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Scale-free Neural and Physiological Dynamics in Naturalistic Stimuli Processing

Scale-free neural dynamics and natural stimuli

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60 **Scale-free Neural and Physiological Dynamics in Naturalistic**
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85 **Abstract**

86 Neural activity recorded at multiple spatiotemporal scales is dominated by arrhythmic
87 fluctuations without a characteristic temporal periodicity. Such activity often exhibits a
88 1/f-type power spectrum, in which power falls off with increasing frequency following a
89 power-law function: $P(f) \propto 1/f^\beta$, which is indicative of scale-free dynamics. Two
90 extensively studied forms of scale-free neural dynamics in the human brain are slow
91 cortical potentials (SCPs) – the low-frequency (<5 Hz) component of brain field
92 potentials – and the amplitude fluctuations of alpha oscillations, both of which have been
93 shown to carry important functional roles. In addition, scale-free dynamics characterize
94 normal human physiology such as heartbeat dynamics. However, the exact relationships
95 amongst these scale-free neural and physiological dynamics remain unclear. We
96 recorded simultaneous magnetoencephalography (MEG) and electrocardiogram (EKG)
97 in healthy subjects under resting state and while performing a discrimination task on
98 scale-free dynamical auditory stimuli that followed different scale-free statistics. We
99 observed that long-range temporal correlation (captured by the power-law exponent β) in
100 SCPs positively correlated with that of heartbeat dynamics across time within an
101 individual, and negatively correlated with that of alpha amplitude fluctuations across
102 individuals. In addition, across individuals, long-range temporal correlation of both SCP
103 and alpha-oscillation amplitude predicted subjects' discrimination performance in the
104 auditory task, albeit through antagonistic relationships. These findings reveal
105 interrelations amongst different scale-free neural and physiological dynamics and initial
106 evidence for the involvement of scale-free neural dynamics in the processing of natural
107 stimuli, which often exhibit scale-free dynamics.

108

109

110 **Significance**

111 Many time-varying natural stimuli such as natural soundscapes, speech and music
112 exhibit scale-free dynamics characterized by a $1/f$ -type power spectrum. In parallel,
113 scale-free neural dynamics are prominent across observational levels in the brain. Two
114 well-established forms of scale-free neural activity are slow cortical potentials and
115 amplitude fluctuations of alpha oscillations. However, it is unknown if they are related. In
116 addition, the inter-beat interval fluctuation of the healthy human heart follows scale-free
117 dynamics, but its relationship with scale-free neural dynamics is not fully characterized.
118 We observed novel relationships between these different scale-free neural and
119 physiological dynamics. Moreover, naturalistic stimuli exhibiting scale-free dynamics
120 modulate scale-free neural dynamics, and baseline characteristics of scale-free neural
121 dynamics predict an individual's ability to process naturalistic stimuli.

122

123 **Introduction**

124 Many natural stimuli exhibit scale-free temporal or spatial patterns, such that no
125 particular temporal or spatial periodicity predominates (Mandelbrot, 1999). In the spatial
126 domain, it is well documented that natural images follow a $P(f) \propto 1/f^\beta$ spatial power
127 spectrum, where f is the spatial frequency (Field, 1987). In the temporal domain, scale-
128 free dynamics are characterized by a $P(f) \propto 1/f^\beta$ temporal power spectrum, where f is the
129 temporal frequency and the power-law exponent β captures the strength of
130 autocorrelation in the signal over time. In dynamics with a larger β , trends tend to persist
131 over longer periods of time (Fig. 1A-C). Time-varying natural images (i.e., natural
132 movies) typically follow a $P(f) \propto 1/f^\beta$ type temporal power spectrum (Dong and Atick,
133 1995). Loudness and pitch fluctuations of natural soundscapes, such as urban and rural

134 environmental noise (De Coensel et al., 2003), speech and music (Voss and Clarke,
135 1975), also exhibit 1/f-type temporal power spectra.

136

137 In the brain, scale-free dynamics are prominent across multiple observational levels (He,
138 2014) and manifest in human behavioral output (Gilden, 2001). Two well-studied forms
139 of scale-free neural dynamics are the slow cortical potentials (SCPs) (He et al., 2010)
140 and amplitude fluctuations of brain oscillations (Linkenkaer-Hansen et al., 2001). The
141 SCPs are the low-frequency (<5 Hz) component of broadband field potentials that exhibit
142 a 1/f-type power spectrum. Changes in arousal state and task performance alter the
143 power-law exponent in the SCP range recorded by electrocorticography (ECoG) in
144 humans (He et al., 2010). In addition, the SCP correlates with fMRI signals in both
145 spontaneous fluctuations and stimulus-driven responses (He and Raichle, 2009; He et
146 al., 2008; Kahn et al., 2013; Pan et al., 2013), and the spontaneous fMRI signals also
147 exhibit prominent scale-free dynamics (He, 2011).

148

149 A parallel line of research has established that amplitude fluctuations of brain alpha
150 oscillations also follow scale-free dynamics (Linkenkaer-Hansen et al., 2001). Its power-
151 law exponent has been shown to vary with task performance (Linkenkaer-Hansen et al.,
152 2004), have a genetic contribution (Linkenkaer-Hansen et al., 2007), increase during
153 development (Smit et al., 2011), and differ between patients with Alzheimer's disease
154 and controls (Montez et al., 2009). Moreover, the power-law exponent of alpha-
155 oscillation amplitude predicts that of behavioral fluctuations across individuals (Palva et
156 al., 2013; Smit et al., 2013), indicating a link between neural and behavioral long-range
157 temporal correlation.

158

159 Although existing data suggest that SCP phase modulates alpha-oscillation amplitude
160 (He, 2014), whether scale-free dynamics in the SCP and alpha amplitude fluctuations
161 are related remains unknown. In addition, a rich literature establishes that the healthy
162 human heart is characterized by scale-free dynamics in its inter-beat interval and failure
163 thereof accompanies heart disease or aging (Goldberger et al., 2002). Currently, the
164 literature remains mixed about whether and how scale-free dynamics in the SCP and
165 alpha-amplitude interact with heartbeat dynamics (Palva et. Al., 2013; Zhigalov et al.,
166 2015). This question is especially intriguing in light of recent data showing that afferent
167 signals from the heart interact with not only the limbic system but also perceptual and
168 cognitive systems in the brain (Park et al., 2014).

169

170 We recorded simultaneous MEG and EKG in human subjects under resting state and
171 while listening to auditory tone sequences whose pitch fluctuations constituted scale-free
172 dynamics with varying degrees of autocorrelation. These auditory stimuli captured 2nd-
173 order statistics in natural stimuli, since their temporal power spectra followed a power-
174 law distribution. Subjects discriminated tone sequences with different degrees of
175 autocorrelation, as captured by the power-law exponent β . We investigated the
176 relationships amongst scale-free neural and heartbeat dynamics across sensors,
177 individuals, and over time within an individual. We further examined whether the degree
178 of auto-correlation in scale-free auditory stimuli modulated scale-free neural and
179 heartbeat dynamics, and whether scale-free neural dynamics predicted an individual's
180 ability to discriminate stimuli with different degrees of autocorrelation. We hypothesized
181 firstly that scale-free dynamics in the SCP, alpha-amplitude fluctuations and heartbeat
182 dynamics are interrelated, and secondly that scale-free neural dynamics are involved in
183 the processing of dynamic, scale-free stimuli.

184

185 **Materials and Methods**

186 *Subjects*

187 The experiment was approved by the Institutional Review Board of the National Institute
188 of Neurological Disorders and Stroke. All subjects were right-handed and neurologically
189 healthy with normal hearing. Nineteen subjects between 19 and 30 years old (mean age
190 24.7; 12 females) participated in a ~3 hour long MEG session with simultaneous EKG
191 recording. Two subjects did not have EKG data because one subject was tested before
192 the EKG recording was implemented, and the other subject's EKG data was too noisy to
193 reliably extract R peaks. All subjects provided written informed consent.

194

195 *Stimulus Creation*

196 We created auditory tone sequences whose pitch fluctuations had five levels of
197 autocorrelation strength, spanning from fractional Gaussian noise (fGn) to fractional
198 Brownian motion (fBm). We used a circulant embedding algorithm (Helgason et al.,
199 2011) to create fGn time series with Hurst exponents of 0.5, 0.6, and 0.75
200 (corresponding to power-law exponent $\beta = 0, 0.2, \text{ and } 0.5$, respectively, where $\beta = 2H -$
201 1), as well as fBm time series with Hurst exponents of 0.25 and 0.5 (corresponding to
202 power-law exponent $\beta = 1.5 \text{ and } 2$, where $\beta = 2H + 1$). We created six unique 600-
203 element long series for each level of β ,

204
$$\mathbf{x}_{\beta, i} = [x_1, x_2, \dots, x_{600}], \quad \beta \in \{0, 0.2, 0.5, 1.5, 2\}, \quad 1 \leq i \leq 6$$

205 where each element x_j of $\mathbf{x}_{\beta, i}$ is taken to represent the pitch of the j 'th tone in the
206 sequence. We verified that each synthesized $\mathbf{x}_{\beta, i}$ indeed had the desired β by computing
207 the autocorrelation function and performing power spectral analysis for each sequence
208 (Fig. 1A & B, respectively). Each auditory sequence i was unique to ensure that subjects
209 would respond to statistical properties of the sequence rather than memorizing particular
210 features.

211

212 After verifying the autocorrelation properties of the sequences, we translated and scaled
 213 each $\mathbf{x}_{\beta, i}$ so that its elements ranged from $\log(220)$ to $\log(880)$, and discretized the
 214 series such that each element took on one of 25 values evenly spaced on the log scale.
 215 Let us refer to the scaled, translated, and discretized series as $\mathbf{p}_{\beta, i}$. Each $\mathbf{p}_{\beta, i}$ thus
 216 represents a time series of tone pitches, where pitch varies in semi-tone steps between
 217 220 Hz and 880 Hz and exhibits autocorrelation prescribed by β . This range of pitch
 218 values was chosen to span the iso-loudness region of human hearing (i.e., with identical
 219 amplitude, subjective loudness varies minimally with changing pitch in this range).

220

221 In order to produce an auditory stimulus for each tone sequence, we first computed the
 222 time series of tone frequencies as $\mathbf{f}_{\beta, i} = \exp(\mathbf{p}_{\beta, i})$ (Hz). For each $f_j \in \mathbf{f}_{\beta, i}$, we constructed a
 223 sinusoidal sound wave of duration 300 ms at a 44,100 Hz sampling frequency (thus
 224 yielding 13,230 samples for each tone) according to

$$225 \quad \mathbf{y}_{j, s} = A \cos(2\pi f_j s / SR + \varphi_j), \quad 1 \leq s \leq 13,230$$

226 where s denotes sample number, f_j denotes tone frequency, SR denotes the sampling
 227 frequency of 44,100 Hz, and $A = 1$. The amplitude of the tones was kept identical
 228 throughout the sequence, i.e., the tones were *not* amplitude-modulated. The 300 ms
 229 duration was chosen for ease of listening (Patel and Balaban, 2000). Because each tone
 230 was 300 ms and each sequence contained 600 tones, each sequence had a total
 231 duration of 180 s.

232

233 Cosine waves $\mathbf{y}_{j, s}$ for each tone j were concatenated, such that there was no silence
 234 period between consecutive tones. For the first tone $j = 1$, the phase φ was set to 0. For
 235 subsequent tones $j > 1$, the absolute value of φ was set to the arccosine of the final

236 sample of tone $j - 1$. The sign of φ for tone j was set such that the first order time
237 derivative was continuous across the transition from the end of tone $j - 1$ to the start of
238 tone j . This ensured that there was a smooth and continuous transition between cosine
239 waves in the junctions where tone frequency changed.

240

241 Auditory sequences were presented using the PsychPortAudio function of the
242 Psychophysics Toolbox (Brainard, 1997) in MATLAB (Mathworks, Natick, MA). The
243 audio was delivered through specialized ear tubes that were custom fit to work within the
244 MEG scanner. We used the Etymotic ER-3 Insert Headphones, in which the frequency
245 response is flat to 5 kHz. The plastic tubing from the transducer to the earpiece had a
246 speed-of-sound delay of around 10 ms, which was corrected in MEG data analyses.

247

248 *Experimental Design*

249 After presentation of each auditory tone sequence (3 min long), subjects were asked to
250 judge its “trend strength” on a scale of 0 to 4. Higher “trend strength” was explained to
251 the subjects as the tendency for a trend to persist over longer period of time, which
252 captured the strength of autocorrelation in the time series. Ascending entries on the
253 “trend strength” scale corresponded to ascending levels of stimulus β . Visual
254 performance feedback was presented after every trial to assist subjects in learning how
255 to use the scale to accurately characterize stimulus β . The feedback indicated what
256 trend strength rating had been entered by the subject, what the true trend strength of the
257 sequence was, and whether the subject’s trend strength rating was correct, close to
258 correct (off by one level of trend strength), or incorrect (off by two or more levels of trend
259 strength). To ensure adequate task performance, all subjects were trained during an
260 initial behavioral session that took place at least a few days prior in which shortened
261 versions of stimuli sequences were used. Subjects who performed adequately

262 (behavioral $\rho > 0.2$, see below) were invited back for the MEG/EKG experiment
263 (82.4% of all subjects tested). At the start of the initial behavioral session as well as the
264 main MEG/EKG experiment, subjects were visually presented shortened examples of
265 each level of trend strength, as exemplified in Fig. 1C, which shows that trend strength
266 was independent of overall range. Subjects also completed one practice block at the
267 start of the main experiment.

268

269 Stimulus sequences were initially created with the intention of having β values of 0, 0.5,
270 1.01, 1.5, and 2, and feedback presented to the subject was consistent with this scheme.
271 However, due to an aliasing artifact, stimuli with an intended $\beta = 1.01$ had an empirical β
272 closer to 0.2 (Fig. 1 A and B), and so we treat these stimuli as having $\beta = 0.2$ in all
273 analyses. Due to this complication, the implicit mapping between trend strength rating
274 and stimulus β communicated to subjects via visual feedback was erroneous for the $\beta =$
275 0.2 case. Nonetheless, subjects demonstrated an ability to accurately detect that pitch
276 autocorrelation was weaker for stimulus $\beta = 0.2$ than for $\beta = 0.5$ (Fig. 1D). This suggests
277 that subjects were able to accurately classify stimulus β in spite of the feedback error
278 and further justifies our treatment of these stimuli as $\beta = 0.2$ rather than $\beta = 1.01$.
279 Additionally, we verified that no analysis presented herein yields different statistical
280 inference if using the originally intended value of stimulus $\beta = 1.01$ rather than the
281 empirically derived value of $\beta = 0.2$.

282

283 We also included a rest condition (3-min long trials) in which no auditory stimulus was
284 presented. Throughout the experiment – during both auditory task and resting state,
285 subjects were asked to keep their gaze fixated on a cross presented at the center of the
286 screen in order to minimize eye movement. Each subject completed 36 trials in total,
287 which included 6 trials per condition (five stimulus β levels plus rest condition). The

288 stimulus sequences differed across trials within the same β level. The trials were
289 grouped in blocks of 3, resulting in 12 blocks in total. Stimulus β was randomized across
290 blocks, while rest trials were evenly dispersed throughout the experiment (always
291 presented as the second trial of even numbered blocks). The head position of the
292 subject was measured with respect to the MEG sensor array using coils placed on the
293 left and right preauricular points and the nasion. Before each block subsequent to the
294 first block, the subject self-corrected their head position to the same position recorded at
295 the start of the first block using a custom visual-feedback program in order to minimize
296 head displacement across the experiment. Video monitoring of the subject during the
297 experiment ensured that subjects stayed alert and did not close their eyes for extended
298 periods of time. After excluding trials that had failure of behavioral response or
299 drowsiness as shown by eye closure, fourteen subjects had all 36 trials, two subjects
300 had 35 trials, two subjects had 33 trials, and one subject had 30 trials.

301

302 *Data Acquisition and Pre-processing*

303 Experiments were conducted in a whole-head 275-channel CTF MEG scanner (VSM
304 MedTech). MEG data were collected with a sampling rate of 600 Hz and an anti-aliasing
305 filter at <150 Hz. Analyses were performed on 271 sensors after excluding 4
306 malfunctioning sensors. The Fieldtrip package (Oostenveld et al., 2011) implemented in
307 MATLAB (MathWorks, Natick, MA) was used for data pre-processing, and analyses
308 were conducted using Fieldtrip and custom-written code. We used Independent
309 Component Analysis (ICA) to remove artifacts related to eye blinks, eye movements,
310 heartbeat, breathing, and slow movement drift. Empty-room recording was collected in a
311 prior experiment to verify that instrument noise was orders of magnitude lower than the
312 signal we analyzed.

313

314 *Measuring Scale-free Parameters*

315 Various scale-invariance measures are mathematically related and thus can be
316 reasonably compared (Eke et al., 2002). Power-law exponents of SCP and alpha-
317 oscillation amplitude fluctuations were estimated using the common power spectral
318 analysis. To estimate the power-law exponent β of the SCP, a Fast Fourier Transform
319 (FFT) was applied to the MEG signal from each sensor in each trial (3 min long) to
320 compute its power spectrum. The power spectrum was plotted in double-logarithmic
321 scale (Fig. 2A). Since a power spectrum following $P(f) \propto 1/f^\beta$ can be rewritten as $\log[P(f)]$
322 $\propto -\beta \log(f)$, the negative slope in the log-log plot provides a convenient measure of the
323 power-law exponent β . In line with previous studies (He et al., 2008; He et al., 2010), the
324 SCP β was estimated in the range of 0.005 – 5 Hz (power spectra were calculated on
325 each trial lasting 180 sec, thus the lowest frequency visible was 0.0056 Hz).

326

327 To estimate the power-law exponent β of alpha-oscillation amplitude fluctuations, we first
328 extracted alpha oscillations from continuous MEG signal in each trial using a 3rd-order
329 Butterworth filter between 6.7 and 13.3 Hz, and computed its instantaneous amplitude
330 envelope by applying the Hilbert transform. An FFT was then applied to the alpha-
331 oscillation amplitude fluctuation to create a power spectrum for each sensor in each trial.
332 The alpha-oscillation amplitude β was estimated from the log-log plot of power spectrum
333 using the 0.1 – 1 Hz range (Fig. 2B).

334

335 Following previously established methodology, we applied detrended fluctuation analysis
336 (DFA) on heartbeat dynamics (Goldberger et al., 2002; Hardstone et al., 2012). This
337 computation was applied to the time variation in inter-beat interval, measured as the
338 interval in seconds between adjacent R peaks (Fig. 2C, left). DFA analysis was
339 conducted as follows. First, the inter-beat interval time series from each trial was

340 integrated, and the mean subtracted. We then estimated the local trend in non-
341 overlapping windows of equal length using a least-squares fit, and determined the
342 fluctuation as variance upon the local trend for a given window. Five different window
343 lengths were used: 4, 8, 16, 32, 64. The log-log plot of mean fluctuation (F) against
344 window length (l) constitutes the DFA plot (Fig. 2C, right), and its slope estimates the
345 DFA exponent α , following the relation: $F(l) \propto l^\alpha$, or $\log[F(l)] \propto \alpha \log(l)$. Theoretically, the
346 power-law exponent β is related to the DFA exponent α , following: $\beta = 2\alpha - 1$ (Eke et al.,
347 2002).

348

349 *Interrelations between Scale-free Neural and Heartbeat Dynamics*

350 To qualitatively assess the relationship between SCP β and alpha-oscillation amplitude β
351 across sensors, we first generated grand-average scalp topography for SCP β and alpha
352 amplitude β across subjects and trials (Fig. 2 A & B, right). No formal statistical test was
353 performed for the relationship between SCP β and alpha-amplitude β across all sensors
354 due to the difficulty in accurately accounting for the degrees of freedom associated with
355 the sensors. However, a scatterplot of SCP β and alpha-amplitude β across sensors is
356 included for descriptive purposes (Fig. 3A).

357

358 To investigate the relationship between SCP β and alpha amplitude β across subjects,
359 we first defined two clusters of sensors based on the topographic map of SCP β (Fig.
360 3C) and then averaged SCP β and alpha-amplitude β , respectively, across sensors
361 within each cluster. Pearson's correlation was calculated between SCP β and alpha-
362 amplitude β across subjects for each of the two clusters.

363

364 To assess the relationship between any two of our three scale-free parameters (SCP β ,
365 alpha-amplitude β , or EKG α) over time, we calculated Pearson's correlation between

366 them across all 36 trials within each subject. Pearson's r values were transformed into
367 Fisher's z -values, which were subjected to a one-sample t -test across subjects.
368 Statistical significance was assessed by a cluster-based nonparametric permutation test
369 (Maris and Oostenveld, 2007; Nichols and Holmes, 2002). To this end, we shuffled one
370 variable across trials for 1,000 iterations. For each iteration, Pearson's correlation
371 between the two variables was recomputed, and the r -value was transformed into
372 Fisher's z -value and submitted to a one-sample t -test across subjects as with the original
373 data. Clusters were defined for both the original and shuffled data as contiguous groups
374 of sensors with p -values less than 0.05 and t -values of the same sign. Summing the t -
375 values created a summary measure of each cluster. To build the null distribution, the
376 absolute value of the summed t -statistic of the largest magnitude was extracted from
377 each iteration. Finally, the absolute magnitude of the summed t -statistic in each cluster
378 from the original data was compared to the null distribution. A cluster survived cluster-
379 based correction if 2.5% or fewer of observations in the null distribution surpassed the
380 absolute value of the cluster's summed t -statistic (corresponding to $p < 0.05$ in a two-
381 tailed test). Correlation between MEG signal power and β was tested similarly.

382

383 *SCP – Alpha Oscillation Nested-Frequency Analysis and Simulation*

384 Given previous EEG and ECoG findings showing a nested-frequency relationship
385 between SCP phase and alpha-oscillation amplitude (He, 2014; He et al., 2010; Monto
386 et al., 2008; Vanhatalo et al., 2004), a natural question is whether this nested-frequency
387 relationship produces any correlation between SCP β and alpha amplitude β . To address
388 this question, we performed simulations to reveal what kind of relationship between SCP
389 β and alpha-amplitude β would be expected if it were driven entirely by the nested-
390 frequency relationship between them.

391

392 First, we quantified the nested-frequency relationship between SCP phase and alpha-
393 oscillation amplitude using the well-established modulation index (MI) (Tort et al.,
394 2008; He et al., 2010). We extracted the SCP phase time series by using a 3rd-order
395 Butterworth filter between 0.005 and 1 Hz (using a 0.005 – 5 Hz filter yielded nearly
396 identical results) and then applying the Hilbert transform. The alpha-oscillation amplitude
397 time series was derived as described above. SCP-alpha nested-frequency plots (for
398 each subject, sensor and condition) were generated by binning the SCP phase time
399 series into twenty evenly spaced phase bins, and averaging the alpha-oscillation
400 amplitude within each phase bin. The MI was computed based on this nested-frequency
401 plot, which uses an inverted entropy measure to quantify its deviation from a uniform
402 distribution. For statistical testing, the MI value was converted into an MI Z-score by
403 comparison with a null distribution generated by shuffling the phase time series using 5
404 equal-length segments, following a previously described method (He et al., 2010). A
405 preliminary analysis suggested that stimulus condition did not modulate MI Z-score, and
406 thus different conditions were combined in the subsequent simulation.

407

408 We next used the empirically measured SCP phase series in conjunction with the
409 nested-frequency relationship between SCP phase and alpha-oscillation amplitude at
410 each sensor to construct simulated alpha-oscillation amplitude time series. To this end,
411 the SCP-alpha nested-frequency plot as described above was averaged across subjects
412 and conditions for each sensor. This distribution was smoothed using a 5-bin-width
413 moving average. For each sample of the SCP phase time series, we used spline
414 interpolation of the nested-frequency distribution at that sensor to determine what alpha-
415 oscillation amplitude would be predicted by the SCP phase. Finally, we computed the β
416 of the empirical SCP time series and the simulated alpha-oscillation amplitude series,
417 averaged these β values over trials and subjects, and examined their Pearson

418 correlation across sensors. This result reveals the contribution of the nested-frequency
419 relationship between SCP and alpha oscillations to the correlation between SCP β and
420 alpha-oscillation amplitude β .

421

422 *Stimulus Modulation of Scale-free Neural and Heartbeat Dynamics*

423 We probed whether the strength of autocorrelation in the auditory stimulus (as captured
424 by its power-law exponent β) modulated scale-free neural and heartbeat dynamics. For
425 each sensor in each subject, stimulus β was correlated with SCP β , alpha-oscillation
426 amplitude β , or EKG α across the 30 task trials using Spearman's rank correlation.

427 Spearman's rho values were transformed into Fisher's z-values (Fieller et al., 1957) and
428 submitted to a one-sample *t*-test across subjects at each sensor. Statistical significance
429 was established using a cluster-based nonparametric permutation test as described
430 earlier.

431

432 *Behavioral Performance Assessment and Correlation with Scale-free Neural Dynamics*

433 To evaluate subjects' behavioral performance in the stimulus β discrimination task, we
434 first visualized the conditional probability of behavioral response β (i.e. the β
435 corresponding to the subject's trend strength rating) at a given stimulus β (Fig. 1D). The
436 behavioral performance of each subject was assessed by Spearman's rank correlation
437 between stimulus β and response β across all task trials. The Spearman's rho, or
438 behavioral rho, captures a subject's behavioral performance for the entire experiment
439 while allowing for some leniency in which subjects could be close to the right answer but
440 not exact. To test whether scale-free neural dynamics predicted behavioral performance
441 on a subject-by-subject basis, we computed Pearson's correlation between behavioral
442 rho and either SCP β or alpha-oscillation amplitude β at each sensor across subjects.

443

444 **Results**

445 **Behavioral performance**

446 The across-trial Spearman's correlation between stimulus β and response β ("behavioral
447 rho") was significant for every subject ($N = 19$, p ranged from $p < 0.0001$ to 0.048^a),
448 indicating that all subjects could perform the stimulus β discrimination task significantly
449 above chance level. Behavioral rho ranged from 0.36 to 0.88, with an average value of
450 0.66. Fig. 1D shows the group-average conditional probability map of behavioral
451 response given stimulus β . The accuracy of subjects' behavioral responses is reflected
452 by the concentration of the probability distribution along the diagonal where response β
453 is equal to stimulus β . Note that incorrect behavioral responses tended to be close to the
454 correct response (i.e. off-diagonal elements that are closer to the diagonal have higher
455 probability than those that are farther away). The Spearman's correlation coefficient thus
456 provides a more informative and natural measure for quantifying overall behavioral
457 performance than proportion correct. In particular, Spearman's correlation, but not the
458 proportion of correct responses, takes into account the magnitude of response error.
459 Interestingly, subjects were better at discriminating between stimulus β in the fBm ($\beta =$
460 1.5 or 2) than the fGn range ($\beta = 0, 0.2$ or 0.5) (Fig. 1D). We note that stimuli in the fBm
461 range tended to sound more melodic than those in the fGn range.

462

463 **Scale-free dynamics in neural activity and heart rate variability**

464 Consistent with earlier reports (Dehghani et al., 2010; He, 2014), the power spectrum of
465 MEG signals followed power-law scaling with peaks at discrete frequencies
466 corresponding to various brain oscillations (see Fig. 2A, left panel for example power
467 spectra from a single subject). We extracted power-law exponent β for SCP from the
468 0.005 – 5 Hz frequency range (Fig. 2A, middle). The grand average (across stimulus
469 conditions and subjects) topographical distribution of SCP β across MEG sensors is

470 shown in Fig. 2A (right panel). SCP β ranged from 0.87 to 1.12 across sensors (mean
471 0.97), and exhibited an anterior-posterior gradient with frontal sensors displaying higher
472 β , and hence longer temporal autocorrelation in the SCP. This finding is consistent with
473 previous MEG (Dehghani et al., 2010) and fMRI (He, 2011) observations.

474

475 We extracted instantaneous amplitude fluctuations of alpha oscillations (filtered in the
476 6.7 – 13.3 Hz range), and computed its power spectrum (see Fig. 2B, left panel for result
477 from an example subject). In line with previous reports (Linkenkaer-Hansen et al., 2001),
478 alpha-oscillation amplitude fluctuations exhibit power-law scaling in its power spectrum.

479 We extracted the power-law exponent β of alpha amplitude in the range of 0.1 – 1 Hz
480 (Fig. 2B, middle). Alpha amplitude β ranged from 0.32 to 0.61 across sensors (mean
481 0.51), and displayed an anterior-posterior gradient opposite to that of SCP, such that
482 posterior sensors had higher β , and accordingly, stronger autocorrelation (Fig. 2B, right).

483

484 Lastly, following established procedures for analyzing heartbeat dynamics (Goldberger
485 et al., 2002), we defined R-peaks from EKG recordings and constructed inter-beat
486 interval time series, which was subjected to DFA analysis to extract the DFA exponent α
487 (Fig. 2C). Theoretically, the DFA exponent α is directly related to the power-law
488 exponent β (see Materials and Methods), both of which capture the strength of
489 autocorrelation in a time series, one using a time-domain approach (DFA exponent α),
490 the other a frequency-domain approach (power-law exponent β). Across 17 subjects with
491 simultaneous EKG-MEG recordings, EKG α ranged from 0.57 to 1.2, with a mean of
492 0.82 across subjects, consistent with previous reports (Goldberger et al., 2002).

493

494 **An anti-correlation between SCP and alpha-oscillation amplitude power-law**
495 **exponents**

496 We next explored the relationship between scale-free dynamics in SCP and alpha-
497 oscillation amplitude fluctuations across the scalp and subjects. Because stimulus
498 condition minimally modulated power-law exponent of SCP or alpha-oscillation
499 amplitude (see below), for this analysis we pooled data across all conditions (including 5
500 stimulus β levels and resting condition).

501

502 The scalp topography of SCP β and alpha-oscillation amplitude β (Fig. 2A-B, right
503 panels) display opposite anterior-posterior gradients, indicating that as the strength of
504 autocorrelation in SCP increases, that in alpha-oscillation amplitude fluctuations tends to
505 decrease. To qualitatively assess this relationship, we plotted the two measures, each
506 averaged over 19 subjects, against each other across all sensors (Fig. 3A). This
507 revealed a negative relationship between SCP β and alpha-oscillation amplitude β
508 across MEG sensors.

509

510 We then assessed whether there might also be an anti-correlation between SCP β and
511 alpha amplitude β across subjects. To this end, we first defined two clusters of sensors
512 based on the scalp topography of SCP β , distributed over frontal and posterior regions,
513 with relatively high and low β , respectively. We then assessed across-subject correlation
514 between SCP β and alpha-oscillation amplitude β for each cluster of sensors. In the
515 posterior cluster, we observed a significant negative correlation between SCP β and
516 alpha amplitude β across subjects (Fig. 3C, $r = -0.48$, $p = 0.037^b$, $N = 19$). In the frontal
517 cluster, there was a negative trend that was not significant (Fig. 3C inset, $r = -0.34$, $p =$
518 0.16^c). Could the significant anti-correlation between SCP β and alpha-oscillation
519 amplitude β in the posterior cluster across subjects be driven by a relation between their
520 respective power? Two pieces of evidence suggest that this is not the case. First, SCP
521 power and alpha-oscillation power were found to correlate *positively* across subjects ($r =$

522 0.91, $p = 8.5e-08^d$; but note that this finding in itself could be due to measurement
523 variation across subjects). Second, a partial correlation analysis revealed that after
524 controlling for the effects of SCP and alpha-oscillation power, the anti-correlation
525 between SCP β and alpha-oscillation amplitude β across subjects in the posterior sensor
526 cluster was unchanged ($r = -0.48$, $p = 0.05^e$).

527

528 The above results reveal an intriguing negative relationship between SCP β and alpha-
529 oscillation amplitude β across the scalp and subjects, such that stronger autocorrelation
530 in the SCP is accompanied by weaker autocorrelation in the amplitude fluctuations of
531 alpha oscillations. In light of previous observations of a nested-frequency relationship
532 between SCP phase and alpha-oscillation amplitude (He, 2014; Vanhatalo et al., 2004),
533 these findings raise a natural question: Is the anti-correlation between SCP β and alpha
534 amplitude β driven by the nested-frequency relationship between them? To test this
535 hypothesis, we quantified the nested-frequency pattern between SCP phase and alpha-
536 oscillation amplitude in each MEG sensor (Fig. 3B, top), and simulated alpha-oscillation
537 amplitude time series for each sensor in each subject, based on the sensor-specific
538 nested-frequency pattern and the empirically measured SCP phase time series. We then
539 computed the power-law exponent β of the simulated alpha-oscillation amplitude time
540 series, and plotted it against the measured SCP β across all sensors (Fig. 3B, bottom).
541 This simulation reveals a positive relationship between SCP β and alpha amplitude β ,
542 suggesting that the negative relationship observed in the empirical data cannot be
543 explained by the nested-frequency relationship between SCP and alpha oscillations.

544

545 Lastly, we investigated whether the amount of power in the SCP or alpha range was
546 related with their respective β across time within an individual (see Materials and
547 Methods). We found a robust positive correlation between SCP power and β : after

548 cluster-based correction for multiple comparisons, all MEG sensors across the entire
549 scalp demonstrated a significant positive correlation (Fig. 3D). By contrast, alpha-
550 oscillation power had no significant correlation with its amplitude β after cluster-based
551 correction. This result is consistent with previous findings showing that SCP β changes
552 by modulating the power in the lowest frequency ranges, thereby causing a positive
553 correlation between its power and β (He et al., 2010).

554

555 **Relationship between scale-free neural and physiological dynamics**

556 We further investigated whether the strength of autocorrelation in scale-free neural and
557 heartbeat dynamics co-modulated across time within an individual. To this end, we
558 computed correlations between SCP β and the DFA exponent α of heartbeat dynamics
559 measured by EKG. This analysis revealed two significant clusters, one over left central
560 cortex, the other over right central cortex extending into frontal areas (Fig. 3E). No
561 significant correlation was found between alpha-amplitude β and EKG α after correction
562 for multiple comparisons.

563

564 **Stimulus condition modulates scale-free dynamics in alpha-oscillation amplitude**

565 Does the strength of autocorrelation in the stimulus sequence (“stimulus β ”) modulate
566 the strength of autocorrelation within scale-free neural or physiological dynamics? To
567 answer this question, we computed Spearman’s rank correlation between stimulus β and
568 the autocorrelation parameter from neural or heartbeat dynamics (respectively, SCP β ,
569 alpha-oscillation amplitude β , and EKG α) across all trials during the auditory task (30
570 trials in total) for each subject.

571

572 We found that as stimulus β increased, alpha amplitude β progressively decreased in a
573 posterior sensor cluster overlying visual cortex at a corrected $p = 0.023^f$ (Fig. 4A, top

574 panels). For the sensors within this cluster, the mean alpha amplitude β across subjects
575 in each condition is plotted in Fig. 4A (bottom panel). Interestingly, white noise input ($\beta =$
576 0) enhanced alpha amplitude β compared to rest ($p = 0.0065^g$, paired t-test across
577 subjects), and there was a trend effect of stimuli with strong autocorrelation ($\beta = 2$)
578 reducing alpha amplitude β compared to rest ($p = 0.0774^h$). A control analysis indicated
579 that stimulus β did not significantly influence MEG signal power in the alpha range. No
580 significant correlation between stimulus β and SCP β was found, nor between stimulus β
581 and EKG α , suggesting that the strength of autocorrelation within SCP and heartbeat
582 dynamics was robust to the range of scale-free stimuli employed in this experiment.

583

584 **Scale-free neural dynamics predicted behavioral performance**

585 Lastly, we investigated whether scale-free neural or physiological dynamics predicted a
586 subject's behavioral performance in the auditory task. Behavioral performance was
587 assessed by Spearman's correlation between stimulus β and response β as described
588 above ("behavioral rho"). We found that behavioral performance correlated negatively
589 with SCP β (averaged across all conditions) in a group of sensors distributed over fronto-
590 central areas (Fig. 4B, $r = -0.62$, $p < 0.0044^i$), and positively with alpha amplitude β in a
591 group of sensors over left fronto-temporal cortices (Fig. 4C, $r = 0.64$, $p = 0.0030^j$). These
592 results suggest that higher autocorrelation within alpha-oscillation amplitude fluctuations,
593 and lower autocorrelation within the SCP, predict better discrimination performance on
594 scale-free auditory stimuli. Importantly, neither SCP power nor alpha-oscillation power
595 correlated with behavioral performance, suggesting that signal power was not a
596 mediating factor between scale-free neural dynamics and behavioral performance. A
597 control analysis further suggested that the above effects are regionally specific: alpha-
598 amplitude β in the frontocentral area (Fig. 4B, left) did not significantly correlate with

599 behavioral performance ($r = 0.15$, $p = 0.55^k$); nor did SCP β in the left frontotemporal
600 area (Fig. 4C, left) ($r = -0.32$, $p = 0.19^l$).

601

602 **Discussion**

603 In this study, we investigated the interrelations amongst scale-free dynamics in the SCP,
604 alpha-oscillation amplitude fluctuations and heartbeat dynamics across MEG sensors
605 and subjects, and over time within an individual. We further explored their modulation by
606 scale-free dynamic stimuli, and tested whether an individual's scale-free neural
607 dynamics predicted their ability to tell scale-free stimuli apart based on autocorrelation
608 property. Below, we summarize our findings in turn and discuss their implications.

609

610 **Interrelations amongst scale-free neural and physiological dynamics**

611 Across the scalp, a qualitative pattern emerged such that sensors exhibiting stronger
612 autocorrelation (hence, larger power-law exponent β) in the SCP tended to have weaker
613 autocorrelation in the alpha-oscillation amplitude fluctuations. In addition, SCP β and
614 alpha-amplitude β were anti-correlated across subjects within a large posterior sensor
615 cluster. This anticorrelation could not be explained by the nested-frequency coupling
616 between SCP and alpha oscillations, as a control analysis based on simulation
617 suggested that the phase-amplitude coupling between SCP and alpha oscillations
618 contributes to a positive correlation between their power-law exponents instead.
619 Together, these results suggest that not only do scale-free dynamics exist within both
620 arrhythmic brain activity and amplitude fluctuations of brain oscillations, but these
621 different scale-free neural dynamics are related and follow a systematic antagonistic
622 pattern. Functionally, this anticorrelation may be important for preventing excessive long-
623 range temporal correlation in the brain, such that strong autocorrelation in one type of

624 neural signals impedes the generation of strong autocorrelation in another. Since proper
625 brain functioning requires a balance of sufficient order and flexibility, such anti-
626 correlation may be evident of a negative feedback mechanism whereby self-organized
627 brain activity is regulated across levels to avoid excessive regularity or overly random
628 fluctuation. The current study does not address the mechanism giving rise to the
629 anticorrelation between SCP β and alpha-amplitude β across subjects. In particular, it
630 remains unknown whether these two measures have a common mechanism or different
631 mechanisms under common influence, or, alternatively, one measure influences the
632 other directly or indirectly. Nonetheless, developmental and genetic contributions that
633 have been shown to influence alpha-amplitude β (Linkenkaer-Hansen et al., 2007; Smit
634 et al., 2011) indicate possible starting points for future investigations to probe.

635

636 We further observed that SCP power positively correlated with SCP β across time within
637 an individual, indicating that higher β in the SCP is a result of higher power in the lowest
638 frequencies. This resonates with a previous finding on the pattern of power spectral
639 changes in this frequency range during task performance (He et al, 2010).

640

641 Our results reveal a novel relationship between scale-free neural and physiological
642 dynamics, with the strengths of autocorrelation in the SCP and heartbeat dynamics
643 (captured by SCP β and EKG α , respectively) positively co-modulating across trials
644 within an individual. Since neither measure was influenced by stimulus condition, this
645 relationship is due to their intrinsic fluctuations over time. By contrast, we did not
646 observe a significant relationship between alpha-amplitude β and EKG α ; such a
647 relationship was reported in Palva et al. (2013) but it failed to be reproduced in a later
648 study from the same group (Zhigalov et al., 2015). Zhigalov et al. reported a correlation
649 between the scaling exponents of delta-oscillation amplitude and heartbeat dynamics;

650 however, they tested many frequency bands and brain systems without correcting for
651 multiple comparisons. In addition, neither of these two previous studies directly recorded
652 EKG, but rather used ICA-extracted component from the MEG recording to substitute for
653 heartbeat signal. Our result with direct EKG recording suggests that fluctuations in slow,
654 arrhythmic neural activity coordinate with heart signals, although the directionality of this
655 influence remains unknown at present. We speculate that a tight correlation between
656 SCP β and EKG α may be due to the fact that the time scales at which SCP and
657 heartbeat dynamics fluctuate are comparable, both taking place on the order of many
658 seconds (SCP: 0.2 – 200 sec; heartbeat: 4 – 64 sec; as compared to alpha amplitude: 1
659 – 10 sec). Together, the anticorrelation between SCP β and alpha-amplitude β and the
660 positive correlation between SCP β and EKG α may suggest the SCP as a central link
661 that connects scale-free neural and physiological dynamics across scales and systems.
662 Nonetheless, neuroanatomical interpretation for the spatial distribution of sensors whose
663 SCP β correlate with EKG α (Fig. 3E) would be better informed by future investigations
664 employing invasive recordings and/or source reconstruction.

665

666 More broadly, it has been shown that the brain exerts strong autonomic influence on and
667 receives feedback from the heart (Craig, 2002; Gray et al., 2007). Previous studies
668 suggest that scale-free heartbeat dynamics may be adaptive with its long-range
669 temporal correlation serving as a self-organizing mechanism for highly intricate
670 processes that generate fluctuations across wide timescales (Ivanov et al., 1996).
671 Indeed, highly periodic or rigid behaviors may narrow functional responsiveness, as
672 shown by the observation that the breakdown of scale-free heart dynamics and
673 appearance of excessive regularity often accompany pathologies such as severe
674 congestive heart failure (Goldberger et al., 2002).

675

676 **Stimulus modulation of scale-free neural dynamics**

677 We observed a systematic modulation of alpha-oscillation amplitude dynamics by scale-
678 free auditory stimuli, such that alpha-amplitude β decreased with increasing stimulus β in
679 a posterior sensor cluster overlying occipital cortex. Our stimuli captured a range of
680 stationary and non-stationary patterns, from fractional Gaussian noise to fractional
681 Brownian motion. This result suggests that listening to stimuli that exhibit strong auto-
682 correlation reduces auto-correlation in alpha amplitude fluctuations in visual regions. A
683 control analysis further suggested that stimulus β had no effect on MEG signal power in
684 the alpha range. Why should an auditory task affect scale-free neural dynamics in visual
685 regions? While underlying mechanisms of this phenomenon require future investigation,
686 a speculative possibility is that higher stimulus β translates into lower alpha-amplitude β
687 in visual regions due to cross-modality interaction carried by an inhibitory pathway from
688 auditory cortex to visual cortex (Iurilli et al., 2012).

689

690 By contrast, we did not observe a significant correlation between stimulus β and SCP β
691 after cluster-based correction. This negative finding could be due to several reasons. It is
692 possible that SCP reflects a backbone of brain network structure that remains
693 unperturbed by changes in arousal state (He et al., 2008) or the range of scale-free
694 stimuli utilized herein. Yet, at present we cannot rule out the possibility that the sample
695 size in the current study was insufficient for detecting an effect in the SCP.

696

697 **Prediction of behavioral performance**

698 We found intriguing evidence suggesting that baseline characteristics of scale-free
699 dynamics in the SCP and alpha amplitude fluctuations predicted an individual's
700 performance in discriminating between scale-free auditory stimuli exhibiting different
701 levels of autocorrelation. Better performance correlated with higher alpha-amplitude β

702 and lower SCP β . Moreover, neither SCP nor alpha-oscillation power correlated with
703 behavioral performance, suggesting specific behavioral relevance of scale-free
704 parameters. Previous studies have shown that alpha-amplitude β correlates with long-
705 range temporal correlation in behavioral fluctuations across normal subjects (Palva et
706 al., 2013; Smit et al., 2013). Yet, it is unclear whether longer or shorter autocorrelation in
707 behavioral fluctuations is adaptive. On the other hand, discriminating natural stimuli
708 based on their time-aggregate statistics should confer behavioral advantage in an
709 ecologically natural environment. To our knowledge, this is the first study demonstrating
710 that properties of scale-free neural dynamics predict behavioral performance across
711 normal individuals.

712

713 Why should lower SCP β and, conversely, higher alpha-amplitude β predict better
714 behavioral performance? One possibility is that SCP fluctuations include frequencies an
715 order of magnitude lower than alpha amplitude fluctuations (0.005 – 5 Hz vs. 0.1 – 1 Hz).
716 Thus, this pattern of result is consistent with the idea that there may be an optimal range
717 of autocorrelation that is most conducive to performing this task: relatively weak
718 autocorrelation in the very long time scales encompassed by the SCP, and relatively
719 high autocorrelation in the comparatively shorter time scales spanned by alpha
720 amplitude fluctuations. Higher alpha-amplitude β might also suggest a state closer to
721 criticality with higher information processing capacity (Poil et al., 2012; Shew et al.,
722 2011). Tantalizing clues supporting the existence of an optimal range of scale-free
723 neural dynamics exist from studies of clinical populations. For example, breakdown of
724 long-range temporal correlation in theta- and alpha- oscillation amplitude fluctuations
725 has been observed in depression (Linkenkaer-Hansen et al., 2005), Alzheimer's
726 Disease (Montez et al., 2009), and schizophrenia (Nikulin et al., 2012). On the other

727 hand, abnormally high long-range temporal correlation in beta-band amplitude
728 fluctuations is found in seizure onset areas (Monto et al., 2007).

729

730 Lastly, in our experiment, the auditory stimuli were constructed such that scale-free
731 statistic, embodied in the power-law exponent β , is the only difference between
732 categories of auditory tone sequences. All other statistics, including tone duration, pitch
733 range, sequence length, and higher-order statistics (which are random), were identical
734 across stimulus categories ($\beta = [0, 0.2, 0.5, 1.5, 2]$). Moreover, behavioral discrimination
735 was carried out on power-law exponent β , not the specific sequence presented; this was
736 ensured by presenting 6 unique sequences at each β level, and asking subjects to make
737 discrimination about β only. Hence, in our task, subjects' ability to discriminate different
738 auditory tone sequences was specifically related to their ability to process the scale-free
739 statistic of the stimuli, and our findings establish the role of scale-free brain activity in
740 processing scale-free statistics of naturalistic stimuli. On the other hand, our results do
741 not imply that the function of scale-free brain activity is specific to the processing of
742 scale-free or natural stimuli. It is possible that similar correlations may be observed for
743 tasks that do not explicitly require the evaluation of scale-free stimulus statistics. Future
744 studies investigating performance in such tasks will delineate the functional specificity
745 (or generality) of scale-free neural activity.

746

747 In summary, we observed novel relationships amongst scale-free dynamics in distinct
748 components of neural and physiological activity, including the SCP, alpha-oscillation
749 amplitude fluctuations and heartbeat dynamics. We further demonstrate that scale-free
750 neural dynamics can be systematically perturbed by scale-free dynamical stimuli that
751 capture 2nd-order statistics (i.e. autocorrelation or power spectrum) of the natural
752 environment. Moreover, the baseline characteristics of scale-free neural dynamics in an

753 individual predict their ability to discriminate scale-free dynamical stimuli based on their
754 autocorrelation property. These results shed light on the complex interrelations amongst
755 scale-free neural and physiological dynamics at different levels and how they may
756 contribute to adaptive behavior in the natural environment.

757

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764

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875

876 **Figure legends**

877 **Figure 1. Stimuli characteristics and behavioral performance.** (A) Lagged auto-
878 correlation function for each class of stimulus sequences, averaged across the 6
879 examples at each β level. (B) Power spectra of stimulus sequences, averaged across
880 the 6 examples at each β level. (C) Visual instruction presented to the subjects, showing

881 example stimulus sequences at different β levels. Sequences of two different overall
882 range were presented (large fluctuation range: the two left columns; small range: the two
883 right columns), to demonstrate that trend strength (i.e., auto-correlation) is independent
884 from overall range. **(D)**. Group-average (N=19) conditional probability of behavioral
885 response given stimulus β , color-coded by the proportion of response β at each
886 stimulus- β level. Each row sums to 1.

887

888 **Figure 2. Characterization of neural and physiological dynamics.** **(A)** Left: MEG
889 signal power spectra from an example subject in each task condition (averaged across
890 all sensors and trials within a condition). Middle: Example MEG signal power spectrum
891 from a single trial in one subject. The red lines indicate the frequency range for
892 extracting SCP power-law exponent β : 0.005 – 5 Hz. Right: Grand-average topographic
893 map of SCP β across the scalp. **(B)** Same as in A, but for alpha-oscillation amplitude.
894 Alpha oscillation was filtered in the 6.7 – 13.3 Hz range, and its amplitude time series
895 was extracted using the Hilbert transform. Alpha-amplitude β was extracted in the 0.1 –
896 1 Hz range (red lines in the middle panel). **(C)** For analysis on heartbeat dynamics, the
897 inter-beat interval was calculated as the difference in time (sec) between adjacent R-
898 peaks in the EKG recording (left panel). The inter-beat interval time series was subjected
899 to detrended fluctuation analysis (DFA) to extract the DFA exponent α , which describes
900 the power-law relationship between fluctuation magnitude and the length of observation
901 in scale-free dynamics (right panel).

902

903 **Figure 3. Interrelations between scale-free neural and physiological dynamics.** **(A)**
904 Scatter plot of SCP β against alpha-amplitude β across all MEG sensors (averaged
905 across subjects and stimulus conditions). The inset shows the grand-average
906 topographical plots of SCP β and alpha-amplitude β , reproduced from Fig. 2. **(B)** Top:

907 Nested-frequency analysis between SCP phase and alpha amplitude. Group-average
908 Modulation Index (MI) Z-score topography plot is shown (middle), along with the phase-
909 amplitude histogram for the two dominant clusters (see insets). Bottom: The scatter plot
910 between empirically measured SCP β and simulated alpha-oscillation amplitude β
911 across all sensors. (C) Left: Scatter plot across subjects between SCP β and alpha-
912 amplitude β in a posterior sensor cluster (see inset). Right: Scatter plot across subjects
913 between SCP β and alpha-amplitude β in an anterior sensor cluster (see inset). (D)
914 Correlation between SCP β and SCP power across trials within an individual. Pearson
915 correlation values were Fisher-z-transformed and subjected to a group-level one-sample
916 t-test. T-values are plotted in the topography plot, with a single cluster encompassing all
917 sensors surviving cluster-based correction. The group-level mean and s.e.m. of Fisher-z
918 values (averaged across all sensors) are shown in the bar-graph to the right ($p < 0.001$,
919 1-sample t-test across subjects). (E) Similar to D, but for within-subject, across-trial
920 correlation between SCP β and EKG α . Two clusters of sensors survived cluster-based
921 correction. The group-level mean and s.e.m. of Fisher-z values (averaged across all
922 significant sensors) are shown in the bar graph to the right ($p < 0.001$, 1-sample t-test
923 across subjects).
924

925 **Figure 4. Stimulus modulation of scale-free neural dynamics and prediction of**
926 **behavioral performance.** (A) Spearman rank correlation was calculated between
927 stimulus β and alpha amplitude β across the 30 task trials for each subject, and the
928 group average is plotted for all sensors (top-left panel). A posterior sensor cluster
929 survived cluster-based correction at $p < 0.05$ level (top-right panel). For this significant
930 sensor cluster, alpha-amplitude β averaged across sensors was plotted for each
931 stimulus β level and rest condition (bottom panel), which shows the mean and s.e.m.
932 across subjects. (B) Left: Pearson's correlation value between behavioral performance

933 (measured as “behavioral rho”) and SCP β (averaged across all conditions) across
 934 subjects, thresholded at a $p < 0.05$ level. Non-significant sensors are shown as a uniform
 935 green background. Right: The SCP β averaged across significant sensors is plotted
 936 against behavioral rho for all subjects. (C) Same as B, but for the correlation between
 937 alpha-amplitude β and behavioral performance.

938

939 **Statistical table.**

	Data Structure	Type of Test	Power
a	non-parametric	Spearman’s correlation	below for each subject*
b	normal	Pearson's correlation	0.55
c	normal	Pearson's correlation	0.29
d	normal	Pearson's correlation	1
e	normal	Pearson's correlation	0.55
f	normal	cluster-corrected permutation test**	cluster p value = 0.023, 1000 permutations
g	normal	paired-t test	0.83
h	normal	paired-t test	0.43
i	normal	Pearson's correlation	0.83
j	normal	Pearson's correlation	0.86
k	normal	Pearson's correlation	0.09
l	normal	Pearson's correlation	0.26

940 **based on one-sample t-tests at each sensor, where the permutation is conducted
 941 at the trial level for each subject

942







