV);  
 483 Brain related input:  $\alpha$  power within ROI. Box plots (horizontal bar: mean; whiskers: 1.5  
 484 interquartile range); individual dots represent individual participants. **A.** Heart-to-brain coupling  
 485 coefficient (HF-HRV  $\rightarrow$   $\alpha$ ; averaged across ROI). There was no evidence for any significant effects  
 486

487 *of arousal, movement nor interaction on HF-HRV  $\rightarrow \alpha$  (all  $p > .05$ ). **B.** Brain-to-heart coupling*  
488 *coefficient ( $\alpha \rightarrow$  HF-HRV; averaged across ROI) during HA than LA. There was no evidence for*  
489 *any significant effects of arousal, movement nor interaction on  $\alpha \rightarrow$  HF-HRV (all  $p > .05$ ).*

## 490 5. Control and Exploratory Analyses

### 491 5.1. ECG waveform

492 There were no significant differences (max  $t(28) = 1.1$ , min  $p = .27$ , FDR-corrected) in the ECG  
493 waveform between HA and LA conditions at all the time-points within the time window of EA  
494 related HEP differences (328 to 360 ms after R-peak).

### 495 5.2. Other frequency bands

496 A summary of the results can be found in Table 1 and figures including topographies in the  
497 Supplements.

498 Exploring arousal-related changes in whole-brain activity, we found different patterns of  
499 activation for HA vs. LA (see Figure S3 in Supplements). For the theta band, we found 17 EEG  
500 electrodes (see Table 1) with lower theta power during higher arousal. For the alpha band, there  
501 were 23 EEG electrodes with lower alpha power during higher arousal. For the beta band, there  
502 were 6 EEG electrodes with lower beta power during higher arousal. For the gamma band, one  
503 EEG electrode showed higher gamma power during higher arousal.

504 Exploring further arousal-related changes in BHI, we found different patterns of activation for  
505 HA vs. LA (see Figure S4 in Supplements). For HF-HRV  $\rightarrow \delta$ , one EEG electrode (see Table 1)  
506 showed lower BHI coupling coefficients during higher arousal. For LF-HRV  $\rightarrow \delta$ , one EEG  
507 electrode showed higher BHI coupling coefficients during higher arousal. For HF-HRV  $\rightarrow \alpha$ ,

508 one EEG electrode showed lower BHI coupling coefficients during higher arousal. For HF-HRV  
509  $\rightarrow \beta$ , two EEG electrodes showed lower BHI coupling coefficients during higher arousal. For  
510 HF-HRV  $\rightarrow \gamma$ , one EEG electrode showed higher BHI coupling coefficients during higher  
511 arousal. For LF-HRV  $\rightarrow \gamma$ , there were 12 EEG electrodes (see Table 1) with higher BHI  
512 coupling coefficients during higher arousal. For  $\gamma \rightarrow$  HF-HRV, there were 17 EEG electrodes  
513 with lower BHI coupling coefficients during higher arousal. Furthermore, concerning the gamma  
514 band, when looking at the interception (FC5, CP5, P3, T7, TP9, TP10, O1, Oz, O2) of both  
515 significant electrodes for the ascending (LF-HRV  $\rightarrow \gamma$ ) and descending ( $\gamma \rightarrow$  HF-HRV)  
516 directions, both effects were still present (LF-HRV  $\rightarrow \gamma$ :  $t(28) = 2.8$ ;  $p = .008$ ;  $\gamma \rightarrow$  HF-HRV:  
517  $t(28) = -2.7$ ;  $p = .012$ ).

518

<b>HA vs. LA</b>	<b>direction effect</b>	<b>electrodes with significant differences (<math>p_{\text{uncorrected}} &lt; .05</math> and <math>p_{\text{FDR}} &lt; .05</math>)</b>
<i>Brain/EEG</i>		
$\theta$ (4–8 Hz)	HA < LA	Fp1, <b>Fp2</b> , Fz, F3, FC1, <b>FC2</b> , FC6, C3, <b>C4</b> , CP1, CP5, P4, P7, <b>TP9</b> , TP10, O1, O2
$\alpha$ (8–13 Hz)	HA < LA	<b>Fp1, Fp2, Fz, F3, F4, FC1, FC2, FC6, Cz, C4, CP1, CP5, CP6, Pz, P3, P4, P7, P8, TP9, TP10, T8, O1, O2</b>
$\beta$ (13–30 Hz)	HA < LA	FC2, C4, <b>CP1, Pz, P3, P4</b>
$\gamma$ (30–45 Hz)	HA > LA	O2
<i>Brain-Heart (SDG)</i>		
<u>Ascending</u>		
LF-HRV $\rightarrow \delta$	HA > LA	P8
LF-HRV $\rightarrow \gamma$	HA > LA	Fp2, Fz, FC5, CP5, P3, P8, T7, TP9, TP10, Oz, O1, O2
HF-HRV $\rightarrow \delta$	HA < LA	O1
HF-HRV $\rightarrow \alpha$	HA < LA	<b>P3</b>
HF-HRV $\rightarrow \beta$	HA < LA	Pz, CP2
HF-HRV $\rightarrow \gamma$	HA > LA	O2
<u>Descending</u>		
$\gamma \rightarrow$ HF-HRV	HA < LA	Fp1, F3, FC5, FC6, C3, CP5, CP6, P3, P4, P7, T7, T8, TP9, TP10, Oz, O1, O2

519 **Table 1.** Summary of the exploratory analyses. At each electrode, the different metrics were  
520 averaged over the head movement conditions, and paired t-tests were performed between the mean  
521 during high arousal (HA) and the mean during low arousal (LA) for each participant.  
522 Topographies can be found in the Supplements (see Figure S3 and S4). SDG: synthetic data  
523 generation modeling; LF/HF-HRV: low/high-frequency heart rate variability.

## 524 **Discussion**

525 We investigated brain-heart interactions during an emotionally arousing experience in immersive  
526 VR. In particular, we analyzed EA-related cardiac activity (particularly its vagal regulation) and  
527 the extent to which it contributed to the previously reported link between EA and parieto-occipital  
528 alpha power (Hofmann, Klotzsche, Mariola et al., 2021). We found differences in heart activity,  
529 brain activity and - less consistently - brain-heart interactions between states of HA and LA. More  
530 specifically, we observed significant arousal-related BHI differences in event-related analyses  
531 (i.e., HEPs) but not in oscillatory analyses (i.e., SDG modeling), although whole-brain exploratory  
532 analyses pointed towards increased ascending heart-to-brain (i.e., LF-HRV  $\rightarrow$   $\gamma$ ) and reduced  
533 descending brain-to-heart (i.e.,  $\gamma \rightarrow$  HF-HRV) functional information flow during higher EA.  
534 Generally, our findings extend previous results from classical studies and confirm the link between  
535 EA and HF-HRV, parieto-occipital alpha power, and HEP amplitude under more naturalistic  
536 conditions.

### 537 1. Heart/ECG

538 Analyzing the heart signal, we found significant effects of EA on both LF- and HF-HRV. This is  
539 in line with previous research showing lower HF-HRV during states of higher EA (Valenza et al.,  
540 2012; Luft & Bhattacharya, 2015; Hildebrandt et al., 2016). As HF-HRV reflects vagal  
541 cardio regulation (Task Force, 1996), a possible interpretation is that the parasympathetic  
542 regulation of heart activity decreased (i.e., vagal withdrawal) during higher EA. Fluctuations in  
543 HF-HRV during emotion have been associated with functional changes in medial prefrontal cortex  
544 (Lane et al., 2009), a brain region shared by the CAN and the SN. The changes in HF-HRV during

545 EA could therefore be also linked to a (bottom-up) modulation of attention in presence of  
546 emotional stimuli.

547 Concerning LF-HRV, the measure reflects both the sympathetic and parasympathetic influences  
548 on the heart rate. While the EA-related changes in LF-HRV could thus be driven by changes in  
549 parasympathetic activity, it remains unclear why we did not find evidence for heart rate differences  
550 between LA and HA. As both ANS branches can be active at the same time (Koizumi et al., 1983;  
551 Paton et al., 2005), their contribution to the heart rate may have canceled each other out (to only  
552 be visible in the variability measures LF- and HF-HRV). Because the heart rate and its sympathetic  
553 regulation are known to change more slowly (order of few seconds) than its parasympathetic  
554 regulation (order of ms), it is also possible that our analysis (with 1 s resolution) did not capture  
555 these delayed changes. Future studies may consider directly assessing the sympathetic regulation  
556 of the heart and its potential link to emotional arousal, for instance by modeling regulations at  
557 different timescales to extract a sympathetic activity index (Valenza et al., 2018) from the ECG  
558 signal and take into account the potential delay of the sympathetic regulation.

## 559 2. Brain/EEG

560 Analyzing the brain activity, we confirmed our previous findings of lower parieto-occipital alpha  
561 power for HA compared to LA states (Hofmann, Klotzsche, Mariola et al., 2021) with a different  
562 statistical approach, using LMM instead of decoding. Of note, exploratory analyses suggest that  
563 this effect is not restricted to parieto-occipital cortical areas. This is also in line with previous  
564 research using event-related designs (Koelstra et al., 2012; Luft & Bhattacharya, 2015). Because  
565 alpha power has also been linked to attentional processes (Klimesch, 2012; van Diepen et al., 2019)  
566 and to the encoding of the emotional salience of stimuli (e.g., in orbitofrontal cortex; Todd et al.,  
567 2014), the change in alpha power might indicate a (bottom-up) modulation of attention in presence



568 of emotional stimuli (Sutherland & Mather, 2018) - which may be present with a more widespread  
569 topography.

570 In additional exploratory analyses, we investigated EA-related differences in other frequency  
571 bands. We observed significant effects in other frequency bands, such as lower theta power (cf.  
572 Aftanas et al., 2002), lower beta power (Schubring et al., 2020; Kim et al., 2021), and higher  
573 gamma power (Cao et al., 2020) during HA vs. LA, but these findings should be interpreted with  
574 caution given the exploratory nature of these analyses and the risk of false positives.

575 The main aim of this work was to investigate if these changes in parieto-occipital alpha oscillations  
576 and the changes we observed in heart activity (i.e., in HF-HRV) were related to each other. Given  
577 the alpha reduction during HA compared to LA, how did vagal cardioregulation come into play?

### 578 3. Brain-Heart

579 Combining heart and brain activities together in a multimodal analysis, we investigated BHI during  
580 different states of emotional arousal. Using two different approaches, an event-related and an  
581 oscillatory analysis, we found - though not consistently across both approaches - that the functional  
582 coupling between the heart and the brain was linked to emotional arousal.

583 Looking at HEPs (event-related analysis), we found a significantly lower (or more negative) HEP  
584 amplitude for high compared to low arousal in left fronto-central electrodes. Because there was no  
585 significant difference in heart rate (i.e., IBIs) nor in ECG waveform between HA and LA, this HEP  
586 difference may not be due to residual CFA nor to a difference of duration between heartbeats. We  
587 did not replicate the findings from Luft & Battacharya (2015), in that we did not find a significantly  
588 higher HEP amplitude in parieto-occipital regions during higher arousal (a pattern, which we only  
589 observed in a non-significant cluster). The topography of the fronto-central cluster, however, might  
590 reflect the anterior pole of a dipole that is also visible at the parietal electrodes. Particularly, a

591 separation with an angle of approximately  $45^\circ$  between the positive and negative pole on the scalp  
592 is often characteristic of a tangential equivalent dipolar source located inside the central sulcus  
593 (e.g., for the somatosensory evoked potential N20; Scherg et al., 2019). Our source localization  
594 results support this view by pointing towards a distribution of sources around the central sulcus,  
595 in sensorimotor areas. The left fronto-central topography observed here and the right parieto-  
596 occipital topography reported by Luft and Battacharya (2015) may thus reflect similar underlying  
597 sources.

598 Our HEP results are also in line with a meta-analysis (Coll et al., 2021) that found a large effect of  
599 arousal (including but not restricted to *emotional* arousal) on HEP amplitudes, with the strongest  
600 effect around 250 ms after R-peak and in fronto-central electrodes (Cz, C1, C2, C3, C4, FCz, FC1,  
601 FC2, FC3, FC4, FC5, FC6 and AFz). More specifically related to *emotional* arousal, a recent study  
602 (Marshall et al., 2019) included in this meta-analysis found a HEP suppression for angry vs. neutral  
603 faces when they were repeatedly presented. This could reflect a different weighing of exteroceptive  
604 vs. interoceptive information to facilitate rapid perceptual processing and behavioral responses, as  
605 well as to mobilize (e.g., metabolic) resources (Gianaros & Wager, 2015).

606 In the confirmatory oscillatory analysis using SDG modeling, we did not find evidence for an  
607 association between EA and directional communication between the brain (indexed by parieto-  
608 occipital alpha power) and the heart (indexed by HF-HRV). The results of the SDG whole-scalp  
609 exploratory analysis of multiple frequency bands indicated that EA was associated with specific  
610 changes in information flow from the heart to the brain (higher LF-HRV  $\rightarrow$   $\gamma$  in a temporo-  
611 occipital cluster, lower information flow from HF-HRV to the brain in single electrodes) and - less  
612 so - from the brain to the heart (lower  $\gamma \rightarrow$  HF-HRV in a temporo-occipital cluster; Table 1 for  
613 details). Although this should, again, be interpreted with caution, these results suggest a link

614 between the level of EA and the coupling between HRV and brain activity in different frequency  
615 bands. Particularly, ascending signals of heart activity seem to inform brain activity and modulate  
616 the emotional experience (Candia-Rivera et al., 2022). Our results are partly consistent with the  
617 findings of Candia-Rivera and colleagues (2022), who reported higher (ascending) heart-to-brain  
618 information flow - although in different frequency bands - during higher arousal, and lower  
619 (descending) brain-to-heart information flow during emotion elicitation compared to rest.  
620 Interestingly, genetically modified mice with chronically elevated heart rate (within the  
621 physiological range) had higher HF-HRV, higher EEG gamma band power, and higher ascending  
622 information flow from LF-HRV to gamma compared to control mice (Agrimi et al., 2023).

623 Overall, these results extend our previous contribution to the physiology of emotional experience  
624 using immersive VR, with our previous “brain-only” results of EEG-derived parieto-occipital  
625 alpha power (Hofmann, Klotzsche, Mariola et al., 2021) now complemented by considering the  
626 rest of the body (here: the heart or ANS). During states of higher emotional arousal, not only  
627 parieto-occipital alpha power was lower but so were LF-HRV, HF-HRV, and HEP amplitudes  
628 over fronto-central electrodes. While we did not find evidence for the hypothesized changes in  
629 BHI between parieto-occipital alpha power and HF-HRV (in either direction), exploratory  
630 analyses suggest several other EA-related BHI changes, notably in temporo-occipital gamma  
631 power, where higher EA was linked to decreased brain-to-heart ( $\gamma \rightarrow$  HF-HRV) and increased  
632 heart-to-brain (LF-HRV  $\rightarrow$   $\gamma$ ) information flow. Thereby, heart-to-brain information flow seems  
633 to change more broadly (in time and space) with different affective states than - in the opposite  
634 direction - the brain-to-heart information flow. This supports the view that signals from the internal  
635 body (e.g., the heart) influence our perception of the world and our interaction with it (Ohl et al.,  
636 2016; Kunzendorf et al., 2019; Motyka et al., 2019; Galvez-Pol et al., 2022). Changes in bodily

637 rhythms, as they occur in different affective states, change attentional processes (Sutherland &  
638 Mather, 2018) or - more generally - the way in which sensory evidence is accumulated (Allen et  
639 al., 2022), for example through increased ascending (heart-to-brain) compared to reduced  
640 descending (brain-to-heart) information flow.

#### 641 4. Limitations and Future Directions

642 Several limitations should be considered when interpreting our findings. While the dataset is  
643 relatively short and potentially noisy due to the more naturalistic conditions of data acquisition,  
644 this is a tradeoff that comes with using a more realistic affective stimulation.

645 Other limitations are due to the approach of a secondary analysis - the experimental design was  
646 not optimized for some analysis methods used here. For example, to avoid transition effects  
647 between the different parts of the VR experience, data needed to be trimmed at the beginning and  
648 end of rollercoasters. This discontinuity was not ideal for time-resolved metrics such as heart rate,  
649 HRV and SDG couplings. Fully continuous data without trimming would be preferable in future  
650 experiments.

651 Furthermore, the EA ratings were binned into HA and LA in order to increase sensitivity and to  
652 maximize comparability to previous findings (Luft & Bhattacharya, 2015) as well as our previous  
653 analyses (Hofmann, Klotzsche, Mariola et al., 2021). Models that include the continuous ratings  
654 (as also part of Hofmann, Klotzsche, Mariola et al., 2021) can provide a more fine-grained picture  
655 of the relationship between emotional arousal and physiological measures.

656 As respiration modulates vagal cardiorespiration (Benarroch, 1993) and HEP amplitudes (Zaccaro  
657 et al., 2022), we cannot exclude potential EA-related changes in respiration (e.g., its rate) and  
658 assess their influence on measures of BHI. In the future, respiratory activity should also be added  
659 to the physiological measurements of BHI studies (e.g., with a respiration belt).

660 Finally, the inclusion of (e.g., behavioral or eye movement-related) measures of attention could  
661 support the interpretation of emotion-related modulations of attention (as reflected in changes in  
662 vagal cardiorespiration and parieto-occipital alpha power).

## 663 **Conclusion**

664 We replicated previous findings from classical studies in a more naturalistic virtual reality setting,  
665 confirming the link between emotional arousal, heart activity, brain oscillations and - albeit less  
666 consistently - brain-heart interactions. Our analysis demonstrates that combining measures of heart  
667 and brain activity provides insights beyond what can be learned from studying each modality in  
668 isolation. Finally, this work illustrates how VR paired with multimodal physiological recordings  
669 can be a valuable approach for simultaneously studying multiple components of emotions. Taken  
670 together, our results suggest that to better understand affective processes, we must consider the  
671 heart alongside the brain, as both play integral roles in emotion.

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