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**Research Articles: Behavioral/Cognitive**

**Neural Entrainment to the Beat: the “Missing Pulse” Phenomenon**

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3 **Abbreviated Title: The “Missing Pulse”**

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22 **Abstract**

23           Most humans have a near-automatic inclination to tap, clap or move to the beat of  
24 music. The capacity to extract a periodic beat from a complex musical segment is remarkable,  
25 as it requires abstraction from the temporal structure of the stimulus. It has been suggested  
26 that nonlinear interactions in neural networks result in cortical oscillations at the beat  
27 frequency, and that such entrained oscillations gives rise to the percept of a *beat*, or a *pulse*.  
28 Here we tested this “Neural Resonance Theory” using MEG recordings as female and male  
29 individuals listened to 30-second long sequences of complex syncopated drumbeats designed  
30 such that they contain no net energy at the pulse frequency when measured using linear  
31 analysis. We analyzed the spectrum of the neural activity while listening and compared it to the  
32 modulation spectrum of the stimuli. We found enhanced neural response in auditory cortex at  
33 the pulse frequency, and showed phase locking at the times of the missing-pulse, despite the  
34 fact that it was absent from the stimulus itself. Moreover, the strength of this pulse-response  
35 correlated with individuals’ speed in finding the pulse of these stimuli, as tested in a follow-up  
36 session. These findings demonstrate that neural activity at the pulse-frequency in auditory  
37 cortex is internally generated rather than stimulus-driven. In line with the Neural Resonance  
38 Theory, the current results are consistent with models based on nonlinear response of the brain  
39 to rhythmic stimuli and thus constraining possible models of beat perception.

40 **Significance statement**

41 Humans perceive music as having a regular pulse marking equally spaced points in time, within  
42 which musical notes are temporally organized. Neural Resonance Theory (NRT) provides a  
43 theoretical model explaining how an internal periodic representation of a pulse may emerge  
44 through nonlinear coupling between oscillating neural systems. We tested key falsifiable  
45 predictions of NRT using MEG recordings, and demonstrate the emergence of neural  
46 oscillations at the pulse frequency, which can be related to pulse perception. These findings  
47 rule-out alternative explanations for pulse-perception and provide evidence supporting neural  
48 entrainment to the pulse, a widely debated topic over recent years.

49 **Introduction**

50 Music often contains complex temporal patterns, with no simple regularity predicting  
51 when a particular note will occur. Nonetheless, listeners typically perceive music as having a  
52 regular *pulse*, or *beat*, marking equally spaced points in time within which sequences of musical  
53 notes are organized. Moreover, an almost automatic response is to move to the beat of the  
54 music (Nettl, 2000; Michaelis et al., 2014). The process through which a percept of pulse  
55 emerges is referred to as induction, and most listeners are quite accurate in identifying and  
56 tapping to a pulse, even for highly non-isochronous rhythms (Large et al. 2002, 2015; Patel et  
57 al., 2005).

58 The neural mechanisms underlying pulse induction are not fully understood, but it is  
59 clear that the phenomenon involves complex dynamics in multiple brain regions including STG,  
60 SMA, frontal cortex, Basel ganglia and cerebellum (Grahn and Brett, 2007; Bengtsson et al.,  
61 2009; Chen et al., 2009; Chapin et al., 2010; Merchant et al., 2015). Large and colleagues  
62 recently proposed a computational model, Neural Resonance Theory (NRT), for explaining how  
63 non-periodic stimuli interact with endogenous brain rhythms to induce the percept of a  
64 periodic pulse (Snyder and Large, 2005; Large, 2008; Large and Snyder, 2009). According to  
65 NRT, the pulse emerges through nonlinear coupling between two oscillatory networks – one  
66 representing the physical properties of the stimulus (labeled “sensory”), and a second (labeled  
67 “motor”) that integrates inputs from the sensory system. The nonlinear interactions give rise to  
68 oscillatory activity not only at the frequencies present in the stimulus, but also at more complex  
69 combinations, including the pulse frequency (and its harmonics).

70           A critical test for empirical evaluation of NRT is to use syncopated rhythms in which the  
71 pulse frequency does not physically exist in the stimulus. It has been shown that syncopated  
72 rhythms containing no energy at the pulse-frequency in their broadband modulation spectrum  
73 (Velasco and Large, 2011), can nonetheless induce the percept of a pulse (Chapin et al. 2010;  
74 Large et al. 2015). Such rhythms are created using phase cancellation – half of the notes occur  
75 in-phase with the intended pulse, the other half occur in anti-phase. Here we tested whether  
76 the neural response to such stimuli contains energy at the pulse frequency, despite its physical  
77 absence in the acoustics. If this were the case, it would support the notion that pulse induction  
78 emerges through nonlinear interaction between the stimulus and endogenous neural dynamics,  
79 and would rule out simpler explanations of apparent entrainment stemming either from  
80 transient responses to individual rhythmic events (Sussman et al. 2008; Tremblay et al. 2004),  
81 or from linear frequency analysis of the stimuli (Todd, 1999; Tomic and Janata, 2008). Previous  
82 studies have demonstrated that the steady-state EEG response to syncopated stimuli shows  
83 enhanced power at the pulse frequency; at magnitudes exceeding what is expected from the  
84 acoustic structure of the stimulus alone, which is in line with NRT predictions (Nozaradan et al.,  
85 2011, 2012 and 2016). However, in most of those studies, the pulse frequency was either  
86 present in the stimulus envelope, or was induced through instruction, making it difficult to rule-  
87 out the possibility that these effects reflect selective amplification of neural responses to on-  
88 beat sounds (Tierney and Kraus, 2014; Bower and Honing, 2015).

89           In the current study we directly test the hypotheses posed by NRT that oscillations at  
90 the pulse frequency would emerge independent of stimulus acoustics, using MEG recordings  
91 while individuals listened to ‘pulse-less’ syncopated rhythms. We were also interested in testing

92 whether the emergence of a neural representation for the pulse was linked to the behavioral  
93 perception of a pulse, since previous studies have suggested that pulse induction for  
94 syncopated rhythms is not ‘automatic’, but requires attention (Chapin et al. 2010) and can be  
95 modified by instruction (Large et al. 2002; Nozaradan et al. 2011).

## 96 **Methods**

### 97 **Experiment 1**

98 *Participants.* 11 subjects (6 males, mean age = 30, SD = 3.7) received payment to participate in  
99 the study and signed a consent form approved by the NYU IRB ethics committee. Participants  
100 did not suffer from any neurological disorders and had normal hearing.

101 *MEG Recordings.* MEG data were collected on a 157-channel whole-head MEG system (5 cm  
102 baseline axial gradiometer SQUID-based sensors, KIT, Kanazawa, Japan) in an actively  
103 magnetically shielded room (Vakuumschmelze GmbH). Data were sampled at 1000 Hz, with a  
104 notch filter at 60 Hz, and an online recording 200Hz low pass filter. Each participant's head  
105 position was assessed via five coils attached to anatomical landmarks both before and after the  
106 experiment to ensure that head movement was minimal using 3D digitizer software (Source  
107 Signal Imaging) and digitizing hardware (Polhemus). The auditory signals were presented  
108 through in-ear earphones (Etymotic ER3-A) at comfortable, conversational levels (~ 72 dB SPL).  
109 Stimulus delivery and triggering was controlled by Presentation (Neurobehavioral systems,  
110 Albany, CA).

111 *Stimuli.* Stimuli consisted of sequences of drumbeats, with a rise time of 0.5 ms (calculated as  
112 the time it took the acoustic signal to cross from 10% to 90% reference levels) and pulse width

113 of 20 ms. Four different sequences were used, differing in their temporal pattern, as illustrated  
114 in Figure 1a. The Isochronous sequence (*ISO*) contained 8 drumbeats presented with a constant  
115 Inter Onset Interval (IOI) of 0.5 seconds. Two syncopated patterns that contained no energy at  
116 the pulse frequency when measured using linear analysis and are thus referred to as Missing-  
117 pulse (*MP1* and *MP2*) were selected from the stimuli used by Chapin et al. (2010). These  
118 complex rhythmic patterns contained 8 drumbeats, and were constructed such that half of the  
119 drumbeats occurred on “strong” beats and half on “weak” beats of a 2Hz rhythm. These highly  
120 syncopated patterns are expected to give rise to the perception of a 1Hz or 2Hz pulse, yet the  
121 Fourier spectrum of the stimuli contain no energy at these frequencies. The random condition  
122 (*RAND*) consisted of 8 drumbeats placed in a temporally-random sequence that did not induce  
123 any perception of a pulse. All sequences had an equal length of 4 seconds. We analyzed the  
124 modulation-spectrum of the stimulus acoustics by computing the broadband amplitude  
125 envelope using the absolute value of the Hilbert transform. Next, we computed the spectrum of  
126 the envelope using FFT on 2 cycles of each sequence (8 sec.), yielding a frequency resolution of  
127 0.125Hz. We used the broadband envelope to assess the modulation-spectrum. In the general  
128 case, the cortical inputs relevant to beat perception would more realistically be described as  
129 event onsets in multiple cochlear frequency channels (Langner, 1992). However, since the  
130 percussive sounds used here as stimuli are brief and broadband, the two input representations  
131 yield nearly identical frequency-domain descriptions. This simpler representation enabled us to  
132 apply a similar analysis to the stimulus and the neural signal.

133 As seen in Figure 2 (top panels), neither syncopated stimuli contained a peak at 1 or 2Hz –  
134 frequencies that are perceived as the pulse of these rhythms. One should note that although



135 both our syncopated rhythms contained instances where the interval between sounds is  
136 precisely 500 ms (2 such intervals in MP1, 3 such intervals in MP2), by design, these intervals  
137 were never consecutive but are separated by other intervals. Consequently, due to the  
138 uncertainty principle, there is no principled way for a linear system (digital or biological) to  
139 produce a 2Hz response from a single interval of 500 ms, even if a shorter time-windows was  
140 used in order to calculate the modulation spectrum.

141 *Experimental Procedure.* The time course of a sample trial is illustrated in Figure 1b. Participants  
142 listened to 8 consecutive repetitions of one of the patterns (total 32 seconds). Following this  
143 passive listening period, the participants heard an additional test item consisting of one  
144 repetition of the same pattern but could have a different tempo (same tempo, 10% faster or  
145 10% slower, equi-probable). Participants were then asked to judge whether the tempo of the  
146 test item was faster, slower or the same as the original pattern. This was done in order to keep  
147 the subjects engaged while passively listening to the long auditory stimulus and attentive to its  
148 temporal properties without explicitly instructing them to extract a pulse. Trials with the four  
149 different temporal conditions (*ISO, MP1, MP2, RAND*) were presented in pseudo-random order  
150 and each condition was repeated 10-15 times throughout the experiment.

151 *MEG preprocessing and analysis.* All analyses were performed using MATLAB (The Mathworks,  
152 Natick MA), as well as the Fieldtrip toolbox (Oostenveld et al. 2010). The data were noise  
153 reduced offline using a time-shift Principled Component Analysis (de Cheveigné and Simon  
154 2007). Heart beats, eye movements and blinks artifacts were removed from the data using an

155 ICA algorithm from the Fieldtrip toolbox. Additional visual inspection of the data was performed  
156 to remove data segments with large muscle or external artifacts.

157 *Spectral analysis.* MEG signals were segmented into 32-second long epochs corresponding to  
158 the 'passive listening' periods, and divided into four conditions. The first 1-second of data was  
159 removed from all epochs, to avoid onset effects. Epochs were then averaged for each  
160 condition, and the spectrum of the averaged data (zero padded) was calculated using Fourier  
161 transform at each of the 157 sensors, separately for each participant. Visual inspection revealed  
162 a peak in the MEG spectrum at 2Hz that did not exist in the stimulus spectrum and matches the  
163 preferred intrinsic pulse tempo for these syncopated stimuli (Moelants, 2002, Honing, 2013,  
164 Large et al. 2015).

165 For statistical analysis of the pulse frequency peaks observed in the MEG spectrum, we  
166 averaged the MEG responses for each subject over all sensors. We then calculated the non-  
167 parametric Wilcoxon signed-rank test between the 2 Hz power and the mean power at  
168 frequencies around it (1.875 Hz and 2.125 Hz). We specifically targeted this frequency a-priori  
169 (as the stimuli were constructed to induce perception of a pulse at this specific rate), and the  
170 *RAND* condition served as a control to test that the observed effects were not biased due to  
171 this a-priori frequency selection.

172 *Phase-Locking Analysis.* The stimuli were constructed such that half of the drumbeats occurred  
173 on strong-beat positions, whereas in half of the strong-beat positions no stimuli occurred. This  
174 allowed us to look directly at the neural activity at these positions which was not contaminated  
175 by sensory-evoked potentials, in addition to analyzing the spectrum of the neural response to

176 the entire continuous stimuli. To this end, single trials data were filtered between 0.5-3 Hz and  
177 the instantaneous phase at each time point was extracted using the Hilbert transform  
178 (implemented in Matlab). For each of the syncopated conditions we averaged the phase values  
179 for each subject at the ‘missing beat’ positions (i.e. the temporal location of strong-beat where  
180 no physical stimuli were present; see Figure 5, red Xs’). These time points occurred either 0.25  
181 or 0.5 sec after a previous auditory stimulus. In order to control for carry-over effects of  
182 evoked-responses to previous stimuli we used the *RAND* condition (in which there was no  
183 expected pulse) as follows: We selected time points in the *RAND* condition where no physical  
184 stimulus was present and were at similar distances from previous sounds as the “missing beat”  
185 positions in the *MP1* condition (i.e. 0.25 and 0.5 sec. from the onset of the auditory stimulus).  
186 This equated any possible effects of responses to previous sounds on the response at time  
187 “zero” between the syncopated and *RAND* conditions, and allowed us to rule out the possibility  
188 that phase locking observed in the syncopated conditions was merely a reflection of carry-over  
189 responses to previous sounds. For all three conditions, we tested the mean-phase consistency  
190 across subjects using the Rayleigh test at each MEG sensor, and corrected for multiple  
191 comparisons of the number of MEG sensors using false discovery rate (FDR).

192 *Behavioral Tapping Paradigm.* Following the MEG scans, participants performed a behavioral  
193 tapping task to assess their subjective perception of a pulse in syncopated rhythms. This task  
194 was performed outside the MEG immediately after the main experiment, and not as part of the  
195 main experiment so as not to contaminate the MEG data with motor activity from the tapping.  
196 We used 10 different pulse-less syncopated patterns, previously used by Chapin et al. (2010)  
197 and Velasco and Large (2011). Each pattern was repeated 8 times consecutively (total 32

198 seconds) and participants were instructed to listen to the auditory patterns and start tapping  
199 on a touch-pad in a periodic manner as soon as they perceive a constant pulse from the  
200 complex rhythms. As means for evaluating the robustness of their pulse perception, for each  
201 participant we evaluated how long it took them to start tapping (Time to Tap; TTT) as well as  
202 the temporal precision of their taps using circular statistics. For each subject in each trial, the  
203 event times closest to the tapping times were used to convert all taps of all subjects into a  
204 sequence of phases  $\phi = 2\pi \frac{t_{event} - t_{tap}}{IOI}$ , where the inter-onset interval (IOI) of the metronome  
205 time was set to 60/tempo (Large and Gray, 2015). The circular mean for each trial was then  
206 computed. The length of the mean vector,  $r$ , is the synchronization coefficient which is a  
207 measure of tapping variability (1: no variability; 0: maximum variability). The angle  $\phi$  of the  
208 mean vector shows the relation to the pulse of the rhythmic pattern.  $\phi > 0$  indicates that taps  
209 came earlier than the pulse,  $\phi < 0$  indicates that taps came later than the pulse (for additional  
210 details of the calculation of circular mean and mean vector see: Large et al., 2015)

211 Tapping data were not available from one of the subjects due to technical problems. Thus, this  
212 analysis was based on the remaining 10 subjects.

### 213 **Experiment 2**

214 We were unable to perform reliable source localization for the data collected in Experiment 1,  
215 due to technical problems. NRT hypothesized that the two interacting systems involved in  
216 generating the 'missing-pulse' responses correspond to sensory and motor networks (Large et  
217 al. 2015). In order to empirically test the predictions of the model as to which brain regions  
218 produced the pulse frequency peaks observed in Experiment 1, we repeated the same

219 paradigm with a different group of subjects, in another MEG scanner. Our analysis focused  
220 specifically on contrasting the neural responses in auditory cortex vs. motor-related regions  
221 (motor cortex and supplementary motor area; SMA).

222 *Participants.* 8 subjects (3 males, mean age = 26, SD = 4.17) received payment to participate in  
223 the study and signed a consent form approved by the Bar Ilan University internal ethics  
224 committee. Participants had no more than one year of musical training (in their childhood), had  
225 normal hearing and did not suffer from any neurological disorders.

226 *MEG Recordings.* Magnetic brain responses were measured with a whole head helmet-shaped  
227 biomagnetometer (4D-Neuroimaging, San Diego). The sensor array consisted of 248  
228 superconducting magnetometers. A head position indicator using five coils attached to the  
229 scalp provided exact information on the position of the head relative to the sensor array before  
230 and after the measurement. Coil positions were determined in relation to external anatomical  
231 landmarks. The head shape and coil position were digitized using a Pollhemus FASTTRAK  
232 digitizer. Brain signals were recorded at a sampling rate of 1017.25Hz and band-pass filtered at  
233 0.1-400Hz.

234 *Stimuli and experimental procedure.* We used the same stimuli and paradigm as in Experiment  
235 1. However, in order to assist analysis of the MEG data in source space, auditory and motor  
236 localizer tasks were added after the main experiment.

237 *Localizer tasks.* The auditory localizer task consisted of passive listening to drumbeat tones  
238 presented at random times with an interval of  $500 \pm 200$  milliseconds. The duration of the  
239 auditory localizer task was  $\sim 1.5$  minutes. For the motor localizer task subjects were instructed

240 to tap repeatedly at a comfortable rate using their index finger for ~1.5 minutes for each hand.  
241 Tapping was performed on flat-surfaced custom-made optic device, which did not produce any  
242 auditory sounds, and allowed recording the precise tap-times for use in subsequent  
243 segmentation of the MEG data. The localizer was performed separately for the right and left-  
244 hands.

245 *Source Localization.* For source localization of the functional MEG data, we co-registered the  
246 head shape digitization from the MEG with the anatomical MRI of the participant. When an  
247 anatomical MRI was not available (3 participants) a template MRI (MNI305) was used and  
248 scaled for co-registration with the digitized head shape of the subject. Co-registration used 3  
249 anatomical landmarks on the subject's head: left pre-auricular point (PA), right PA and Nasion.  
250 Then, we created a Nolte model (Nolte, 2003) hull according to the brain surface of the MRI  
251 data using Brainhull software (NIMH, Bethesda, Maryland) and used this hull as a model for  
252 source localization.

253 Brain activity was localized using a Synthetic Aperture Magnetometry (SAM) beamformer  
254 (Robinson and Vrba, 1999) that derived a single optimal dipole orientation vector and  
255 amplitude for each target voxel that produced the maximal power-to-noise output ratio. We  
256 only used the amplitude for further analysis. Voxels were placed on a 5x5x5 mm rectangular  
257 grid. Only voxels within the hull were considered.

258 *ROI selection.* Statistical analysis of the power at the pulse frequency was performed in six  
259 independently-selected regions of interest (ROI) focusing on bilateral auditory and motor  
260 cortices and supplementary motor area (SMA). ROIs for auditory and motor cortex were

261 identified using data from two independent localizer procedures. To this end we calculated the  
262 average response in each task (event-related fields; ERFs) locked either to the onset of the  
263 sounds (auditory localizer) or the time of taps (motor localizer). We selected the time-window  
264 of maximal ERF for each participant to use for ROI localization. Beamformer weights for each  
265 voxel were derived from the covariance matrix of the raw localizer data filtered at 1-40Hz, and  
266 these weights were multiplied by the mean ERF in the selected time-window to estimate the  
267 source currents at each voxel. After aligning the subjects' anatomical and functional data to  
268 Talairach coordinates we chose the 20 voxels exhibiting the strongest responses in each of the  
269 localizer tasks within each hemisphere. For the SMA ROI we used the Human Motor Area  
270 Template, a composite atlas based on the meta-analysis of 126 motor-based fMRI studies  
271 (Mayka et al. 2006; <http://lrnlab.org>). In total, 6 ROIs were selected for each subject in the left  
272 and right auditory and motor cortices and SMA, which were used to constrain the statistical  
273 analysis of the data in the main experiment.

274 *Localization of pulse frequency.* MEG signals were segmented into 32-second long epochs  
275 corresponding to the 'passive listening' periods and divided into four conditions (*ISO, MP1,*  
276 *MP2, RAND*). Beamformer weights were calculated for each voxel from the covariance matrix of  
277 the raw single trial data filtered at 0.1-35Hz to avoid slow drifts or high frequency noise. Next,  
278 the average time-course for each condition was multiplied by these weights to obtain the time-  
279 course of neural responses at each voxel and calculate the spectrum of this response, as in  
280 Experiment 1. We normalized the entire spectrum for each voxel by its mean power at 80-  
281 120Hz to avoid bias due to different noise levels at each source location (Lots et al., 2016). The  
282 whole-brain analysis was used in order to obtain a qualitative description of the regions where

283 the strongest missing-pulse response was observed. However, statistical analysis focused on  
284 the six independently-selected ROIs, in bilateral auditory and motor cortices and SMA. The  
285 existence or lack of a ‘missing-pulse’ response in each of these ROIs were determined using the  
286 non-parametric Wilcoxon signed rank test between the amplitude of the 2Hz ‘missing pulse’  
287 frequency vs. the average of amplitude at surrounding frequencies (1.875 and 2.125Hz). This  
288 analysis was conducted on the average spectra across both syncopated stimuli (MP1 and MP2).

## 289 **Results**

### 290 ***Tempo Task***

291 The tempo task was designed to keep the subjects attending to the auditory stimuli and to its  
292 timing without explicit instruction to extract the pulse from the syncopated rhythms. All  
293 subjects, in both experiments, performed well in the task (mean = 83% correct, SD = 8%)  
294 indicating that they indeed attended to the auditory stimuli. There was no significant  
295 correlation between the results in the tempo task and the TTT or the synchronization  
296 coefficient of the subjects in the subsequent tapping task, although the two subjects who  
297 showed the worst performance in the tempo task also performed poorly in the tapping task.

### 298 ***MEG results – Experiment 1***

299 The main goal of this study was to test whether we could identify the emergence of the pulse in  
300 the dynamics of neural activity despite its absence in the acoustics. Figure 2a shows a  
301 comparison of the frequency content of each of the 4 stimuli used (top) and the spectrum of  
302 the MEG responses to each stimulus (bottom), averaged over all subjects.



303 The spectrum of the isochronous stimulus contains power at 2 Hz and its harmonics, and this  
304 pattern is faithfully represented in the neural response. The spectra of the two syncopated  
305 stimuli (*MP1*, *MP2*) have peaks at many frequencies (e.g. 0.75, 1.25, 2.75 and 4 Hz), but contain  
306 no energy at 2 Hz which is the expected pulse frequency. The MEG-recorded neural responses  
307 to these stimuli show peaks at all the frequencies contained in the stimuli. However, in  
308 addition, clear 2Hz peaks are observed for both *MP1* and *MP2*, despite the absence of this  
309 frequency in the stimulus spectrum. Moreover, in *MP1*, a peak was seen at 1Hz as well (a sub-  
310 harmonic which can also be perceived as the pulse in some cases; Parncutt, 1994). These results  
311 demonstrate the brains' capacity for generating an internal representation of the perceived  
312 pulse, above and beyond the acoustic of the stimulus. In the *RAND* condition, the stimulus  
313 spectrum contains several small peaks corresponding to peaks in the stimulus spectrum, but  
314 does not show any peak at 2Hz, nor any other frequency that is not present in the stimulus  
315 itself.

### 316 ***Correlations with tapping to the beat***

317 Pulse-perception for complex rhythms is not necessarily ubiquitous, but may vary across  
318 individuals. Therefore, we conducted an independent assessment of our participants' ability to  
319 extract the pulse from syncopated stimuli in a tapping task, performed outside the MEG  
320 immediately after the main experiment. There was substantial variability in the time it took  
321 each participant to perceive the pulse and start tapping (Time to Tap - TTT; Figure 3a), with  
322 some tapping within the second repetition and others requiring almost 3-4 repetitions of the  
323 rhythm (more than 10 sec.) to start tapping. However, once they started tapping most subjects

324 successfully synchronized to the stimulus and tapped at either 1Hz or 2Hz, both of which could  
325 be induced as the pulse of these stimuli (Honing, 2013, Large et al. 2015). Individual  
326 participants did not necessarily exhibit a clear ‘preference’ for tapping at one of these  
327 frequencies for all 10 stimuli, and in some instances started tapping at one frequency (e.g. 2Hz)  
328 and shifted to another frequency (e.g. 1Hz) mid-trial. This variability in pulse-perception is  
329 consistent with existing literature demonstrating that the same stimulus can induce the  
330 perception of a pulse at different (integer-related) frequencies across and even within  
331 individuals (reviewed by Repp et al. 2013). Variability in tap-rate was accounted for when  
332 calculating the synchronization coefficients and the angle of the mean vector, which ranged  
333 between  $0.67 < r < 0.97$  (Figure 3b, blue trace) and between  $-0.17 < \varphi < 0.87$  (Figure 3b, red  
334 trace), respectively. There was no significant correlation between the TTT and the  
335 synchronization coefficients of the subjects indicating that once participants perceived the  
336 pulse and started tapping, they did so accurately.

337 The variability in the time it takes individuals to perceive a pulse provides an opportunity to test  
338 whether the emergence of a neural response at the pulse-rate was uniform across all  
339 participants or whether it co-varied with their subjective perception of a pulse. Figure 4 shows a  
340 comparison of the MEG spectrum in the syncopated conditions for two example fast and slow  
341 pulse-perceivers, as assessed by their TTT values. Indeed, the fast pulse-perceiver showed the  
342 emergence of power at the 2Hz pulse frequency whereas this peak is absent in the spectra of  
343 the slow pulse-perceiver, supporting the notion that the 2Hz peak is related to the perception  
344 of a pulse rather than the acoustics of the stimulus. To quantify this effect, we calculated  
345 Spearman’s rank correlation between the TTT and the 2 Hz amplitude in the neural signal,

346 averaged over all MEG sensors. We found a strong negative correlation between the TTT and  
347 the 2 Hz power ( $r_s=-0.82$ ,  $p<0.01$ ; Figure 4c), such that subjects who started to tap to the pulse  
348 sooner had higher amplitude at 2Hz when passively listening to syncopated stimuli, whereas  
349 2Hz amplitude was lower in participants who took longer to detect a pulse. TTT was not  
350 significantly correlated with 2Hz amplitude in the isochronous or random condition ( $p>0.5$  for  
351 both).

### 352 ***Phase locking to the missing-pulse***

353 Thus far we have inferred the existence of a pulse-response by looking at the spectra of the  
354 neural response, averaged across the entire stimulus. However, the special nature of the  
355 syncopated stimuli used here allows us to specifically test the hypothesis that pulse induction is  
356 manifest in entrainment/phase-locking of low-frequency neural activity to the pulse-rhythm  
357 (Large et al., 2015). We use the term “entrainment” to describe the synchronization of neural  
358 responses to an external (or perceptual) rhythm, which in this case is the ‘pulse’ rhythm.  
359 According to this hypothesis, we would expect to find increased low-frequency phase-locking at  
360 strong-beat positions within syncopated sequences. The syncopated stimuli used here were  
361 constructed specifically so that individual sounds coincided with strong-beat positions only half  
362 of the time, whereas in the other half of the strong-beat positions no sounds occurred. Thus, in  
363 this analysis we focused only on the neural responses time-locked to strong-beat positions  
364 where no sounds occurred (red Xs’ in top panels of Figure 5a), thus avoiding contamination  
365 with sensory-evoked potentials. The bottom-panels in Figure 5a show the average sounds-wave  
366 locked to these positions, verifying that these were indeed locked to ‘quiet’ periods within the

367 sequence, and shared similar acoustic properties with control time-periods selected from the  
368 *RAND* condition.

369 Figure 5b shows the grand-average for neural responses time-locked to these positions for the  
370 two syncopated conditions and for the *RAND* condition. For both syncopated conditions a  
371 negative deflection is observed locked to the soundless strong-beat positions ( $t=0$ ), whereas in  
372 the *RAND* condition the responses is flat.

373 In order to quantify this response, we filtered the single-trials responses between 0.5-3Hz and  
374 extracted the momentary phase at this position separately for each trial, sensor and participant  
375 and calculated the mean phase across trials. We then tested the phase-consistency across  
376 participants using the Rayleigh test. A distribution of the mean phase across subjects is shown  
377 in Figure 5c for one representative MEG sensor. ~30% of the MEG sensors showed significant  
378 phase-locking at the time of the ‘soundless strong-beat position’ in both syncopated conditions  
379 (50 sensors for *MP1*; 51 for *MP2*;  $p<0.05$ , FDR corrected). The topographical distribution of  
380 sensors with significant phase-locking corresponded to the typical auditory topography (Figure  
381 5d). No significant phase locking was found in the *RAND* condition, indicating that the effects  
382 found for the syncopated stimuli do not result merely from a carry-over of evoked responses to  
383 preceding sounds (see Methods).

#### 384 ***Where is the neural correlate of the missing-pulse generated? – Experiment 2***

385 After establishing the emergence of a pulse-related neural dynamic which is dissociated from  
386 simple evoked-responses, we ask which brain regions are involved in generating this ‘missing-  
387 pulse’ response profile. In order to test the origin of the ‘missing-pulse’ response, we repeated

388 the experiment with a new set of participants, in another MEG facility. The whole-brain analysis  
389 revealed that the strongest ‘missing-pulse’ response was found in two clusters localized to the  
390 right and left superior temporal gyrus, with the response stronger on the right (Figure 6c).  
391 These clusters overlapped with the clusters that were detected in the auditory localizer task.  
392 Statistical analysis was performed in six independently-selected ROIs, corresponding to bilateral  
393 auditory and motor cortices and SMA. The spectra of the neural response to syncopated stimuli  
394 in each ROI are shown in Figure 6a, revealing a ‘missing-pulse’ response at 2Hz only in the STG  
395 ROIs. Non-parametric statistical analysis confirmed that the 2Hz ‘missing-pulse’ response was  
396 significantly higher than neighboring non-pulse frequencies (averaged over 1.875 and 2.125Hz)  
397 in the right STG (Wilcoxon Signed-rank test,  $p < 0.05$ ) and the left STG showed a trend towards  
398 significance ( $p = 0.071$ ), whereas the 2Hz response was not significant in the motor (R:  $p > 0.36$ ; L:  
399  $p > 0.18$ ) or SMA ROIs (R:  $p > 0.52$ ; L:  $p > 0.26$ ). Thus, we replicated the ‘missing-pulse’  
400 phenomenon found in Experiment 1, and found that a correlate of this effect was primarily  
401 localized to the right STG.

402 Note that the spectra in all ROIs, including motor regions, showed peaks at frequencies that  
403 exist in the stimulus itself (which was the case for the isochronous stimulus as well; data not  
404 shown), consistent with previous studies suggesting activation in motor-related regions in  
405 response to auditory stimuli (Grahn and Bret, 2007; Patel and Iversen, 2014; Arnal et al. 2014;  
406 Grahn and Rowe, 2009).

407 **Discussion**

408           The current results are in line with theoretical predictions of Neural Resonance Theory  
409 (NRT; Large and Snyder 2009) associating pulse-perception with emergence of neural phase-  
410 locking at the pulse-frequency. NRT predicts that, due to higher order resonances, when neural  
411 oscillators are driven by an acoustic stimulus, oscillations may emerge at favored frequency  
412 ratios (harmonics, sub-harmonics, and integer ratios), not always present in a linear frequency  
413 analysis of the acoustics (Velasco and Large 2011). Empirical findings consistent with this model  
414 show enhancement of pulse related frequencies in EEG-recorded steady-state evoked  
415 potentials (SS-EPs) compared to non-pulse frequencies (Nozaradan et al. 2012), and its  
416 correlation with behavioral measures of pulse perception (Nozaradan et al. 2016). However, in  
417 those studies most stimuli contained the pulse-frequency in their modulations spectra, allowing  
418 alternative interpretations that SS-EP modulations reflect enhancement of evoked responses to  
419 on-beat sounds (Potter et al., 2009; Schaefer et al., 2011). That said, at least one stimulus used  
420 in those studies could be considered a ‘missing-pulse’ rhythm, supporting the current findings.

421           Our study comprehensively test the predictions of NRT using ‘missing-pulse’ rhythms in  
422 order to rule out two alternative explanations: a) That apparent entrainment of SS-EPs merely  
423 reflects overlapping transient responses to individual sounds (Sussman, et al. 2008; Tremblay et  
424 al. 2004) or; b) arises from linear neural frequency analysis, such as a bank of band-pass filters  
425 (Todd, 1999, Tomic and Janata, 2008). In both cases the spectra of the neural response to  
426 ‘missing-pulse’ rhythms should mirror the modulations-spectrum of the stimuli, and would not  
427 contain energy at the pulse-frequency. However, our results show clear ‘missing-pulse’

428 responses – both in the spectrum of the neural response and in phase-locking at the time of  
429 unsounded beats - findings that cannot be explained by simple linear neural dynamics.

430         That said, current findings do not unequivocally prove that the observed pulse-response  
431 results from entrainment of endogenous neural oscillation. An alternative model also  
432 consistent with the current results is that of neural time delay, which predicts responses at  
433 subharmonics of the dominant 4 Hz frequency in the stimuli (Eck, 2006; Scheirer, 1998).  
434 Additional experiments are required to determine which model is superior in describing the  
435 underlying computations involved in neural encoding of complex rhythms.

436         Interestingly, the phenomenon identified here – perceptual and neural responses to a  
437 ‘missing-pulse’ - is analogous to the ‘case of the missing fundamental’ where the perceived  
438 pitch of harmonic tones correspond to the fundamental frequency (F0) even if that frequency is  
439 physically removed from the stimuli (Licklider, 1954). Although the mechanistic infrastructure  
440 underlying the two phenomena likely differ (Kerr et al. 2013; Huang and Rinzel 2016), in both  
441 cases the most salient percept corresponds to a frequency that is missing in an objective  
442 frequency analysis of stimulus acoustics, demonstrating a disparity between sensation and  
443 perception in audition.

#### 444 ***Phase locking to the missing-pulse***

445         The analysis of low-frequency phase-locking at soundless strong-beat positions enabled  
446 us to further disentangle the manifestation of neural entrainment from stimulus-driven evoked  
447 responses. It has been proposed that slow cortical oscillations can be used to tune neural  
448 excitability to the timing of upcoming events and thus form the basis for predictive timing

449 (Schroeder and Lakatos, 2009; Arnal and Giraud, 2012). Low-frequency phase can be modulated  
450 by top-down processes in order to enhance stimulus processing (Buschman and Miller, 2007,  
451 Lakatos et al. 2008, 2013, 2016; Arnal et al., 2014) and has been linked to increased perceptual  
452 sensitivity (Large and Jones 1999; Ng et al., 2012; Zoefel and VanRullen, 2015). The occurrence  
453 of phase-locking in the absence of physical stimuli suggests the influence of intrinsic processes  
454 related to extracting the underlying temporal structure of the sequence on local neuronal  
455 excitability.

#### 456 ***Variability in pulse perception***

457 Pulse perception is not ubiquitous within the population (Sowiński and Bella, 2013), with  
458 an extreme case being beat-deaf individuals who fail in perceiving the pulse of syncopated  
459 rhythms (Phillips-Silver et al., 2011). Here, we observe variability in the time it takes for pulse  
460 induction, reflected in participants' Time to Tap (TTT), which was correlated with the magnitude  
461 of the neural 'missing-pulse' response. While TTT remains an indirect measure of pulse  
462 induction, it probably gives us an upper bound estimate, especially since once participants  
463 started tapping they did so accurately, indicating that no one started tapping *before* perceiving  
464 the pulse. Thus, our results suggest a direct link between the neural pulse-frequency response  
465 and subjective pulse perception. These results align well with findings that activity in pulse-  
466 related regions does not occur "automatically" (Chapin et al. 2010; Doelling and Poeppel, 2015).  
467 The current findings also predict that beat-deaf individuals will not exhibit a 'missing-pulse'  
468 response in their neural activity. This correlation may be interpreted either as a stronger pulse-  
469 response, or as an earlier onset of the pulse-response in people who are faster at detecting the



470 pulse. Unfortunately, attempts to test these two options by studying the development of pulse-  
471 responses over time did not yield substantial results.

472 Another source of potential variability across (and within) individuals is the specific  
473 frequency induced as the ‘pulse’. For the stimuli used here, a 2Hz pulse is typically perceived  
474 however a 1Hz pulse can also be induced (Large et al. 2015). Indeed in the behavioral session  
475 participants tapped at both rates for different stimuli, without any discernable individual  
476 preference. Moreover, the neural response to stimulus MP1 exhibited a peak at 1Hz, in addition  
477 to the 2Hz peak. It is well established that pulse perception is dynamic and flexible, and the  
478 perceived pulse-frequency for a given stimulus can vary across and even within individuals (for  
479 review see: Repp, 2013), and can be intentionally changed (Large et al. 2002; Nozaradan et al.  
480 2011). Thus, another prediction to be tested in future studies is whether the dominant  
481 ‘missing-pulse’ frequency in the neural signal reflects the specific pulse-frequency induced in a  
482 given trial. Unfortunately, given the difference in stimuli used in the behavioral and MEG  
483 sessions here, and the fact that these were tested separately, the current data is not suitable  
484 for addressing this question.

485 ***What is the source?***

486 The ‘missing-pulse’ response was predominantly localized to right auditory cortex. This  
487 is consistent with the Asymmetrical Sampling in Time framework (AST), which suggests that the  
488 auditory cortices in the two hemispheres differ in their sensitivities to temporal information  
489 (Poeppel 2003; Giraud et al., 2007). The right hemisphere is proposed to be more sensitive to

490 slow time-scales, relevant for musical pulse, whereas the left hemisphere shows advantages for  
491 processing rapid sound variations.

492         Several studies suggest that the motor system is also involved in pulse perception  
493 (Merchant et al., 2015). For example, activation of motor areas bilaterally has been reported  
494 during rhythm perception in the absence of movement (Grahn and Bret, 2007; Patel and  
495 Iversen, 2014; Michaelis et al., 2014). However, in the current study we did not detect  
496 significant pulse-related responses in motor areas. While this does not necessarily contradict  
497 existing literature that the motor-system plays a role in pulse perception, it does leave open the  
498 question of the specific nature of the neural dynamics and representation of the pulse within  
499 these regions.

500         The NRT framework, which describes two interacting oscillatory networks intended to  
501 model “auditory” and “motor” dynamics, may also need to be modified and updated in future  
502 iterations of the model, based on the current findings. Specifically, the dynamic interactions  
503 predicted by the model may occur primarily in sub-networks within a single area (e.g. auditory  
504 cortex), and not between spatially distinct brain regions as originally proposed. Such re-labeling  
505 of the coupled networks would not change the core predictions of the model as to the dynamic  
506 pattern of neural responses, but would alter predictions as to where these responses would be  
507 observed. Additional research is ongoing to clarify this point prior to updating the NRT model.  
508 However, as we see it, one of the strengths of this study is the empirical testing of specific  
509 predictions put forth by a theoretical model, which may well result in updating some aspects of  
510 the model to improve its biological plausibility.

511 **Conclusions**

512 We demonstrate the capacity of auditory cortex to phase-lock to the pulse of complex  
513 rhythms, and successfully dissociate this activity from evoked responses. Moreover, we show  
514 that this phenomenon is not seen in individuals who have difficulty perceiving the pulse, linking  
515 it directly to pulse perception. These findings bear significance not only for music perception,  
516 but for speech processing as well, which also contains temporal regularities at similar time-  
517 scales (Zion Golumbic et al., 2012). Entrainment of cortical activity to rhythmic stimuli has been  
518 suggested as a mechanism for enhancing processing efficiency; decoding high-level information  
519 and directing selective attention in a noisy environment (Schroeder and Lakatos 2009; Lakatos  
520 et al., 2016; Zion Golumbic et al., 2013; Kayser et al., 2015; Zoefel and VanRullen, 2016). Use of  
521 complex yet precisely controlled stimuli, coupled with empirical testing of specific theoretical  
522 models, provides a unique opportunity to study such mechanisms leading to a better  
523 understanding of neural dynamics underlying the processing of continuous naturalistic sounds.

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665 **Figure captions**

666 **Figure 1. Stimulus and paradigm.** (a) Notation of the auditory stimuli for the isochronous (top), syncopated pattern  
 667 MP1 (middle) and syncopated pattern MP2 (bottom) stimuli. (b) Time course of a sample trial. In the passive  
 668 listening period, the basic pattern (2 musical bars) was repeated 8 times. Then, following a cue, a test item was  
 669 played consisting of the same basic pattern but the tempo could be the same/10% faster/ 10% slower. Participant  
 670 performed a tempo-judgment task on the test item.

671 **Figure 2. Stimulus and MEG spectrum.** a-d: The modulation spectra of each stimulus (top) and of the neural  
 672 response it generated, averaged over 10% of the sensors with the highest 2Hz amplitude (bottom). (a and b)  
 673 Syncopated patterns MP1 and MP2 – There is no visible 2 Hz peak in the stimulus spectrum, however, pulse  
 674 frequency peaks (indicated by the black arrows) are observed in the MEG spectrum for both syncopated rhythms.  
 675 (c) Isochronous condition – 2Hz peaks and its harmonics are clear in both stimulus and MEG spectrum. (d) Random  
 676 pattern – 2 Hz peaks are missing in both the stimulus and the MEG spectrum. (e) Amplitude at 2 Hz vs. the  
 677 frequencies around it for each condition. Neural data are averaged over all MEG sensors. In the ISO and both  
 678 syncopated conditions there was a significant difference between 2Hz power and the frequencies around it,  
 679 indicating a peak at the pulse frequency (Wilcoxon Signed-Rank test, \*  $p < 0.05$ , \*\*  $p < 0.01$ ). In the random  
 680 condition there was no significant peak at 2Hz. Error bars indicate standard error of the mean (SEM).

681 **Figure 3. Behavioral performance in the tapping task.** (a) Time-To-Tap (TTT); The time elapsed from the beginning  
 682 of the stimulus until subjects started tapping at the perceived pulse frequency. (b) Blue – synchronization coefficient  
 683 for each subject, all subjects eventually managed to tap in synchrony with the beat. Red – angle of the mean vector.  
 684 Almost all subjects showed positive values indicating that tapping came earlier than the strong-beat positions. Error  
 685 bars indicate SEM. The numbers on the bottom of the red trace indicate the average number of taps for each  
 686 subject over the 10 syncopated rhythms during the behavioral task.

687 **Figure 4. MEG spectrum for individual subjects.** The spectrum is shown averaged over both syncopated conditions  
 688 and over 7 channels (5% of the total number of channels) showing the highest 2 Hz power. (a) A subject with low  
 689 average TTT value, who perceived the pulse of the syncopated rhythms early-on during the behavioral task. (b) A

690 subject with high TTT value for whom it took over 15 second to perceive the pulse. The MEG spectrum of the early  
 691 pulse-perceiver shows a clear 2 Hz peak that matches the expected pulse frequency of the stimulus while the late  
 692 pulse-perceiver failed to generate such oscillations. Note that both subjects showed peaks at frequencies that were  
 693 present in the stimulus itself (e.g. 1.25 and 4 Hz). (c) Correlation between 2 Hz amplitude and TTT for the two  
 694 syncopated conditions. Subjects that showed higher 2 Hz amplitude during the MEG scans in the syncopated  
 695 conditions perceived the pulse of the syncopated patterns and start tapping earlier during the subsequent  
 696 behavioral task. Blue and Red squares indicate the subjects shown in (a) and (b) respectively.

697 **Figure 5.** Phase locking to the ‘missing-pulse’ for the two syncopated rhythms (MP1 & MP2; top two rows) and the  
 698 RAND condition (bottom row). (a) Illustration of the ‘soundless strong-beat’ positions. Black dots mark the locations  
 699 of each physical sound and, for the two syncopated rhythms, Xs’ mark the strong-beat positions. Red Xs’ denote  
 700 strong-beat positions where no sounds were present, which served as t=0 in this analysis. The lower panels show  
 701 averaged sound files time-locked to these positions, verifying that these were indeed quiet times. Similar soundless  
 702 periods were selected from the RAND condition (depicted by the red Xs’), matched on their distance from previous  
 703 sounds so as to control for carry-over effects of evoked responses from previous sounds. (b) MEG signals averaged  
 704 over all participants for one representative MEG sensor. The signals were time-locked to the position of soundless  
 705 strong beats (t=0) in the syncopated conditions, or control epochs in the RAND condition, filtered between 1-40Hz  
 706 (blue) and between 0.5-3Hz (red). (c) Phase histograms at the time of the expected pulse, across all participants for  
 707 the MEG sensor shown in (b). (d) Topography of the phase-locking values across MEG sensors. The colors indicate  
 708 the Z-value of the Rayleigh test. Significant sensors are indicated by an asterisk ( $p < 0.05$ , FDR corrected).

709 **Figure 6.** Localization the ‘missing-pulse’ response. (a) Spectra of the neural response in response to the two  
 710 syncopated rhythms in the right (blue) and left (red) hemisphere for each ROI. Inserts indicate the anatomical  
 711 locations of the voxels used for each ROI (see Methods). (b) Statistical comparison of 2Hz amplitude (blue) vs.  
 712 amplitude in adjacent frequencies (red) in each ROI. Error bars indicate SEM. (c) Whole-brain analysis of the  
 713 ‘missing-pulse’ response found in whole-brain analysis. The two clusters with the strongest ‘missing pulse’  
 714 responses were localized in right and left STG.













