

Fronto-temporal coupling dynamics during spontaneous activity and auditory processing

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14 **Abstract**

15 Most mammals rely on the extraction of acoustic information from the environment in order to
16 survive. However, the mechanisms that support sound representation in auditory neural networks
17 involving sensory and association brain areas remain underexplored. In this study, we address the
18 functional connectivity between an auditory region in frontal cortex (the frontal auditory field, FAF)
19 and the auditory cortex (AC) in the bat *Carollia perspicillata*. The AC is a classic sensory area
20 central for the processing of acoustic information. On the other hand, the FAF belongs to the frontal
21 lobe, a brain region involved in the integration of sensory inputs, modulation of cognitive states, and
22 in the coordination of behavioural outputs. The FAF-AC network was examined in terms of
23 oscillatory coherence (local-field potentials, LFPs), and within an information theoretical framework
24 linking FAF and AC spiking activity. We show that in the absence of acoustic stimulation,
25 simultaneously recorded LFPs from FAF and AC are coherent in low frequencies (1-12 Hz). This
26 “default” coupling was strongest in deep AC layers and was unaltered by acoustic stimulation.
27 However, presenting auditory stimuli did trigger the emergence of coherent auditory-evoked gamma-
28 band activity (>25 Hz) between the FAF and AC. In terms of spiking, our results suggest that FAF
29 and AC engage in distinct coding strategies for representing artificial and natural sounds. Taken
30 together, our findings shed light onto the neuronal coding strategies and functional coupling
31 mechanisms that enable sound representation at the network level in the mammalian brain.

32 **1 Introduction**

33 Many animals rely on the processing of acoustic information for survival. Nevertheless, the
34 mechanisms by which sounds are represented in neural networks involving distant areas in the brain
35 remain obscure. In the mammalian cortex, sensory and integration areas have been described as part
36 of putative neural networks tasked with sound processing. The auditory cortex (AC), for example,
37 plays an important role in sound analysis and even in coordinating acoustically guided behaviours
38 (Song et al., 2010; Li et al., 2017). Neuronal activity within the AC represents a large range of
39 acoustic properties including spectrotemporal structure (Gaese and Ostwald, 1995; Lu et al., 2001;
40 Yin et al., 2011; Gaucher et al., 2013; Kanold et al., 2014; Gao and Wehr, 2015; Lu et al., 2016;
41 Martin et al., 2017; Sheikh et al., 2019), sound source location encompassing azimuth/elevation
42 coding (Recanzone, 2000; Mrsic-Flogel et al., 2005; Salminen et al., 2015; Trapeau and
43 Schonwiesner, 2018) and target distance processing (Suga and O'Neill, 1979; Hechavarria et al.,
44 2013; Bartenstein et al., 2014; Beetz et al., 2016), as well as abstract properties such as sound
45 “emotional valence” (Concina et al., 2019) and future behavioural outcomes based on auditory
46 stimuli (Francis et al., 2018).

47 Regions within the frontal lobe of the mammalian brain also participate in auditory processing and
48 could in principle synchronize their activity with that of canonical auditory areas, such as the AC (see
49 (Winkowski et al., 2018)). Frontal and AC regions are strongly connected through feedforward and
50 feedback anatomical pathways (Kobler et al., 1987; Medalla and Barbas, 2014; Plakke and
51 Romanski, 2014; Winkowski et al., 2018). Neurons within the prefrontal cortex (PFC, a region in the
52 frontal lobe) respond to sounds when the latter possess rich spectrotemporal dynamics (Eiermann and
53 Esser, 2000; Kanwal et al., 2000; Romanski and Goldman-Rakic, 2002). Additionally, PFC is
54 thought to engage in cognitive processes ranging from attention, learning, and memory
55 formation/retrieval, to decision making (Miller, 2000; Floresco and Ghods-Sharifi, 2007; St Onge et
56 al., 2011; Gourley et al., 2013; Gilmartin et al., 2014; Pezze et al., 2014; Helfrich and Knight, 2016;
57 Kim et al., 2016; Werchan et al., 2016; Helfrich et al., 2017). This area could thus be a fundamental
58 node for sound evaluation in auditory networks, and even for the implementation of acoustically
59 guided behaviours.

60 Though there is increasing evidence supporting the idea of frontal-AC functional networks for
61 auditory processing, specifics regarding activity coupling within this network remain unknown. For
62 example, it remains unclear if different types of neural signals (i.e. spikes and local field potentials,

63 LFPs) measured simultaneously in frontal and AC areas synchronize during spontaneous activity and
64 during listening. Moreover, it is unknown whether frontal activity displays preferential coupling
65 patterns with certain layers of the AC. Assessing the latter can only be achieved by conducting
66 simultaneous measurements from frontal and AC regions using layer-specific intracranial recordings
67 to study spikes and LFPs.

68 In the current study, we address the functional connectivity in a fronto-auditory cortical circuit in bats
69 (species *Carollia perspicillata*). The bat AC has been studied extensively, and it has been shown that
70 oscillatory and spiking activity patterns in the bat cortex are in accordance with those observed
71 during the processing of artificial and naturalistic sounds in other animal models, including speech in
72 humans. This comprises phenomena such as multiscale temporal processing of acoustic streams
73 (Giraud and Poeppel, 2012; Hyafil et al., 2015; Hechavarria et al., 2016b; Teng et al., 2017; Garcia-
74 Rosales et al., 2018a), interactions between spikes and LFPs for audition (Lakatos et al., 2005;
75 Kayser et al., 2009; Arnal and Giraud, 2012; Kayser et al., 2012; Gilmartin et al., 2014; Garcia-
76 Rosales et al., 2018b; Garcia-Rosales et al., 2019), and gamma-band activity for communication call
77 processing (Medvedev and Kanwal, 2008). In bats, there exists a region within the frontal lobe that is
78 responsive to sounds: the frontal auditory field (FAF; (Kobler et al., 1987; Eiermann and Esser, 2000;
79 Kanwal et al., 2000)). This region is anatomically connected with the AC (Kobler et al., 1987), but it
80 also receives auditory afferents via a non-lemniscal pathway through the suprageniculate nucleus of
81 the thalamus, bypassing main auditory centres in the midbrain (Kobler et al., 1987). In addition to
82 pure tones, neurons in the FAF encode spectrotemporally complex sounds with variable latencies and
83 response properties (Eiermann and Esser, 2000; Kanwal et al., 2000; Lopez-Jury et al., 2019). Our
84 goal was to examine specifics of fronto-AC activity in awake bats during the processing of acoustic
85 streams. We tackled this question by quantifying neural synchronization in the FAF-AC network in
86 terms of oscillatory coherence (a mechanism underlying interareal communication; (Fries, 2015)),
87 during both spontaneous activity and the processing of natural and artificial acoustic sequences.

88 We found that the FAF-AC network is synchronized by default (i.e. without sensory stimulation) in
89 low-frequencies (up to 12 Hz), and that coherence with the FAF is strongest in deep laminae of the
90 AC. In addition, low-frequency coherence between the two structures remains unchanged during
91 acoustic processing, and auditory-evoked gamma-band synchronization emerges at stimulus onset
92 without clear layer specificity. Finally, based on an information theoretical framework, our data
93 suggest that the neuronal coding of acoustic streams in FAF and AC may occur with non-overlapping

94 neural codes. Taken together, the data presented in this manuscript offer insights into the strategies
95 for sound representation in fronto-AC neural networks.

96 **2 Results**

97 **2.1 Stimulus-related LFPs in AC lag relative to those in FAF**

98 We recorded electrophysiological data from the primary AC, paired with penetrations from the FAF,
99 in 5 awake *Carollia perspicillata* bats (all males; n = 50 penetrations). Recordings in the AC were
100 performed with laminar electrodes inserted perpendicularly into the brain, spanning depths of 0-750
101 μm as measured from the cortical surface. Each penetration in AC was paired with a simultaneous
102 recording from the FAF using a single carbon electrode at an average depth of $313 \pm 56 \mu\text{m}$ (mean \pm
103 std). Auditory stimuli consisted of artificially constructed syllabic trains with repetition rates of 5.28
104 and 97 Hz in order to test for slow and fast periodicities in acoustic streams, plus another syllabic
105 train that had no clear rhythmicity as syllables were presented in a Poisson-like sequence with 70 Hz
106 average rate (see Methods). The trains consisted of a repeated short duration, broadband distress
107 syllable from *C. perspicillata*, recorded in previous work (Hechavarria et al., 2016a), whose
108 spectrotemporal design is typical of distress syllables emitted by this species. In addition, we
109 presented a natural distress vocalization (“nat” throughout the text) that has been used in previous
110 research (Hechavarria et al., 2016b; Garcia-Rosales et al., 2018a; Garcia-Rosales et al., 2019), and
111 which comprises temporal modulations in low (ca. 4 Hz) and high-frequency ranges (> 50 Hz),
112 corresponding to the bout and syllabic periodicities, respectively, typical of this animal’s distress
113 vocalizations (Hechavarria et al., 2016a).

114 Grand average traces of simultaneously recorded LFPs from FAF and AC (the latter at a depth of 450
115 μm , corresponding to input layers in AC) during acoustic stimulation are shown in **Fig. 1A**. LFP
116 responses from frontal and auditory cortical regions showed clear modulation by the acoustic streams
117 that were well-correlated across structures for each stimulus tested, particularly at depths > 200 μm
118 (**Fig. S1**). Remarkably, population averaged LFPs appeared “faster” in the FAF than in the AC (see
119 **Fig 1A**, right column; blue: FAF; orange: AC at 450 μm) relative to stimulus onset. In fact, cross-
120 correlation analyses of the traces depicted in **Fig. 1A** showed that LFPs recorded in frontal regions
121 preceded those recorded from the AC by at least 4 ms (**Fig. 1B**), effectively indicating that primary
122 auditory cortical stimulus-related LFPs in input layers “lag” relative to those in the FAF. We
123 confirmed this trend by systematically determining the temporal lag between LFPs in the AC at

124 various depths, and LFPs from the FAF. **Figure 1C** summarizes the results by illustrating, for each
125 stimulus, the distribution of lags between FAF and AC across depths (note that negative lags indicate
126 FAF “leading”). Indeed, we observed a significant effect of LFPs in the FAF being “faster” than
127 those in the AC, robust across depths in the latter structure, and also across stimuli (**Fig 1C**; FDR-
128 corrected tailed Wilcoxon signed rank tests, testing that the medians of the lag distributions were
129 significantly less than 0 across electrodes; $p_{\text{corr}} < 0.05$; precise p_{corr} values are indicated next to each
130 heatmap). These results were corroborated by testing FAF-AC lags in LFPs but considering only LFP
131 pairs that were well correlated across structures (correlation coefficients higher than 0.5, shown in
132 **Fig. S1**).

133 That LFPs in the frontal auditory field “lead” relative to those in the auditory cortex suggests the
134 presence of fast inputs into frontal auditory areas, agreeing with a non-lemniscal auditory pathway
135 converging into the FAF and consisting of as few as four synapses in bats (Kobler et al., 1987). We
136 sought for evidence of fast neuronal responses in FAF that would support these observations by
137 measuring response latencies of the neuronal spiking recorded simultaneously in both structures (see
138 Methods). We observed that spiking responses from the FAF could in fact be as fast as spiking
139 responses from the AC, although this effect was found only in a subpopulation of neurons (on
140 average $5.65\% \pm 3.19\%$ of the units considered, across stimuli and channels; see **Fig. 2A, B**, which
141 depicts example responses from one FAF and one AC unit at $450 \mu\text{m}$ recorded simultaneously).
142 Measured neuronal response latencies from both structures yielded that AC spiking was on average
143 faster than the FAF spiking (**Fig. 2C**; for illustrative purposes AC responses are those recorded at
144 $450 \mu\text{m}$). Still, some FAF units exhibited response latencies below 10 ms, indicative of fast acoustic
145 inputs into this structure. By subtracting latencies from simultaneously recorded units in the FAF and
146 the AC (across depths; latencies were pooled from all tested stimuli, but paring was only done within
147 a particular stimulus), it became evident that auditory cortical spiking was typically faster than its
148 FAF counterpart, although some latencies from frontal regions were shorter than those in the AC.
149 **Figure 2D** shows the distribution of latency differences (across cortical depths in the AC), depicting
150 the abovementioned observations. Latency differences were significantly higher than 0 for all
151 recording depths in the AC, except in the case of the most superficial channel (FDR-corrected
152 Wilcoxon signed rank tests, significance when $p_{\text{corr}} < 0.05$; corrected p values across channels are
153 given to the right of the latency distribution heatmap in **Fig. 2D**).

154 Altogether, these results provide evidence supporting that the FAF receives fast auditory inputs.
155 Notwithstanding, such inputs do not necessarily elicit equally fast spiking, suggesting that the
156 neuronal dynamics in frontal areas are “sluggish” in comparison to primary AC. Sluggish dynamics
157 can arise from multiple factors, and may be essential for sensory integration in the frontal cortex (see
158 Discussion).

159 **2.2 FAF and AC synchronize in low frequency LFP bands during spontaneous activity**

160 Local-field potentials recorded in the FAF and the AC typically showed visible phase
161 synchronization, even in the absence of acoustic stimulation (see **Fig. 3A**, where LFP traces from
162 both structures during a single 3 s epoch of spontaneous activity are depicted). We quantified phase
163 coherence between the two structures by means of the imaginary part of the coherency (“iCoh” in
164 this manuscript; see Methods and (Nolte et al., 2004)), for data recorded both during spontaneous and
165 sound-driven activities. The iCoh metric allows to minimize spurious phase-synchrony attributable,
166 for example, to common referencing and passive spreading of field potentials, by effectively
167 removing non-lagged phase correlations (Bastos and Schoffelen, 2015).

168 Coherence analyses revealed that, as shown in **Fig. 3A**, FAF and AC were synchronized in low
169 frequencies. **Figure 3B** depicts population averaged z-normalized (to a surrogate distribution where
170 phase relationships were abolished; see Methods) iCoh values (z-iCoh) across electrode depths in the
171 AC. Elevated low-frequency coherence is evident in deep layers of the AC, suggesting as well that
172 FAF-AC synchrony was depth-dependent. A time-resolved analysis of iCoh (**Fig. 3C**) over the same
173 LFP traces used to calculate values in **Fig. 3B** also showed that low-frequency phase synchrony was
174 strongest in deeper channels, and furthermore limited to the low-frequency region of the coherence
175 spectrum. The data depicted in **Fig. 3C** are shown here for illustrative purposes and serve as a
176 comparison with the time-resolved coherence estimations performed on LFPs recorded during
177 acoustic processing (see below).

178 To statistically corroborate our observations, we divided the coherence spectrum into canonical
179 frequency bands encompassing delta (1-4 Hz), theta (4-8 Hz), alpha (8-12 Hz), beta (12-25 Hz) and
180 low-gamma (25-45 Hz). We then tested if z-normalized iCoh values in each band were significantly
181 different than 0 across the population. Because of the nature of the surrogate analyses (see Methods),
182 non-consistent phase synchronization in the data would yield a distribution of z-iCoh statistically
183 indistinguishable from 0. In other words, z-iCoh values significantly higher than 0 suggest consistent,

184 population-wise phase-locking between LFPs in FAF and AC during spontaneous activity. **Figure**
185 **3D** (top) depicts the z-iCoh calculated between FAF and AC oscillations for each frequency band at
186 various AC depths. For frequency bands between 1-12 Hz (i.e. delta to alpha), we observed
187 significantly higher than 0 z-iCoh estimates (FDR-corrected Wilcoxon signed rank tests, $p_{\text{corr}} < 0.05$
188 for significance; log-converted p values are shown in **Fig. 3D**, bottom), which became gradually
189 lower towards higher frequencies (note also the decay in **Fig. 3B**). Beta or gamma z-iCoh
190 distributions were not significantly different than 0 at any cortical depth.

191 It was also apparent that coherence values were depth dependent in the AC, particularly in the delta
192 band (where z-iCoh was strongest, see **Fig. 3B, D**). We tested the depth dependence of coherence by
193 comparing the distributions of z-iCoh for all pairs of channels, across all penetrations and frequency
194 bands. Results are summarized in significance matrices depicted in **Fig. 3E**. Each cell (i, j) in a
195 matrix represents the log-converted, corrected p value (FDR Wilcoxon signed rank tests), obtained
196 after statistically comparing FAF-AC coherence using an AC channel at depth i , and another at depth
197 j . In the matrices, cells within red contour lines correspond to statistically significant p_{corr} values (p_{corr}
198 < 0.05). As shown in **Fig. 3E**, deep electrodes in the AC were significantly better synchronized with
199 the FAF, an effect only visible in the delta band.

200 **2.3 FAF-AC synchronization during acoustic processing**

201 To quantify synchronization during acoustic processing in the FAF-AC circuit, we calculated time-
202 resolved iCoh values in response to four acoustic stimuli (a natural call, syllabic trains of 5.28 and 97
203 Hz, and a syllabic train with Poisson temporal structure; see above). Population average coherograms
204 (i.e. time-frequency representations of iCoh values) are shown in **Fig. 4A-D** for all stimuli tested, and
205 at representative depths in the AC (50, 450 and 700 μm). The most conspicuous pattern across
206 stimuli was the appearance of low-gamma coherence (typically in the range of 25-45 Hz), which was
207 associated with stimulus onset (at time 0) and apparently independent of auditory cortical depth.
208 Gamma synchrony was auditory-evoked, a notion strengthened when considering responses to the
209 5.28 Hz syllabic train (**Fig. 4B**), where the evoked coherence tracked individual syllable
210 presentations. Remarkably, we observed little evidence for an increase of low-frequency synchrony
211 when compared to spontaneous activity (compare heatmaps in **Fig. 4** with **Fig. 3C**). That is, even
212 though low-frequency coherence was present before sound presentation (in line with our results using
213 spontaneous LFPs), it did not change visibly after stimulus onset. To illustrate the occurrence of low
214 and high frequency coherence, **Figure 4E-H** depict single-trial LFPs from a representative pair of

215 simultaneous penetrations in the AC (450 μ m depth) and FAF. Raw LFPs are shown in their
216 broadband form (0.1-300 Hz), and filtered in frequency ranges of 4-12 Hz and 25-45 Hz (i.e. low and
217 high frequencies oscillations). The range 4-12 Hz was chosen for low-frequency activity because
218 spectral parameters at lower frequencies could not be reliably estimated with the window size chosen
219 for time-resolved coherence analyses (200 ms; see Methods). Note that the occurrence of
220 synchronized waves in the AC and FAF is clear after stimulus onset (0-ms mark).

221 The defined low- and high-frequency ranges were then used to quantify changes from spontaneous to
222 stimulus-driven coherence in the FAF-AC network. A systematic, time-resolved analysis of low-
223 frequency synchrony revealed that, across stimuli and auditory cortical depths, there was little change
224 (calculated as percentage increase from spontaneous to sound-driven activity: $[iCoh_{stim} - iCoh_{spont}] /$
225 $iCoh_{spont} * 100$) in coherence between both structures (**Fig. 5A, D, G, J**, top heatmaps). The data
226 showed that low frequency synchrony preceded stimulus presentation in deep layers, seldom reached
227 50% increase from spontaneous across stimuli (black contour lines in **Fig. 5A, D, G, J**), and when it
228 did, it typically happened at middle AC depths. We did not observe statistical evidence showing
229 significant increase of low frequency coherence at stimulus onset (i.e. first 100 ms after sound
230 presentation; **Fig. 5B, E, H, K**, black traces; FDR-corrected Wilcoxon signed rank tests, significance
231 when $p_{corr} < 0.05$).

232 **Figure 5C, F, I, L** (top heatmaps) illustrate effect size calculations (r ; see Methods) for the low-
233 frequency coherence increase in a time resolved manner across channels. In the heatmaps, only time
234 points where the increase was significantly different from 0 (uncorrected Wilcoxon signed-rank test,
235 $p < 0.05$) are shown. From this analysis the following was evident: (i) the pattern of significance was
236 inconsistent across stimuli for low frequency coherence; and (ii) effect sizes were typically small,
237 with areas of medium effect size (those within grey contour lines) appearing also with an inconsistent
238 pattern across sounds. Large effect sizes (within red contour lines) were overall only observed in
239 small clusters, lacking consistency throughout the stimulus set. The boundaries between small,
240 medium and large effect sizes were defined as follows: $r < 0.3$, small; $0.3 \leq r < 0.5$, medium; $r \geq 0.5$,
241 large (Fritz et al., 2012). Altogether, these results corroborate a lack of reliable increase in low-
242 frequency coherence between FAF and AC during passive listening, compared to spontaneous
243 activity.

244 High frequency FAF-AC coherence was considerably more sensitive to acoustic stimulation. As
245 expected from the data depicted in **Fig. 4**, we observed a strong increase of low-gamma interareal

246 synchronization associated to the stimulus onset (**Fig. 5A, D, G, J**, bottom heatmaps). Stimulus-
247 evoked gamma synchrony was typically higher than 50% (reaching values as high as 80%) and
248 tracked the syllable presentations of the 5.28 Hz syllabic train (**Fig. 5D**, bottom). Indeed, the increase
249 of low-gamma synchrony at stimulus onset was significantly above 0 for all stimuli (**Fig. 5B, E, H,**
250 **K**, grey traces; same statistical analysis as for low-frequencies; $p_{\text{corr}} < 0.05$), and more reliably so for
251 channels located in input layers of the AC (in this context, electrodes at depths of 250-350 μm ; layers
252 III-IV in *C. perspicillata*'s AC span depths of 200-450 μm , see (Garcia-Rosales et al., 2019)). For the
253 5.28 Hz and the Poisson syllabic trains, the onset-related increase in low-gamma coherence occurred
254 essentially along all AC depths studied. In terms of effect size (**Fig. 5C, F, I, L**; bottom heatmaps),
255 we observed large effects of increased low-gamma coherence at stimulation onset across stimuli (less
256 clearly in the case of the natural vocalization), with sustained, seemingly periodic increases along the
257 time-course of the 5.28 Hz syllabic sequence. Taken together, coherence analysis results indicate that
258 acoustic stimulation elicits auditory-evoked low-gamma synchronization between the frontal auditory
259 field and the auditory cortex.

260 **2.4 Gamma-band activity in FAF and AC**

261 Previous studies showed the occurrence of gamma-band activity in the AC of primates, bats, and rats
262 (Brosch et al., 2002; Medvedev and Kanwal, 2008; Vianney-Rodrigues et al., 2011). These studies
263 reported auditory cortical gamma which was not time-locked to the onset of a stimulus, and that
264 appeared even hundreds of milliseconds after sound presentation. Given the nature of the coherence
265 analyses performed here, it is possible that the presence of non-locked gamma oscillations could have
266 been overlooked in the FAF and the AC of *C. perspicillata*. To explore the occurrence of these
267 rhythms in our dataset, we focused on the onset period of the 5.28 Hz syllable train as it was the
268 stimulus that permitted the analysis of an onset window without the influence of subsequent sounds
269 (after the first syllable presentation), for a sufficiently long time-lapse of at least 180 ms. The time
270 period around the first syllable presentation in the 5.28 Hz train was subdivided into three segments:
271 (1) a window of 90 ms spanning times before stimulus onset (*pre*); (2) a window of 90 ms starting at
272 stimulus onset (*onset*); (3) a window of 90 ms starting 90 ms past stimulus onset (*late*); and (4) a
273 window of 180 ms starting at stimulus onset (*full*). The span of these segments is illustrated in **Fig.**
274 **6A** together with representative LFP traces from a penetration pair. The segments were chosen in
275 order to contrast LFP power at different frequency bands (low frequencies, 0-15 Hz; low-gamma, 25-

276 45 Hz; high-gamma 45-80 Hz; and broad gamma 25-80 Hz) with spontaneous LFP power before
277 stimulus presentation (*pre* window).

278 There was a consistent increase of onset-related gamma activity in FAF and AC, particularly during
279 the *onset* period, which was potentially linked to an evoked activation in cortex as it was associated
280 with a broadband increase in LFP power (see **Fig. 6B**, green traces, and **Fig. S2A**). To uncover the
281 presence of gamma within later time periods in our data, the power of different frequency bands in
282 the *late* period was statistically compared (Wilcoxon signed rank test, significance threshold at $p =$
283 0.01; see Methods) with the power in the *pre* period on a trial-by-trial basis, per penetration (**Fig.**
284 **6C**). The percentage of penetrations in FAF where there was a power increase in low frequencies was
285 of 8%, reaching between 14-24% in the AC. We also observed a relatively small number of
286 penetrations (<10%) either in AC or FAF in which there was a significant power increase in gamma
287 for the *late* period as compared to the *pre* segment. We further calculated the time course of the
288 percentage of penetrations showing significant power increase at times surrounding the stimulus
289 presentation for both FAF and AC, at various LFP frequencies (**Fig. 6D**; see Methods). As expected
290 from the data shown in **Fig. 6B-C** and **Fig. S2A**, up to about 50 ms after stimulus onset there was a
291 high percentage of penetrations (ca. 80%; cf. with **Fig. S2A**) where the power in gamma increased
292 significantly in either structure. This number was relatively low (< 20%) for times beyond 50-60 ms
293 after stimulus onset.

294 The FAF-AC circuit exhibited increased auditory-evoked gamma band coherence, related to the onset
295 of acoustic stimulation (**Figs. 4, 5**). We tested to what extent we could disentangle gamma activity in
296 our data from a non-specific broadband response, by means of previously used approach which relies
297 on comparing the relative power distributions of gamma and low frequency LFPs (Medvedev and
298 Kanwal, 2008). In this case, evidence for the gamma-band activity being a different component from
299 the broadband evoked-related potentials relies on the statistical independence between low- and high-
300 frequency power in the LFPs. For this analysis the *full* window was used (see **Fig. 6A**). The power
301 distributions of gamma (either 25-45 or 45-60 Hz) and low frequencies typically did not differ in our
302 dataset (see **Fig. 7A, E** for a representative penetration). A systematic population analysis was
303 performed to quantify the percentage of penetrations in the data for which there was evidence of
304 statistical independence between the power of gamma and that of low-frequency potentials. As
305 depicted in **Fig. 7B, F**, power distributions of gamma (in the 25-45 and 45-60 Hz ranges) and low
306 frequencies (0-15 Hz) were significantly different from each other (2-sample Kolmogorov Smirnov

307 tests, significance when $p < 0.01$) only in a small proportion ($< 15\%$) of the total amount of
308 penetrations, either in FAF or AC. This could suggest that gamma-band activity in these frequency
309 ranges cannot be readily disentangled from a broadband power increase related to an onset response,
310 assuming that if they were separable processes (i.e. gamma and low frequency activities) their power
311 distributions would differ significantly (Medvedev and Kanwal, 2008).

312 We reasoned, however, that a lack of significant differences between the distributions does not
313 necessarily imply that the relative powers of gamma and low-frequencies are well correlated when
314 considering trial specific information. Strong correlations would occur if low and high frequency
315 relative powers were tightly determined by the strength of the broadband activation. Therefore, given
316 a weak correlation, it could be argued that the dynamics of low- and high-frequency (gamma) LFPs
317 might be more complex than an unspecific power increase related to the evoked response. We
318 observed poor correlations, across penetrations in FAF and AC, between low-frequency and gamma-
319 band relative power on a trial-by-trial basis (see, for example, **Fig. 7C, G**). The distribution of
320 correlation coefficients for the population data is depicted in **Fig. 7D, H**. Overall, correlation
321 coefficients were low, having a median in the FAF of 0.22 (25th and 75th percentiles: 0.12 and 0.35)
322 for the 25-45 Hz gamma range, and of 0.07 (25th and 75th percentiles: -0.05 and 0.23) for the 45-60
323 Hz band. In the AC, the median across channels was of 0.17 (25th and 75th percentiles: 0.03 and 0.31)
324 for the 25-45 Hz gamma, and of 0.08 (25th and 75th percentiles: -0.04 and 0.1) for the band of 45-60
325 Hz. Typically, no more than 20-25% of the penetrations in AC and FAF showed a significant
326 correlation (significance when $p < 0.01$) between relative power at low-frequencies and gamma (25-
327 45 Hz, median 20% of sites; 45-60 Hz, median 8% of sites; see **Fig. S2B**).

328 We also quantified how the overall energy of early activation correlates with the gamma coherence
329 increase in the FAF-AC circuit. Gamma-band coherence increase (compared to spontaneous activity,
330 see **Fig. 5**) was poorly correlated with evoked potential energy for all AC channels (median across
331 channels: 0.15; 25th and 75th percentiles: 0.08 and 0.22), as illustrated in **Fig. 7I** for representative
332 depths in AC, and in **Supplementary Fig. S3** for all depths. Although gamma-band activity is not
333 straightforwardly separable from a broadband activation pattern, the data shown in **Fig. S3** and the
334 poor trial-by-trial correlation between gamma and low-frequency powers (see above) suggest the
335 possibility of interesting gamma-band dynamics in *C. perspicillata*'s FAF and AC.

336 **2.5 Mutual information in FAF and AC spiking**

337 We investigated spike-spike interactions in the FAF-AC network within an information theoretical
338 framework (Shannon, 2001). Mutual information (MI or “information” throughout the text) between
339 the stimuli and neuronal responses allows to quantify the theoretical ability of a neuron (or a set
340 thereof) to represent the acoustic input on a single trial basis (see Methods). MI captures all non-
341 linear dependencies of any statistical order in the data, and its quantification depends on the neural
342 code being considered (Kayser et al., 2009). Here, we aimed to determine the coding abilities in AC,
343 FAF, and a joint response from both structures based on a spike rate code (I_{rate} for single units, I_{joint}
344 considering responses from AC and FAF together; (Kayser et al., 2009; Garcia-Rosales et al.,
345 2018a)). A rate code was considered so that our results could be comparable with previous data
346 obtained from *C. perspicillata*'s AC (Garcia-Rosales et al., 2018a).

347 Overall, we relied on an information theoretic approach because we observed that representations in
348 AC and FAF were quite different and on occasions, at least in appearance, complementary. For
349 example, **Fig. 6A** depicts spiking from two simultaneously recorded FAF and AC units in response to
350 the natural stimulus. Note how the firing rate of the FAF unit increases as the stimulus progresses,
351 whereas the AC unit is time-locked to slow temporal modulations in the stimulus and does not
352 respond like its FAF counterpart. Information theory would allow to measure possible interactions
353 between these responses in a quantitative manner.

354 **Figure 6B** shows a schematic of the rate code used to quantify MI for single units and joint
355 responses. For subsequent analyses and in order to guarantee that all units considered were auditory-
356 responsive (both in FAF and AC), we used only responses that provided at least 0.1 bit/s of
357 information (with a window size of 4 ms this corresponds to 4×10^{-3} bits; see Methods). The number
358 of units used to quantify I_{rate} , per channel (including the FAF electrode, and across the AC linear
359 probe) is depicted in **Fig. 6C**, left. Note that the number of penetrations is equivalent to the number
360 of units per channel in this case: $n \geq 13$ in FAF, and $n \geq 29$ in AC. For paired responses (FAF-AC)
361 the number of units considered was less because the inclusion criterion ($I_{\text{rate}} \geq 0.1$ bit/s) had to be
362 fulfilled by units in AC and FAF simultaneously ($n \geq 8$ pairs; **Fig. 6C, right**).

363 Population values of I_{rate} for the FAF and the AC at different depths are depicted in **Fig. 6D**, for each
364 stimulus. Two main conclusions can be drafted from this figure. (i) In the AC, the highest
365 information about the stimuli was found at depths between 200-650 μm . (ii) Neurons in the FAF
366 were on average less informative than AC ones, but were well above the limit set in the inclusion
367 criterion across stimuli (*nat*: 0.56 ± 0.09 bits/s, 5.28 Hz train: 0.45 ± 0.06 bits/s, 97 Hz train: $0.48 \pm$

368 0.04 bits/s, Poisson train: 0.42 ± 0.05 bits/s; given as mean \pm s.e.m). We also quantified the
369 information provided by paired neuronal responses from both regions (I_{joint}), which is illustrated as
370 black traces in **Fig. 6E**. This figure also shows a direct comparison between I_{joint} and the I_{rate} of FAF
371 and AC neurons that conform each pair ($I_{\text{rate_pair_FAF}}$ and $I_{\text{rate_pair_AC}}$, respectively). The contribution of
372 I_{rate} from the FAF was significantly smaller than the contribution of I_{rate} from the AC (FDR-corrected
373 Wilcoxon signed rank tests, $p_{\text{corr}} < 0.05$; corrected p values of all comparisons are given in **Fig. S4**).
374 Although I_{rate} in the FAF was always > 0.1 bit/s, we did not observe I_{joint} to be significantly higher
375 than the I_{rate} from the AC ($I_{\text{rate_AC}}$; orange traces in the **Fig. 6E**), across electrodes and stimuli tested
376 (**Fig. S7**). We did observe I_{joint} to be well correlated with the sum of I_{rate} calculated using the
377 information of FAF and AC spiking ($I_{\text{sum}} = I_{\text{rate_pair_FAF}} + I_{\text{rate_pair_AC}}$; **Figs. S5-S9**).

378 When considering the interactions of spiking across structures in terms of the codes defined in this
379 study, the linear relationship between I_{sum} and I_{joint} , evident in **Figs. S5-S9**, would support the notion
380 of “independence” in the information provided by the spiking in each structure. Independence arises
381 theoretically when $I_{\text{joint}} = I_{\text{sum}}$, and implies that each structure represents different aspects of the
382 sensory stimulus. However, the results illustrated in **Fig. 6E** suggest that independence cannot be
383 inferred from the data with certainty. Mathematically, independence would require I_{joint} to be higher
384 than both I_{rate} in AC and FAF simultaneously, which was not fulfilled at a population level: I_{joint} was
385 not significantly different than I_{rate} obtained from AC units (see **Fig. S4**). Calculating information
386 estimates using time windows of up to 12 ms yielded comparable results, indicating that the temporal
387 resolution of the codes had little effect in the described outcomes (data not shown). Overall, our
388 quantification of stimulus-related spiking information, occurring simultaneously in the AC and FAF,
389 suggests different sound coding strategies in these two structures. These observations are further
390 addressed in the Discussion section.

391 **3 Discussion**

392 In this study we investigated the functional connectivity between frontal and auditory cortical regions
393 of the bat *Carollia perspicillata*. Specifically, we examined the coupling dynamics of the FAF, a
394 frontal area which receives auditory afferents from cortical and subcortical structures, and the
395 primary AC. Functional connectivity was assessed during spontaneous activity and during the
396 processing of natural and artificially generated acoustic sequences. Our main results are: i) LFPs
397 recorded simultaneously in both regions suggest that the FAF receives faster auditory inputs relative
398 to the AC, yet these inputs do not necessarily elicit faster spiking in the FAF; ii) during spontaneous

399 activity, the FAF-AC network is coupled in low frequencies (up to 12 Hz), with stronger coherence
400 values at deep layers of the AC; iii) while acoustic stimulation does not considerably alter the default
401 low-frequency coupling, auditory-evoked gamma-band synchronization in the FAF-AC circuit
402 emerges upon sound presentation; iv) considering a spiking rate code, the FAF is less informative
403 than the AC about the acoustic stimuli, while a joint code using simultaneous spiking from both
404 regions suggests that FAF and AC engage in distinct coding dynamics. Altogether, our data shed
405 light onto how distant brain areas in the mammalian brain engage in sound representation. The results
406 of this paper are summarized in **Fig. 9**.

407 **3.1 Auditory afferents into the FAF**

408 Stimulus-related LFPs recorded simultaneously from FAF and primary AC, at various depths in the
409 latter structure, indicate the presence of fast synaptic inputs into the frontal region that precede those
410 arriving into the AC even at input layers. The work of Kobler, Casseday, and colleagues in the late
411 1980s (Kobler et al., 1987; Casseday et al., 1989), showed that the FAF receives auditory afferents
412 via a non-canonical pathway that bypasses major auditory centres in the midbrain, including the
413 inferior colliculus (IC). In this pathway, acoustic information from neurons in the cochlear nucleus is
414 sequentially relayed to the anterolateral olivary complex, the suprageniculate nucleus of the thalamus
415 (SGN), and from there into the FAF. Thus, although auditory inputs reach the frontal region also
416 through the AC, acoustic information may reach the frontal field, directly from the cochlea, in as few
417 as four synapses (Kobler et al., 1987). Synaptic currents related to inputs from the SGN into the FAF
418 could lead to changes in LFPs (Buzsaki et al., 2012) faster than their counterparts at input layers of
419 the AC, which are predominantly driven by thalamocortical synapses originating in the ventral region
420 of the medial geniculate body. Therefore, a rapid, non-canonical pathway into FAF accounts for our
421 observations regarding the temporal relation between LFPs in both regions studied.

422 The results described in this manuscript indicate that, although sound-related LFPs from the FAF
423 lead those from the AC, the neuronal spiking latencies are shorter in AC. In other words, our data
424 indicate that faster inputs in FAF are not sufficient to elicit faster spiking in most cases.
425 Electrophysiological studies in frontal auditory areas have shown that neuronal responses are usually
426 of relatively large latencies (although short latencies are also to be found), sparse and of high
427 variability (Newman and Lindsley, 1976; Eiermann and Esser, 2000; Kanwal et al., 2000; Plakke and
428 Romanski, 2014). Recent data from *C. perspicillata*'s FAF highlighted the possibility that the
429 sparseness in the response properties of frontal neurons could be explained by slow, low-threshold,

430 and long-lasting synaptic dynamics, at least considering projections from the AC (Lopez-Jury et al.,
431 2019). These slow, long-lasting synaptic dynamics could support sensory integration, by conditioning
432 FAF neurons to spike after accumulating synaptic inputs over time, and/or to integrate multiple
433 synaptic inputs originating from different sensory modalities. Certainly, cross-modal sensory
434 integration occurs in the frontal cortex (Fuster et al., 2000; Romanski, 2007; Hwang and Romanski,
435 2015), whereas integration over relatively long timescales appears to be a feature of higher-order
436 cortical areas in general (Runyan et al., 2017).

437 Fast acoustic afferents, even without eliciting reliable stimulus-evoked spiking, imply nonetheless
438 that auditory information is already present in the FAF before it receives inputs from the AC. Within
439 the predictive coding framework (Arnal and Giraud, 2012; Friston, 2018), it is then possible to
440 hypothesize that the frontal field may be a region where prediction errors could also be generated.
441 That is, the rapid non-lemniscal pathway could relay faithful information into FAF about the auditory
442 stimuli, which can in turn be compared with information received from primary AC and the
443 thalamus. Alternatively, a further proposition would be that prediction errors, relayed “upwards”
444 along the auditory hierarchy (Carbajal and Malmierca, 2018), and generated in the SGN and the AC,
445 are integrated in the FAF. The result of such integration could in turn be used to update the
446 “expectations” of the system. In rodents, prediction error signals appear all along the auditory
447 pathway, but occur more strongly in higher-order structures (Parras et al., 2017), while prediction
448 error signals related to sounds have also been described in the frontal cortex of rats (Imada et al.,
449 2012) and humans (Durschmid et al., 2016; Durschmid et al., 2018). The involvement of the FAF in
450 predictive coding could be thoroughly tested in future experimental work.

451 A number of FAF neurons project directly to the superior colliculus (SC), a structure related to motor
452 control of head and pinna movement in bats (Kobler et al., 1987). The presence of early acoustic
453 information in FAF, the fact that frontal neurons in *C. perspicillata* show preference for naturalistic
454 echolocation acoustic stimuli (high-frequency pulses used to navigate by bats; (Eiermann and Esser,
455 2000)), and the existence of projections from FAF into motor-related structures such as the SC,
456 suggest that the FAF plays an important role in coordinating auditory-guided behaviour. This would
457 be in line with proposed roles of prefrontal cortex in motor control (Risterucci et al., 2003), including
458 volitional motor (vocal) production after acoustic stimulation (Hage and Nieder, 2015). However,
459 whether neuronal activity in the FAF mediates motor outputs is still to be tested in depth.

460 **3.2 FAF-AC synchronization during spontaneous activity**

461 We examined the default (i.e. in the absence of external stimulation) functional connectivity in the
462 FAF-AC network in terms of oscillatory coherence (**Fig. 3**). The data presented in this manuscript
463 show that simultaneously recorded LFPs from both structures are phase-synchronized in low-
464 frequencies of the spectrum (1-12 Hz), although more strongly so in the delta band (1-4 Hz).
465 Empirical evidence points towards a role of oscillatory coherence in the coupling of distant brain
466 regions, a view that is summarized in proposed theoretical mechanisms such as the communication-
467 through-coherence framework (Fries, 2015). Several studies have pinpointed an involvement of low-
468 frequency synchronization in the functional coupling between the frontal cortex and a variety of brain
469 structures. Coherent oscillations between distant cortical areas (including the frontal cortex) in the
470 low-frequency range correlate with working memory (Daume et al., 2017), fear memory
471 consolidation (Popa et al., 2010), attentional selection (Womelsdorf and Everling, 2015), and long-
472 term fear recall (Cambiaghi et al., 2016; Karalis et al., 2016). In the auditory domain, top-down
473 control exerted from frontal cortical areas, through low-frequency oscillatory activity, increases
474 coupling to speech signals in the human AC (Park et al., 2015). Our results indicate that, in the bat
475 brain, frontal areas that participate in audition are functionally interconnected by means of low-
476 frequency LFPs with primary auditory cortex. Critically, such coupling does not require external
477 input, which hints towards the presence of a default synchrony in the fronto-auditory cortical
478 circuitry. The latter could constitute a functional basis for high-order, interareal auditory processing
479 in the mammalian brain.

480 Because recordings in the AC were performed with a laminar probe, we were able to study the
481 laminar dependence of FAF-AC synchrony in AC. During spontaneous activity, low-frequency
482 coherence was strongest in deep layers (depth > 700 μm), but the strength of coherence was only
483 affected by depth in the delta band. Interestingly, a recent study revealed that, also during
484 spontaneous activity, spike-LFP synchronization was strongest in deep layers of the AC (Garcia-
485 Rosales et al., 2019). Such spike-LFP coupling was associated to the presence of discrete
486 spontaneous states of increased spiking rate (UP-states) in laminae V and VI. The origins of deep
487 layer UP-states are unclear, but it has been hypothesized that they could be driven by higher-order
488 structures (Sakata and Harris, 2009). In the current study, we observed a putative higher-order
489 auditory structure (the FAF in the frontal lobe) synchronized via a low-frequency oscillatory channel
490 with deep layers of a primary sensory area (the AC). From the phase correlation of delta-band LFPs
491 in the FAF-AC network, it is possible to speculate that delta oscillations in FAF could modulate UP-

492 states in AC. However, we note that causality cannot be inferred from our current dataset and needs
493 to be addressed thoroughly with further experimental approaches.

494 In all, the “default” coupling in the FAF-AC circuit is supported by the presence of anatomical
495 connections between frontal and auditory cortices (Kobler et al., 1987)). Although it has to be
496 properly addressed, we propose that homologous frontal regions tasked with audition in other species
497 may be functionally interconnected with AC in a similar manner. This possibility is still unexplored,
498 yet addressing this question might be crucial for unravelling the mechanisms of high-order auditory
499 processing, cognition, and behaviour based on audition.

500 **3.3 Functional coupling in the FAF-AC network during acoustic processing**

501 Functional coupling between FAF and AC was also addressed in the context of acoustic processing
502 (Figs. 4, 5). Animals were exposed to four distinct acoustic streams, including a conspecific distress
503 vocalization, and three “trains” constructed by repeating a distress syllable at distinct rates.
504 Independently of the stimulus used, we observed little change in the low-frequency phase synchrony
505 of the FAF-AC network, as compared to spontaneous activity. This is a puzzling result which,
506 assuming that low-frequency oscillatory coupling in the network is useful for auditory perception,
507 could in principle be explained largely by our experimental design. Although the animals were awake
508 during the experiments, they listened to the sequences passively: i.e. they were not expected to
509 behave in response to the stimulus, and other variables (e.g. attentional processes) were not
510 modulated according to a controlled experimental approach. Thus, statistically negligible and
511 unreliable changes in the low-frequency dynamics of FAF-AC connectivity could be explained by
512 the fact that the passive listening of acoustic streams is not sufficient to alter the default functional
513 coupling in the network. Whether attention (a top-down process) or behavioural planning could
514 modify the neuronal connectivity in the circuit by either enhancing it or decreasing it, as compared to
515 spontaneous activity, needs to be tested in further research.

516 Experimental evidence suggests that oscillatory activity in the gamma range is crucial for neuronal
517 computations, including sensory processing and cognitive mechanisms (Fries, 2009). Previous
518 studies have shown the presence of gamma-band activity in primary auditory cortex of rats (Vianney-
519 Rodrigues et al., 2011), monkeys (Brosch et al., 2002) and bats (Medvedev and Kanwal, 2008)
520 during passive listening. These studies reported the presence of gamma oscillations at even later time
521 periods (150-300 ms) in what could be considered “induced” (as opposed to “evoked”) activity, not-

522 locked to the auditory stimulus. Our results show that, past 90 ms and up to 180 ms after stimulus
523 presentation, such late, non-locked gamma oscillations are relatively scarce (~5% of out of 50
524 penetrations). These results should not be taken as evidence for the lack of late gamma oscillations in
525 the AC or FAF of *C. perspicillata*, because later periods (190-300 ms after sound presentation) in
526 which oscillatory activity may have occurred were not analysed due to the nature of the stimulus
527 (note that the second syllable presentation of the 5.28 Hz occurs already at ~189.4 ms). Further
528 research can be aimed at detecting gamma activity at later time points in the cortex of *C.*
529 *perspicillata*.

530 In humans, sources of auditory-evoked gamma-band activity (aeGBA) can be found both in primary
531 auditory and frontal (anterior cingulate cortex, ACC) cortices (Mulert et al., 2007; Polomac et al.,
532 2015). Frontal aeGBA is modulated by attention and correlates with performance in auditory
533 detection tasks (Debener et al., 2003; Gurtubay et al., 2004). Moreover, aeGBA in the frontal lobe
534 and gamma-band synchronization between frontal and auditory cortical regions correlate too with
535 task difficulty (Mulert et al., 2007; Polomac et al., 2015), suggesting a role of gamma-band
536 coherence in a fronto-auditory cortical circuit for cognitive control in audition. In fact, disorders of
537 the central nervous system such as schizophrenia are marked by a dysregulation of aeGBA in frontal
538 regions (Cho et al., 2006; Leicht et al., 2010; Curic et al., 2019), further supporting the importance of
539 gamma-band activity for cognition.

540 Our data indicate that low-gamma (25-45 Hz) coherence in the FAF-AC circuit significantly
541 increases with sound presentation, independently of the stimulus considered. This supports a role of
542 gamma synchronization between frontal and auditory cortices for auditory processing, although the
543 functional significance of aeGBA and its coherence across cortical areas should be considered with
544 care. Coherent activity does not imply directly that there exists effective communication between two
545 given regions. Moreover, the nature of the gamma activity is also to be examined cautiously. Here we
546 attempted to disentangle gamma oscillations from a frequency unspecific power surge related to
547 auditory evoked responses (**Fig. 7**), which would in principle explain gamma coherence between
548 FAF and AC. Based on a method proposed by Medvedev and Kanwal (2008), we did not observe
549 statistical evidence supporting that the distributions of low-frequency and gamma-band LFP power
550 were significantly different from one another across penetrations in FAF and AC (**Fig. 7B, F**).
551 However, we did observe, across multiple penetrations, a lack of trial-by-trial correlation between the
552 LFP power in the abovementioned frequency bands (**Fig. 7C, D, G, H, and Fig. S2B**). In addition,

553 our data also showed a very weak correlation between the energy of the evoked response in the LFP
554 and the gamma-band coherence increase (**Fig. 7I** and **Fig. S3**). While these results do not
555 conclusively demonstrate that gamma-band activity can be separated from a frequency unspecific
556 onset response, they hint towards the possibility of evoked gamma activity being an important
557 component for audition, as suggested by previous work (Brosch et al., 2002; Medvedev and Kanwal,
558 2008; Vianney-Rodrigues et al., 2011). The functional roles of onset-related gamma activity in the
559 FAF-AC circuit of *C. perspicillata* (and in the mammalian auditory system in general) should be
560 thoroughly addressed with dedicated experimental approaches in the future.

561 We would like to note that it remains speculative what might be potentially signalled by the FAF-AC
562 gamma synchronization reported in this study. Short onset-related coherence increase might convey
563 information about the presence of an acoustic stimulus, but not necessarily allow to elucidate the
564 stimulus' spectrotemporal features. In the AC of the bat *Pteronotus parnelii*, Medvedev and Kanwal
565 (2008) reported that the spectral properties of the gamma component of the response could be used to
566 differentiate among a battery of conspecific communication calls. In primary visual cortex, for
567 example, distinct characteristics of stimulus-induced gamma rhythms (e.g. peak frequency or
568 amplitude) encode for distinct properties of presented visual stimuli (e.g. contrast or orientation;
569 (Hermes et al., 2015; Murty et al., 2018)), although it has been argued that the variability of gamma
570 based on stimulus properties may constrain the utility of the rhythm for complex integrative
571 computations, at least in early visual cortex (Henrie and Shapley, 2005; Ray and Maunsell, 2010;
572 Bartoli et al., 2019). Our stimulus set is not ideal to determine in an unbiased manner whether the
573 nature of FAF-AC gamma synchronization changes given the spectrotemporal characteristics of the
574 stimuli, in particular because LFPs synchronize to a stimulus' temporal structure also in the gamma
575 range (see (Hechavarria et al., 2016b; Garcia-Rosales et al., 2018a). The latter could alter the spectral
576 patterns of coherence without necessarily meaning that the nature of the underlying coherence is
577 changing, which is an artefact that needs to be controlled for. The careful and systematic variation of
578 acoustic properties of sounds could be used in further research to explore in full the patterns of FAF-
579 AC gamma-band coherence and its role for audition.

580 **3.4 Mutual information in the FAF-AC circuit**

581 Quantifying the amount of information provided by FAF and AC about the acoustic stimuli revealed
582 that the former structure was, in comparison, significantly less informative than the latter. In addition,
583 when considering responses from frontal or auditory cortices in a joint rate code, it was not possible

584 to determine a clear population trend towards independence, redundancy or synergy between the
585 spiking activities of both structures, from an information theoretic perspective. We propose two
586 candidate explanations for our results, which need not be mutually exclusive. First, it is possible that
587 the way in which FAF encodes incoming auditory stimuli is not sufficiently well-captured by means
588 of a code based on spiking rate, and therefore the true encoding capabilities could be underestimated
589 by assuming such scheme (see (Masquelier, 2013; Insanally et al., 2019)). Second, we note that the
590 fact that the FAF conveys, in comparison, significantly less information than the AC, is an expected
591 result as the AC is a structure specialized for auditory computations. As part of the frontal cortex, it is
592 plausible that the FAF encodes for other variables that go beyond acoustic features (e.g. ethological
593 relevance of the sound, multimodal sensory information, etc.). In that case, FAF units would yield
594 low I_{rate} values when attempting to quantify their abilities to encode a sound based on relatively
595 simple methodological approaches, which rely solely on acoustic processing. The former allows to
596 hypothesize that FAF and AC might engage in distinct, non-overlapping coding strategies.

597 **4 Methods**

598 **4.1 Animal preparation and surgical procedures**

599 All experimental procedures were performed in compliance with current German and European
600 regulations on animal experimentation. Experiments were approved by the Regierungspräsidium
601 Darmstadt (experimental permit #FU-1126). The study was performed on 5 adult bats of the species
602 *Carollia perspicillata* (all males). Animals were obtained from a colony in the Institute for Cell
603 Biology and Neuroscience, Goethe University, Frankfurt am Main. Bats used for experiments were
604 kept separately from the main colony.

605 Before undergoing surgical procedures, bats were anaesthetized with a mixture of ketamine (10
606 $\text{mg}\cdot\text{kg}^{-1}$, Ketavet, Pfizer) and xylazine (38 $\text{mg}\cdot\text{kg}^{-1}$, Rompun, Bayer). For surgery and any
607 subsequent handling of the wounds, local anaesthesia (ropivacaine hydrochloride, 2 mg/ml, Fresenius
608 Kabi, Germany) was applied subcutaneously in the scalp area. A rostral-caudal midline incision was
609 made in the scalp, after which skin and muscle tissues were removed carefully in order to expose the
610 skull. A sufficiently large area of the bone was also exposed to make possible the attachment of a
611 custom-made metal rod (1 cm length, 0.1 cm diameter), used during recordings to fixate the
612 animal's head. The rod was attached with dental cement (Paladur, Heraeus Kulzer GmbH, Germany).
613 Animals were given at least one full day of recovery after surgery, and before experiments were

614 performed upon them. The AC and the FAF were located based on well-established landmarks such as
615 blood vessel patterns, and the sulcus anterior (see (Esser and Eiermann, 1999; Eiermann and Esser,
616 2000)). On the first day of recordings each cortical region was exposed by cutting a small hole (~ 1
617 mm²) in the skull with a scalpel blade.

618 Recordings, which lasted no more than 4 hours a day, were performed chronically on awake bats.
619 Water was given to the animals at a period of approximately 1-1.5 hours. Between recording
620 sessions, a bat was allowed to recover for at least a full day. Experiments for the day were halted if
621 the bat showed any sign of discomfort.

622 **4.2 Electrophysiological recordings**

623 Recordings were made inside an electrically isolated and sound-proofed chamber. Inside the
624 chamber, bats were placed upon a custom-made holder which was kept at a constant temperature of
625 30 °C with a heating blanket (Harvard, Homeothermic blanket control unit). A speaker (NeoCD 1.0
626 Ribbon Tweeter; Fountek Electronics, China), located inside of the chamber 12 cm away from the
627 animal's right ear (contralateral to the hemisphere where recordings were performed), was used for
628 free-field stimulation. The speaker was calibrated using a ¼-inch microphone (Brüel & Kjær, model
629 4135, Denmark), which was connected to a custom-made amplifier.

630 Data were acquired from the bat's left AC as described in a previous study (Garcia-Rosales et al.,
631 2019). Neurophysiological data were recorded from the AC using 16-channel laminar electrodes
632 (Model A1x16, NeuroNexus, MI; impedance: 0.5–3 MΩ), with a channel separation of 50 μm. The
633 probe was carefully inserted into the brain perpendicular to the cortical surface using a piezo
634 manipulator (PM-101, Science 455 products GmbH, Hofheim, Germany) until the top-channel was
635 barely visible on the surface of the tissue. Thus, we were able to record from depths ranging 0-750
636 μm, reaching all layers in AC. Histological confirmation of the extent of the electrodes inside the
637 cortex are detailed elsewhere (Garcia-Rosales et al., 2019). Recordings were made in primary AC,
638 although we cannot discard the presence of columns from high frequency fields (Esser and Eiermann,
639 1999). The laminar probes were connected to a micro-amplifier (MPA 16, Multichannel Systems
640 MCS GmbH, Reutlingen, Germany), and acquisition was done via a portable multichannel system
641 with integrated analogue-to-digital converter (Multi Channel Systems MCS GmbH, model ME32
642 System, Germany) with a sampling frequency 20 kHz and a precision of 16 bits. Data acquisition was

643 on-line monitored and stored in a computer using MC_Rack_Software (Multi Channel Systems MCS
644 GmbH, Reutlingen, Germany; version 4.6.2).

645 For recordings in the FAF, a single carbon electrode (Carbostar-1, Kation scientific; Impedance at 1
646 kHz: 0.4–1.2 M Ω) was inserted into the frontal region of the left hemisphere and lowered to depths
647 of ~300-450 μ m with the aid of a second piezo manipulator (same characteristics as the previous
648 one). The electrode was connected to a micro-amplifier which was also connected to the integrated
649 multichannel recording system as described above. It was possible to use the same hardware because
650 the integrated system accommodates up to 32 simultaneous channel recordings. Ground and
651 reference electrodes (silver wires) were inserted as to only touch the dura mater of non-auditory
652 regions of the bat's brain, preferentially located in occipital areas of the contralateral hemisphere.

653 **4.3 Acoustic stimulation**

654 Acoustic stimulation was controlled from the recording computer using a custom-written Matlab
655 (version 7.9.0.529 (R2009b), MathWorks, Natick, MA) software. As acoustic stimuli we used a
656 natural distress call from *C. perspicillata* and three synthetic trains constructed from a single distress
657 syllable, repeated at different rates. Procedures for recording the natural sequence are described in a
658 previous study (Hechavarria et al., 2016a). The call is representative of *C. perspicillata*'s vocal
659 repertoire, and has been used by us in previous studies addressing auditory processing at the level of
660 the AC (Hechavarria et al., 2016b; Garcia-Rosales et al., 2018a; Garcia-Rosales et al., 2019). Distress
661 calls of *C. perspicillata* exhibit two prominent, coexistent temporal modulations: the syllabic- and
662 bout rhythmicities. Syllabic rates in *C. perspicillata*'s distress utterances are in the range of > 30 Hz
663 (median, 71.4 Hz; iqr: 57.1 Hz), whereas bouts (groups of syllables emitted in close sequence) are
664 repeated with rates typically < 12 Hz (Hechavarria et al., 2016a). In the natural call used here,
665 syllables are repeated on average with a rate of 63.7 Hz (see (Garcia-Rosales et al., 2018a)), whereas
666 bouts are uttered with a rate of 4 Hz (i.e. 8 bouts in 1.96 s).

667 To emulate the temporal dynamics of the communication sequences, a stereotypical distress syllable
668 was used to construct artificial acoustic sequences. A first syllabic train had a repetition rate of 5.28
669 Hz, matching the slow temporal dynamics of *C. perspicillata*'s distress utterances. A second one,
670 with a repetition rate of 97 Hz, was used to simulate fast temporal dynamics in communication
671 streams. Finally, we constructed a syllabic train where syllables were repeated in a Poisson-like
672 manner, with an average rate of 70 Hz. This simulated fast-repetition rates without any periodicity

673 and without a slow temporal structure. The 5.28 and 97 Hz trains had a duration of 2 s, while the
674 Poisson train was 4 s long. The syllables had an intensity of 70 dB SPL (root-mean square), close to
675 the intensity of the natural call (see (Garcia-Rosales et al., 2018a)).

676 Sounds were digital-to-analogue converted by means of a sound card (M2Tech Hi-face DAC, 384
677 kHz, 32 bit) and amplified (Rotel power amplifier, model RB-1050) in order to be presented through
678 the speaker inside of the chamber. Prior to presentation the call and syllabic trains were down-
679 sampled to 192 kHz, and low-pass filtered (80 kHz cut-off). All sounds were pseudorandomly
680 presented 50 times each, with and inter-stimulus interval of 1 s. A period of 300 ms, and another of
681 500 ms, was appended at the beginning and the end of each sequence, respectively.

682 Prior to any acoustic stimulation, per penetration, electrophysiological data were acquired for a
683 period of 180 s. These data were used for coherence analyses during spontaneous activity.

684 **4.4 Separation of spiking activity and local-field potentials**

685 All analyses were performed offline with custom-written Matlab (version 8.6.0.267246 (R2015b))
686 scripts. Initially, the raw electrophysiological signal from each channel (all electrodes in AC and
687 FAF) was bandpass filtered (fourth-order Butterworth filter) in order to extract traces pertaining
688 spiking activity (300-3000 Hz cut-off frequencies) and LFPs (0.1-300 Hz cut-off frequencies). For
689 computational reasons, LFP data were down-sampled to 1 kHz and stored for subsequent analyses.

690 Spike detection and sorting from FAF and AC electrodes were performed using the SpyKING
691 CIRCUS toolbox (Yger et al., 2018). Spike detection threshold was set at 5 median absolute
692 deviations from the noise baseline, and spike sorting was done automatically by the SpyKING
693 CIRCUS algorithm based on the probe's geometry to avoid detecting the same templates in two
694 adjacent electrodes. Each template was assigned to the electrode where its amplitude was the
695 strongest. Per electrode (either in AC or FAF), we chose as representative spiking the template with
696 the highest spike count. Spiking responses relative to a single electrode are referred to as a "unit" in
697 the manuscript.

698 **4.5 Spike latency estimation**

699 Spike latency was defined as the time point in which a unit's spiking rate was statistically different
700 from the expected rate during spontaneous activity, based on a previous study (Chase and Young,
701 2007). In brief, the algorithm proposed by Chase and Young compares a unit's response to a stimulus

702 across several time windows, with the expected spiking rate under the assumption that the unit fires
703 spontaneously with Poisson statistics, given a certain rate. A unit's firing rate in the 250 ms silence
704 period before stimulus onset, across the 50 repetitions from all stimuli tested (a total 200 trials), was
705 considered its spontaneous spiking rate for the abovementioned assumption. The response of a unit to
706 a certain stimulus (i.e. spiking after stimulus onset) was pooled across trials. Taking this pooled
707 response, the probability of observing at least n spikes in a given window t_n (after stimulus onset),
708 assuming Poisson firing in the absence of acoustic inputs, can be defined as follows (Chase and
709 Young, 2007):

$$710 \quad P_{t_n}(\geq n) = 1 - \sum_{m=0}^{n-1} \frac{(N\lambda t_n)^m e^{-N\lambda t_n}}{m!}, \quad [1]$$

711 where N is the number of repetitions of the given stimulus, and λ is the spontaneous firing rate.
712 Starting from stimulation onset, the probability that each elicited spike indicates a stronger than
713 chance deviation in rate from the firing rate estimated in the absence of stimulation (the 250 ms
714 window), is taken as the probability that the spontaneous firing rate would have produced that
715 particular spike as the last of n spikes in a window t_n . In this context, t_n is the width of the window
716 containing the n spikes observed so far. Hence, the time of the first spike for which the
717 aforementioned probability is sufficiently low (here, $P_{t_n}(\geq n) < 10^{-5}$) is considered as the unit's
718 latency. This method circumvents caveats regarding classical peak latency estimations using peri-
719 stimulus time histograms or spike-density functions over time (Levakova et al., 2015).

720 **4.6 Interareal coherence analyses**

721 All coherence analyses were done using the Chronux toolbox (Bokil et al., 2010). As a metric of
722 interareal phase synchronization we used the imaginary part of the coherency ("iCoh" in the
723 manuscript; (Nolte et al., 2004)), both during spontaneous activity and acoustic processing.
724 Coherency is complex value that measures phase consistency between two time series, across several
725 trials. The coherency between two signals x and y , at a certain frequency ω , can be defined as follows
726 (Bastos and Schoffelen, 2015):

$$727 \quad coh_{xy}(\omega) = \frac{\frac{1}{n} \sum_{k=1}^n A_x(\omega, k) A_y(\omega, k) e^{i(\phi_x(\omega, k) - \phi_y(\omega, k))}}{\sqrt{(\frac{1}{n} \sum_{k=1}^n A_x^2(\omega, k)) (\frac{1}{n} \sum_{k=1}^n A_y^2(\omega, k))}}, \quad [2]$$

728 where $A_x(\omega, k)$ and $A_y(\omega, k)$ are the amplitudes of signals x and y at frequency ω and trial k , while
729 coh_{xy} represents the coherency between both signals, and n is the number of trials per stimulus ($n =$
730 50). Coherency is a complex quantity, but its absolute value ranges from 0 to 1, indicating the
731 relative, normalized strength of phase synchronization between time series. Taking the imaginary
732 part of coh_{xy} is a straightforward manner to remove non phase-lagged interactions that could be
733 attributable to, for example, passive field spread or common referencing (Bastos and Schoffelen,
734 2015). In order to minimize further common influences related to the temporal structure of the
735 stimuli, we subtracted from each trial the mean (across all trials of a given stimulus) LFP of each
736 channel (Kikuchi et al., 2017), and calculated coherence using the de-measured traces. Note that this
737 could affect low frequencies more than high frequencies, because the latter are more sensitive to
738 temporal jitter. Additionally, while the approach alleviates obtaining simply stimulus-evoked
739 coherence, it could also mask phase-locking that is time-locked to the stimulus but not entirely
740 attributable to acoustic temporal features.

741 From the 180 s trace of spontaneous activity recorded simultaneously from FAF and AC
742 penetrations, 50 chunks of 3 s length each were taken. The precise time at which chunks started was
743 chosen randomly in a way that the resulting sub-segments would still be non-overlapping. Each of
744 these paired chunks from FAF and AC were treated as a trial, and iCoh was estimated from all 50 of
745 them for the corresponding penetration (data shown in **Fig. 3B**). A surrogate calculation was
746 performed whereby the precise phase relationship between FAF and AC “trials” in spontaneous
747 activity was abolished. This was accomplished by pairing FAF chunks with AC chunks randomly.
748 The former affects the timing of the phase-relationships but maintains the overall power across
749 selected chunks. The pairing was performed randomly a sufficiently large number of times (250), and
750 iCoh was calculated at each repetition of the surrogate analysis. Thus, it was possible to obtain a
751 distribution of iCoh values that represented coherence estimates in the absence of consistent phase
752 relationships between AC and FAF during spontaneous activity. The iCoh calculated from the
753 original data was then related to the surrogate iCoh values by means of z-normalization (z-iCoh). At
754 a population level, lack of consistent phase coherence between FAF and AC at a certain frequency
755 would yield z-iCoh values close to 0.

756 Time-frequency resolved iCoh values were obtained by means of coherogram calculations (*cohgram*
757 function in Chronux; data depicted in **Figs. 3C, 4 and 5**). A time-resolved approach allowed us to
758 examine changes of coherence over time while animals listened to acoustic streams. Each

759 coherogram was constructed by calculating coherence in a sliding window of 200 ms length, which
760 was advanced in steps of 2 ms. Because of the spectral resolution due to window length, the
761 coherence spectrum for frequencies below 4 Hz could not be estimated with precision. As with any
762 time-frequency resolved approach, there is a compromise between temporal and spectral resolutions,
763 which we empirically found to be best balanced with a 200 ms window. All power spectra in the
764 time-resolved analysis were obtained with the multitaper method (Percival and Walden, 1993),
765 available in the Chronux toolbox, using 3 tapers and a time-bandwidth (TW) product 2.

766 The frequency range of 4-12 Hz was used as a representative of low-frequencies in the spectrum, and
767 the 25-45 Hz band was considered as low-gamma. For comparing iCoh values during sound
768 presentation vs. iCoh values during spontaneous activity, we calculated time-resolved iCoh during
769 spontaneous activity using the same segments with which non-time resolved coherency was
770 calculated (shown in **Fig. 3C**). Because the length of the spontaneous segments (3 s) was not
771 precisely equal to the length of the stimuli (the Poisson process, for example, was 4 s long), we
772 collapsed the time-resolved spontaneous iCoh values in the temporal dimension (median across
773 timepoints per frequency). Thus, it was possible estimate the percentage increase during sound
774 processing in a time-resolved manner as follows:

775
$$iCoh_{increase}(\omega, t) = \frac{iCoh_{stim}(\omega, t) - iCoh_{spont}(\omega)}{iCoh_{spont}(\omega)} * 100, \quad [3]$$

776 where $iCoh_{stim}(\omega, t)$ is the iCoh value during stimulus presentation at frequency ω and time t , while
777 $iCoh_{spont}(\omega)$ is the collapsed time-resolved iCoh during spontaneous activity at the same frequency.
778 The percentage increases were narrowed to the frequency bands of interest (i.e. 4-12 and 25-45 Hz)
779 by calculating the median iCoh increase in the corresponding frequency range over time (data
780 depicted in **Fig. 5A, D, G, J**). For evaluating iCoh increase at stimulus onset, the median was
781 calculated not only for the frequency range, but also across time in the first 100 ms after the sequence
782 onset.

783 **4.7 LFP onset power analyses**

784 To test to what extent coherent gamma oscillations in the FAF-AC network could be attributable to a
785 broadband evoked response in the LFP, we explored the statistical dependence of gamma power on a
786 trial by trial basis. Spectral properties were obtained using three different temporal windows (**Fig. 6**):
787 *pre* (-110 ms – -20 ms relative to stimulus onset), *onset* (0 – 90 ms relative to stimulus onset), *late*

788 (90 – 180 ms relative to stimulus onset), and *full* (0 – 180 ms relative to stimulus onset). All analyses
789 were performed using the 5.28 Hz syllabic train, thereby guaranteeing that responses to only one
790 syllable (i.e. the first syllable presented) were considered in the time windows of choice. All spectra
791 were calculated using the Chronux toolbox, with 2 tapers and a TW product of 2, on a trial-by-trial
792 basis. Power spectra were compared for every penetration, per trial, statistically probing changes in
793 the power of low-frequency (0-15 Hz) and gamma bands (25-45, 45-80, and 25-80 Hz) in the *pre* vs.
794 *onset* windows (**Fig. S2A**; Wilcoxon signed rank tests, significance when $p < 0.01$), as well as during
795 the *pre* vs. *late* periods (**Fig. 6C**). A percentage of significant difference (ratio across 50 penetrations)
796 is depicted in the abovementioned figures. The time-frequency analyses shown in **Fig. 6D** was
797 obtained by evaluating significance differences, per penetration, at given time windows (90 ms
798 length) which were slid (10 ms steps) over times surrounding stimulus onset. Each time window
799 spectra were compared, on a trial-by-trial basis given a penetration, with a window located before
800 stimulus onset (center at ca. -90 ms relative to onset; Wilcoxon signed rank tests, significance when p
801 < 0.01).

802 As per Medvedev and Kanwal (2008), the power spectra from each penetration were z-normalized
803 across trials, and the power in a given band was calculated by integrating (*trapz* function, Matlab)
804 over the z-normalized spectrum (per trial). Care was taken that the number of frequency samples
805 were comparable when integrating at different bands; the gamma band was therefore divided into 25-
806 45 and 45-60 Hz sub-bands. We then determined whether the distribution of power in gamma and
807 low-frequencies were different, per penetration, by means of a 2-sample Kolmogorov Smirnov test
808 (alpha at 0.01). Because differences or lack of differences in the power distributions do not
809 necessarily imply the existence (or lack) of trial-by-trial correlation between the power of low and
810 gamma frequency bands, we tested whether these powers were correlated for every penetration, on a
811 trial by trial basis. In this context, correlations were significant given a $p < 0.01$.

812 **4.8 Information theoretic analyses**

813 Information in the neuronal response regarding the acoustic stimuli was quantified by means of
814 Shannon's mutual information (MI; (Shannon, 2001)). The MI between a stimulus set S and a
815 response set R is mathematically expressed as follows:

$$816 \quad I(R; S) = H(R) - H(R|S), \quad [4]$$

817 where $H(R)$ is the response entropy (i.e. the overall variability of the response set), which is
818 expressed as:

$$819 \quad H(R) = -\sum_{r \in R} P(r) \log_2[P(r)], \quad [5]$$

820 while

$$821 \quad H(R|S) = -\sum_{s \in S} P(s) \sum_{r \in R} P(r|s) \log_2[P(r|s)], \quad [6]$$

822 is referred to as the “noise entropy”, representing the irreproducibility of the response given a
823 stimulus. The probabilities $P(r)$, $P(s)$ and $P(r/s)$ indicate the probability of observing response r taken
824 from the set R , the probability of observing stimulus s from the set S , and the probability of observing
825 response r given stimulus s , respectively. If the logarithm in **Eqs. 5** and **6** is of base 2, the MI has
826 units of bits. Each bit of information means that an external observer is able to reduce, by observing
827 the response, the uncertainty about the stimulus by a factor of 2 on a single trial basis. These
828 quantities were estimated by means of the Information Breakdown Toolbox (ibTB; (Magri et al.,
829 2009)).

830 **4.8.1 Stimuli for MI computations**

831 With aims of quantifying the amount of information provided by FAF and AC spiking regarding a
832 specific acoustic stream, we calculated each unit’s ability to discriminate consecutive chunks of the
833 stimulus from each other (de Ruyter van Steveninck et al., 1997; Kayser et al., 2009; Kayser et al.,
834 2010; Garcia-Rosales et al., 2018a). A particular sequence S (be it, for example, the natural the
835 distress call) was subdivided into non-overlapping, consecutive segments s_k ($k = 1, 2, 3, \dots, M$), all of
836 length $T = 4$ ms. We chose this segment length so that results from this paper would be comparable
837 with previous data from the AC of *C. perspicillata* (Garcia-Rosales et al., 2018a). Using lengths in
838 the range of 2-12 ms did not alter the results qualitatively. Each segment s was treated as an
839 independent substimulus from the set S . Note that, in this framework, all substimuli are equiprobable.

840 **4.8.2 Rate and joint neuronal codes**

841 The manner in which $P(r)$ is quantified depends directly on the assumptions made to characterize the
842 neuronal response (i.e. the neural code considered). Here we used a rate code (I_{rate}), which determines
843 how well a unit discriminates between each substimulus s , based on its spiking rate. The response set
844 represented whether a spike occurred or not, and can be characterized as follows: $R = \{0, 1\}$, where 1
845 and 0 represent the occurrence or absence of a spike, respectively. $P(r)$ was then the probability that a

846 unit fired or not a spike across all trials, whereas $P(r/s)$ was the probability of firing to a certain
847 substimulus. The time window was sufficiently short to assume that, in general, a single spike would
848 occur within each time segment, and therefore binarized responses were used for MI calculations.

849 The information provided by joint responses from the FAF and the AC (I_{joint}) was calculated by
850 taking into account which unit elicited a spike in a merged response (see **Fig. 6B**; also referred to as
851 “line code” in the literature (Panzeri et al., 2007; Kayser et al., 2009)). That is, the response set was
852 defined as $R = \{ (0, 0); (0, 1); (1, 0); (1, 1) \}$, where each member of the set represents whether and
853 which unit fired a spike (e.g. $(0, 1)$ could indicate that the FAF unit did not fire, whereas the AC one
854 did; $(1, 0)$ would represent the opposite).

855 **4.8.3 Quantifying information from limited samples**

856 The probabilities in **Eqs. 5** and **6** are estimated empirically from the data, based on the representation
857 of neuronal responses described above (i.e. the neural codes). These empirically estimated
858 probabilities (such as $P(r)$, or $P(r/s)$) are biased because it is impossible in practice to sample all
859 possible values of R a sufficiently large number of times (ideally, infinite). A number of methods
860 have been developed to deal with the sampling bias (Panzeri et al., 2007). In this study, we used the
861 Quadratic Extrapolation (QE) procedure (Strong et al., 1998), implemented in the ibTB. In addition
862 to the QE, we subtracted possible remaining biases by means of a bootstrap procedure (Montemurro
863 et al., 2008; Garcia-Rosales et al., 2018a), using 250 repetitions. For paired responses, we also used
864 the shuffling procedure (Panzeri et al., 2007) implemented in the iBTB together with the bootstrap
865 method. To corroborate that the information estimates presented in the results were not affected by
866 the limited sampling bias, we conducted numerical simulations in order to measure the dependence
867 of the bias on the number of trials. The results of these simulations are shown in **Fig. S8**, and indicate
868 that the number of trials used in this study (50) was sufficient to robustly estimate the information
869 quantities presented.

870 **4.9 Statistical analyses**

871 All statistical analyses were conducted in Matlab (version 8.6.0.267246 (R2015b)), with custom-
872 written scripts using the Statistics and Machine Learning Toolbox. Tests for comparisons between
873 the distributions of the quantities described above were always indicated in the main text. When
874 multiple comparisons were done, we performed False-Discovery Rate (FDR) corrections (e.g.,
875 comparing across multiple channel pairs in **Fig. 3E**) with the Benjamini and Hochberg procedure

876 (Benjamini and Hochberg, 1995). The significance threshold was set at an alpha of 0.05. If the p
877 values reported were uncorrected, it is stated so in the text. Effect sizes were calculated with the r
878 metric, which is defined as follows (Fritz et al., 2012):

879
$$r = \frac{W}{\sqrt{N}}, \quad [7]$$

880 where r is the effect size, W is the test statistic of the Wilcoxon signed rank test used in this context,
881 and N is the sample size of the quantities being compared ($N = 50$). Values of $r \leq 0.3$ were
882 considered small effects, while $0.3 \leq r \leq 0.5$ were considered as medium effects, and large effects
883 were considered when $r > 0.5$ (Fritz et al., 2012).

884 **5 Conflict of Interest**

885 The authors declare that the research was conducted in the absence of any commercial or financial
886 relationships that could be construed as a potential conflict of interest.

887 **6 Author Contributions**

888 **F.G.R** and **J.C.H** designed the study. **F.G.R** collected the data. **F.G.R** analyzed the data and wrote
889 the manuscript. **F.G.R**, **L.L.J**, **E.G.P**, **Y.C.C**, and **J.C.H** discussed the results and reviewed the
890 manuscript.

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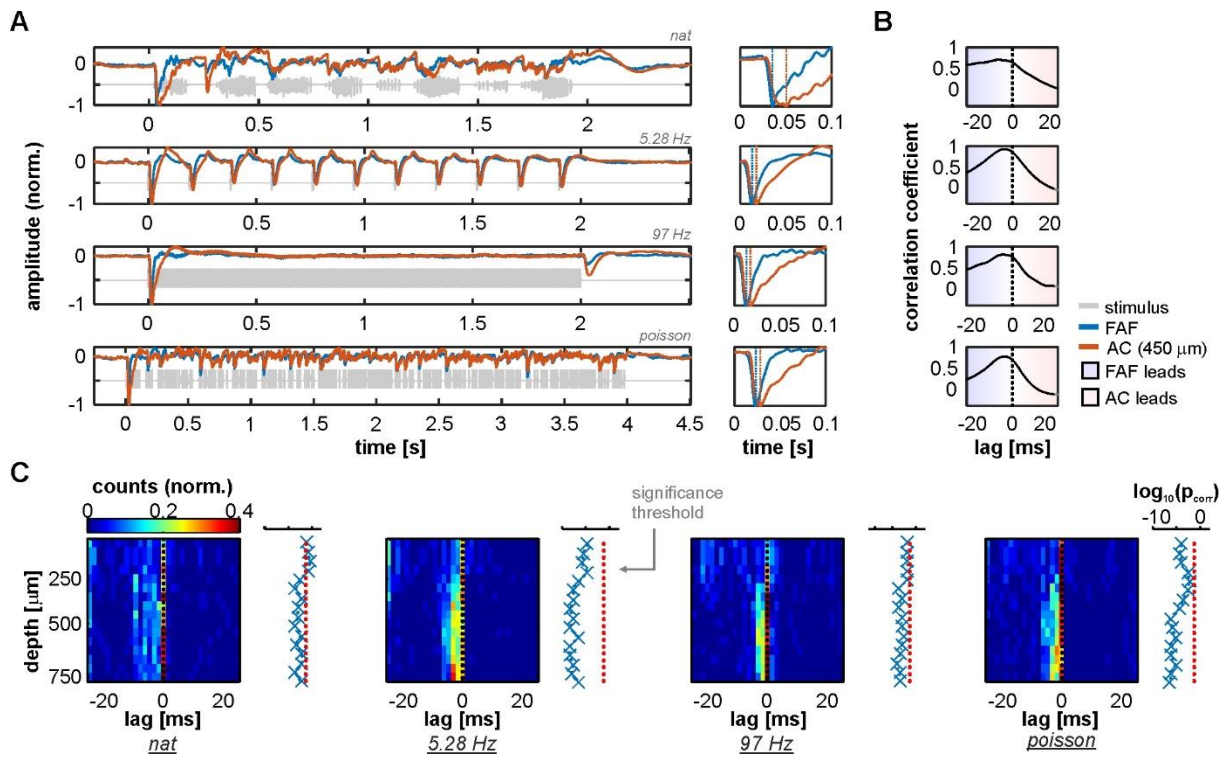
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1152 **1 Data Availability Statement**

1153 The data that support the findings of this study are available from the corresponding authors upon
1154 reasonable request.

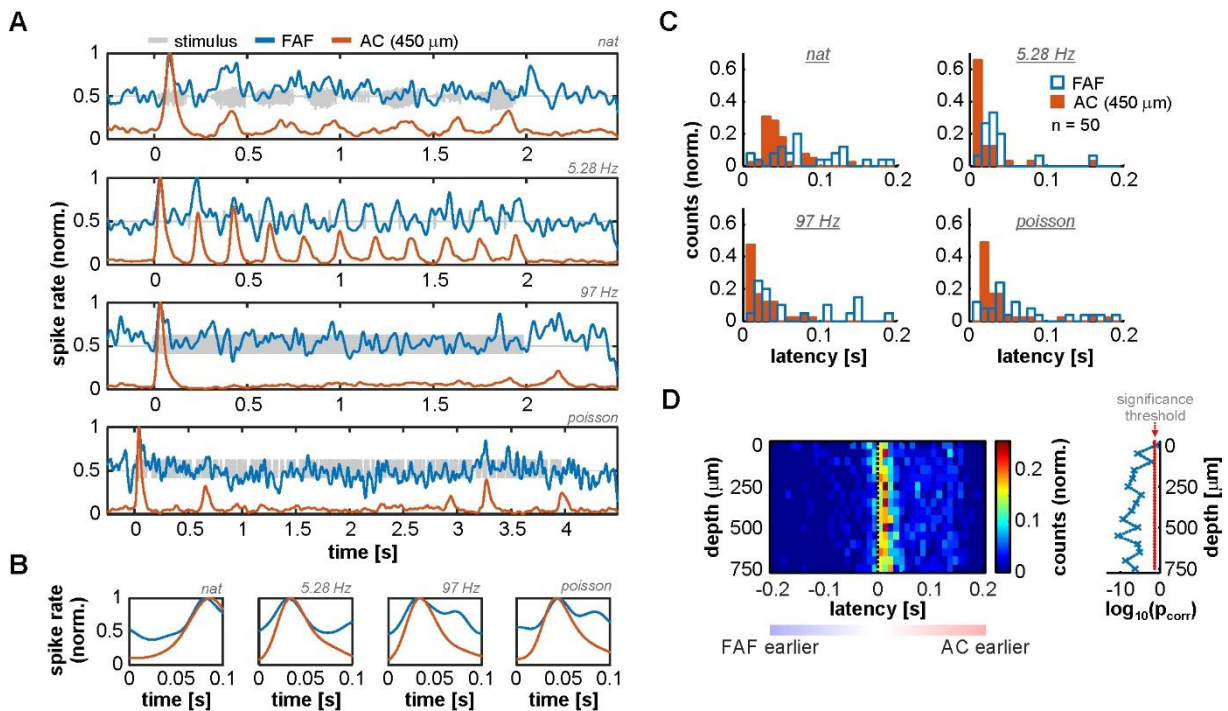
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1157 **Fig. 1. LFP stimulus-related activity in the frontal auditory field (FAF) precedes that of the**
 1158 **auditory cortex (AC).** (A) *Left column:* Grand average across all 50 penetrations of LFPs
 1159 recorded from the FAF (blue) and the AC at a depth of 450 μ m (orange) in response to the four
 1160 stimuli tested (ordered from top to bottom: natural sequence (*nat*), 5.28 Hz train, 97 Hz train, and
 1161 the Poisson syllabic sequence (*poisson*); grey traces). *Right column:* zoom into the first 100 ms
 1162 after stimulus onset. Negative peaks in the evoked potential are marked with vertical dashed
 1163 lines. Note that peaks in the FAF occur earlier than in the AC. (B) Cross-correlation between
 1164 traces in A (*left column*). Peaks in negative lags indicate that FAF field-potentials lead those in
 1165 the AC. (C) Peak lags between the cross-correlation of FAF LFPs and AC LFPs, for all
 1166 penetrations ($n = 50$) and across recording depths. Next to each heatmap, log-scaled corrected p
 1167 values testing that the peak distribution is significantly below 0 (FDR corrected tailed Wilcoxon
 1168 signed rank tests; $p_{corr} < 0.05$ for significance).

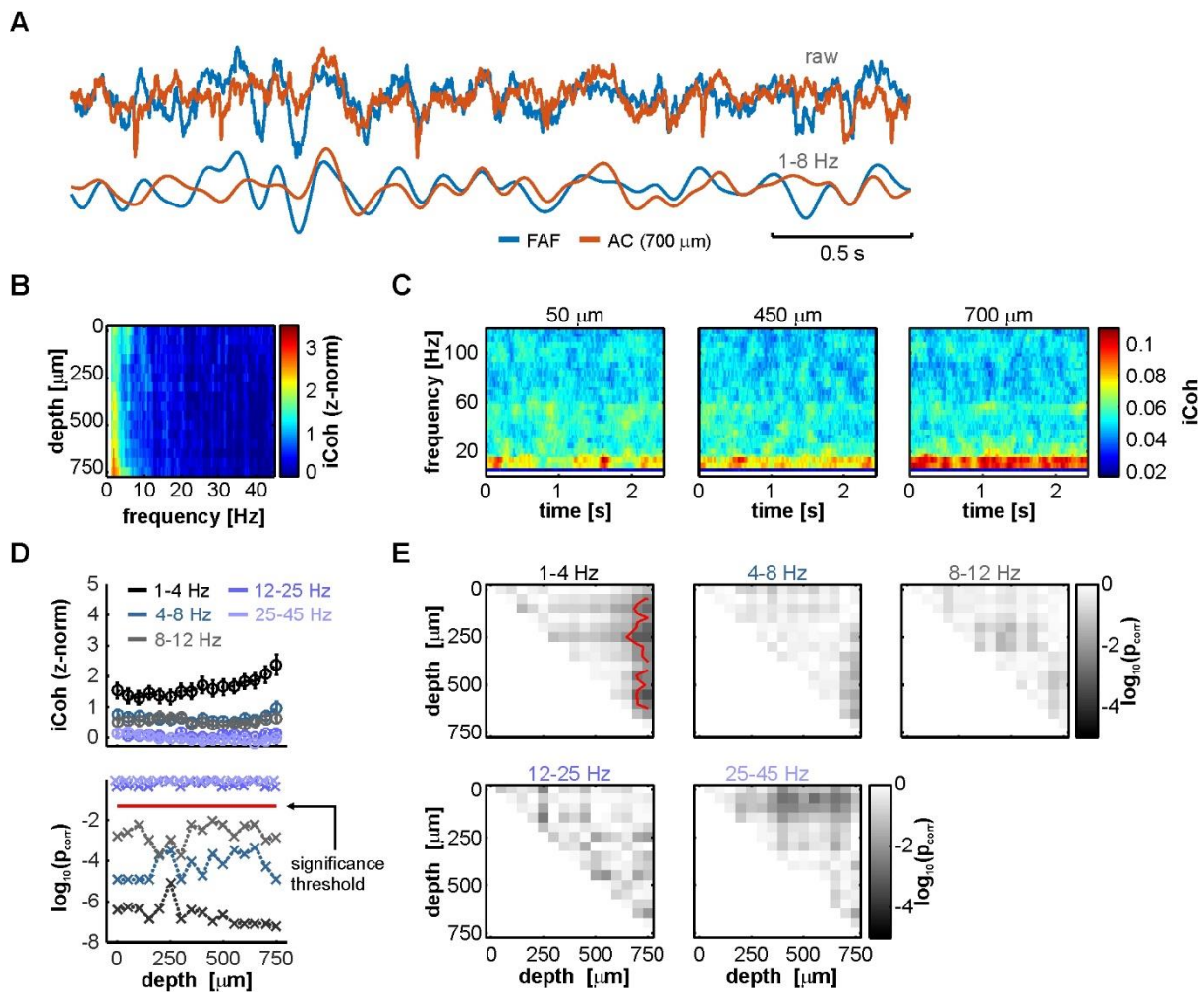
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1171 **Fig. 2. Spiking activity suggests the presence of fast inputs into the FAF.** (A) Spiking responses
 1172 from two simultaneously recorded units in the FAF (blue) and the AC (at 450 μm ; blue), in
 1173 response to all stimuli tested (top to bottom). (B) Zoom-in into the first 100 ms after stimulus
 1174 onset of the examples shown in A. Note that, for this pair, the peak response for the FAF unit
 1175 was at least as fast as the for auditory cortical one. (C) Latency distribution of FAF (blue) units
 1176 and AC units at 450 μm , for all stimuli ($n = 50$ penetrations). The FAF was, overall, sluggish in
 1177 comparison to the AC. (D) Response latency difference between simultaneously recorded
 1178 spiking for FAF and AC at different depths (positive difference, FAF slower than AC; negative
 1179 difference indicates the opposite). In some cases, FAF spiking responses occurred earlier than
 1180 AC responses, although the AC was in general significantly faster than the FAF across channels,
 1181 except in the case of the most superficial contact (FDR-corrected Wilcoxon signed rank tests,
 1182 significance when $p_{\text{corr}} < 0.05$). Log-converted p values and significance threshold are shown to
 1183 the right of the latency distributions. The threshold is indicated as a red dashed line.

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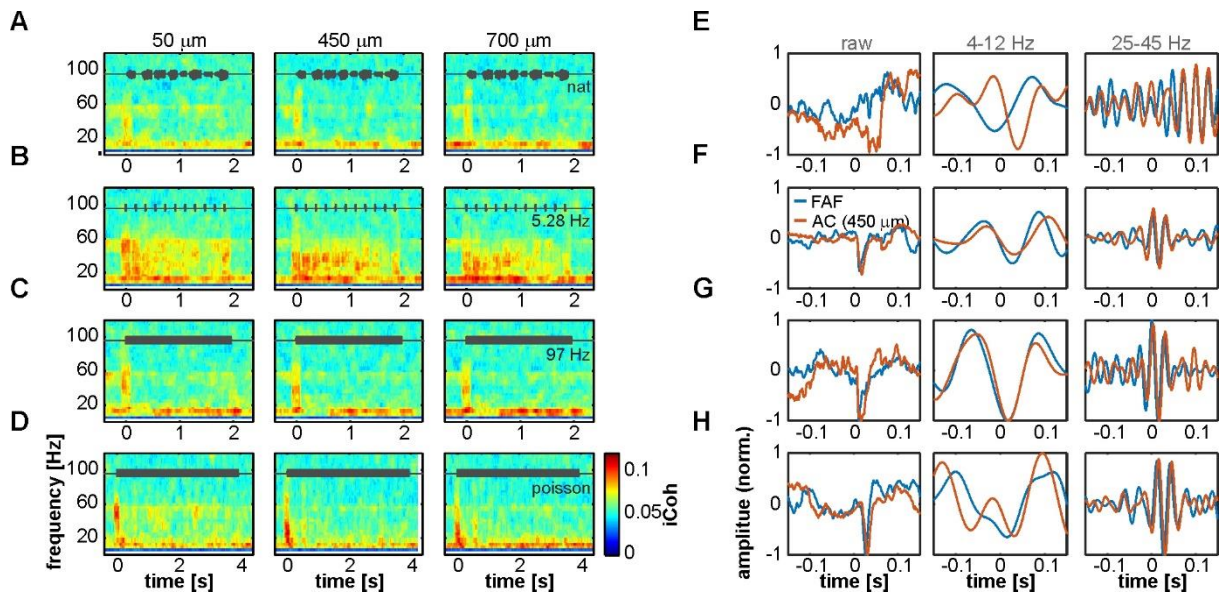


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1186 **Fig. 3. LFPs from FAF and AC are low-frequency coherent during spontaneous activity in a**
 1187 **depth-dependent manner.** (A) Simultaneously recorded LFP trace from the FAF (blue) and the
 1188 AC at a depth of 700 μm (orange). Raw (top pair) and low-frequency filtered (bottom pair)
 1189 traces are shown. (B) Frequency-dependent average imaginary coherence (iCoh), z-normalized
 1190 to a surrogate distribution, across recording depths in the AC. Deep channels showed, on
 1191 average, the strongest coherence values at low frequencies. (C) Time-resolved iCoh using the
 1192 same segments as in B, with a sliding window of 200 ms (see Methods), the same used for
 1193 analyzing stimulus-related synchronization. (D) *Top*: depth-dependent population z-normalized
 1194 iCoh from B, for distinct frequency bands (delta, theta, alpha, beta and low gamma, see
 1195 Methods; frequency ranges indicated in the plot), across all penetrations (shown as mean \pm
 1196 SEM). *Bottom*: log-scaled corrected p values after testing, per frequency band, whether z-
 1197 normalized iCoh values were significantly higher than 0 across penetrations, per AC depth
 1198 (FDR-corrected Wilcoxon signed rank tests, $p_{\text{corr}} < 0.05$ for significance; threshold indicated as a
 1199 horizontal red dashed line). (E) Significance matrices comparing, per frequency band, z-

1200 normalized iCoh values across different depths. Each cell (i, j) in a matrix depicts the log-scaled
1201 p_{corr} obtained from statistically comparing coherence at channels with depths i and j in the AC.
1202 Red contour lines delimit regions of statistical significance (FDR-corrected Wilcoxon signed
1203 rank tests, significance when $p_{\text{corr}} < 0.05$).

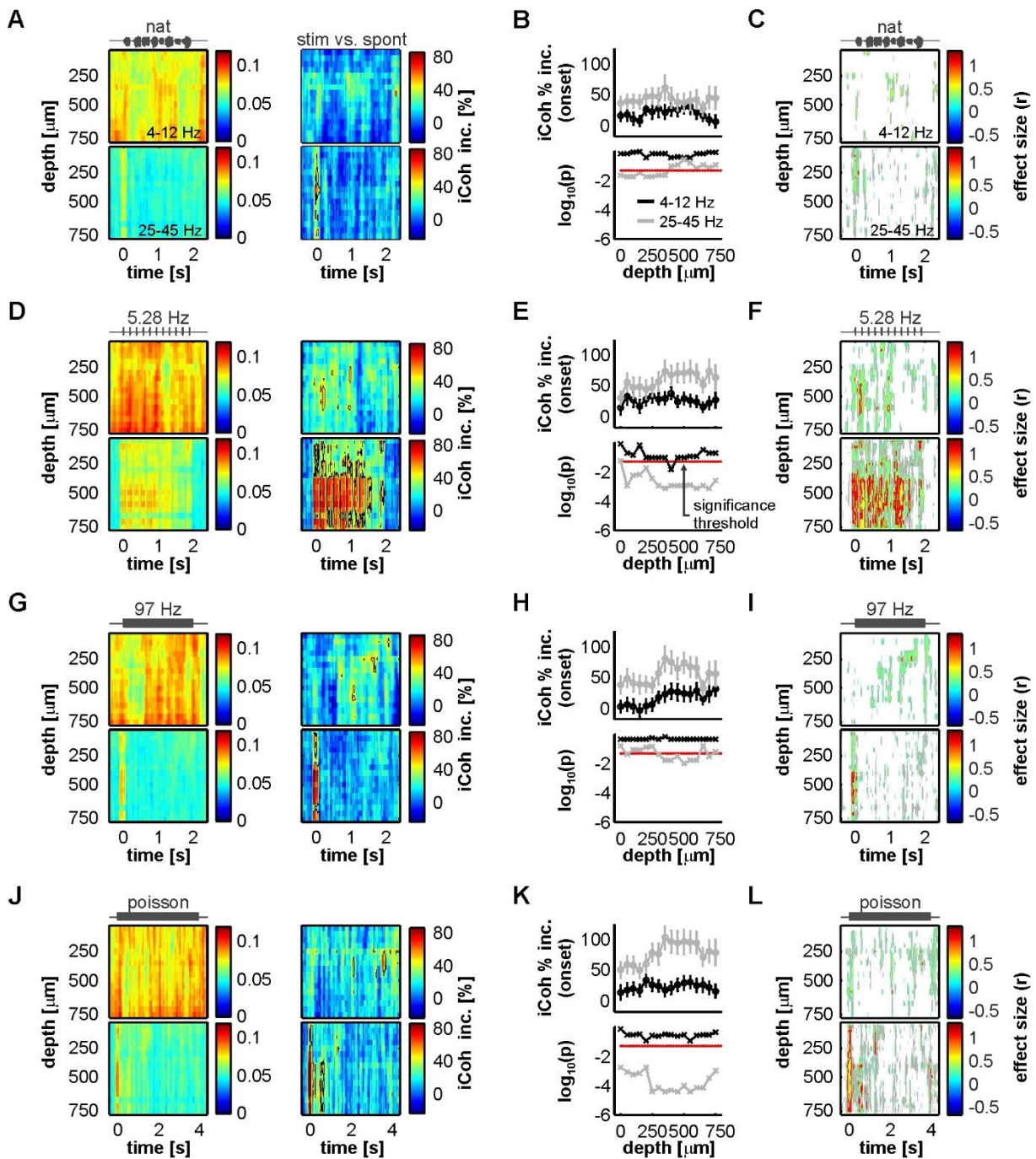
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1206 **Fig. 4. Interareal phase synchrony during acoustic sequence processing.** (A-D) Mean time-
 1207 resolved coherence between LFPs from the FAF and the AC at three representative depths (50,
 1208 450 and 700 μm), in response to the natural sequence (A), a syllabic train of 5.28 Hz (B), a
 1209 syllabic train of 97 Hz (C), and the syllabic train with a Poisson structure (D). Note that low
 1210 frequency synchrony is high even without acoustic stimulation, and the appearance of gamma-
 1211 band evoked synchronization at the stimulus onset (time 0), albeit more weakly in response to
 1212 the natural call in A. (E-H) LFP recordings from the AC (orange) and FAF (blue) around the
 1213 time of stimulus onset (at 0 s; order in E-H corresponds to order in A-D), from single trials in a
 1214 representative penetration. Left column depicts the raw LFP, whereas middle and right columns
 1215 depict field-potentials filtered in 4-12 and 25-45 Hz low-frequency and gamma-bands,
 1216 respectively.

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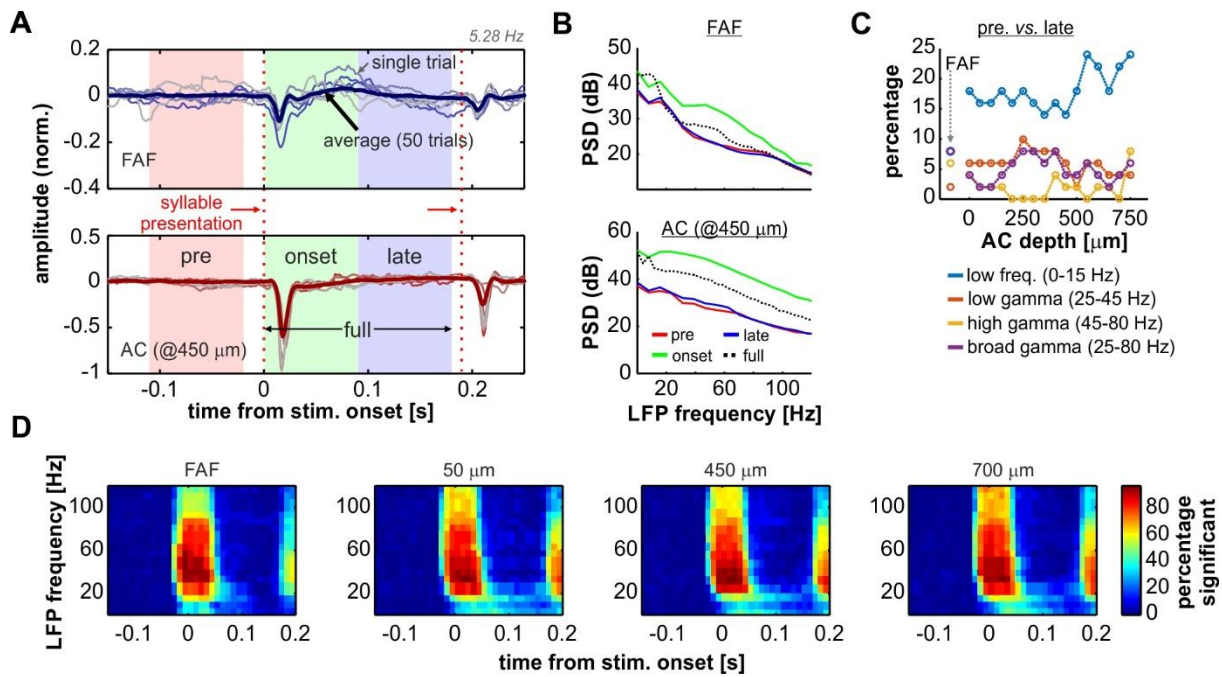


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1219 **Fig. 5. Acoustic stimulation alters FAF-AC coherence mostly in the gamma-band.** (A) *Top*:
 1220 average time course of iCoh while animals listened to the natural sequence (left) across
 1221 recording depths for low frequencies (4-12 Hz), and percentage increase of coherence in that
 1222 range relative to the spontaneous activity (right). *Bottom*: same as *Top*, but for iCoh values in the
 1223 gamma range (25-45 Hz). Black contour lines delimit regions with average increase of coherence
 1224 > 50%. (B) Population onset-related iCoh increase (median in the period of 0-150 ms after
 1225 stimulus onset) across depths in the AC (black traces, low-frequency band iCoh; grey traces,

1226 gamma-band iCoh; shown as mean \pm SEM). On the bottom subpanel, log-scaled corrected p
1227 values obtained after testing that such increase was significantly different from 0% (black, low-
1228 frequency band; grey, gamma-band; FDR-corrected Wilcoxon signed rank tests, significance
1229 when $p_{\text{corr}} < 0.05$, indicated as a red dashed line). **(C)** Time-resolved effect size of population
1230 iCoh percentage increase (r ; see Methods) for the low-frequency band (top) and the gamma-
1231 range (bottom). Grey contour lines delimit regions of $r > 0.3$, whereas red contours mark regions
1232 of $r > 0.5$ (medium and large effect sizes, respectively). r values are only shown for time points,
1233 across channels, where the coherence increase was significantly higher than 0% (Wilcoxon
1234 signed rank test, $p < 0.05$). **(D-F)** Same as **A-C** but considering a syllabic train at 5.28 Hz as
1235 stimulus. **(G-I)** Same as **A-C**, the stimulus being a syllabic train at 97 Hz. **(J-L)** Same as **A-C**,
1236 except the stimulus was the Poisson syllabic train.

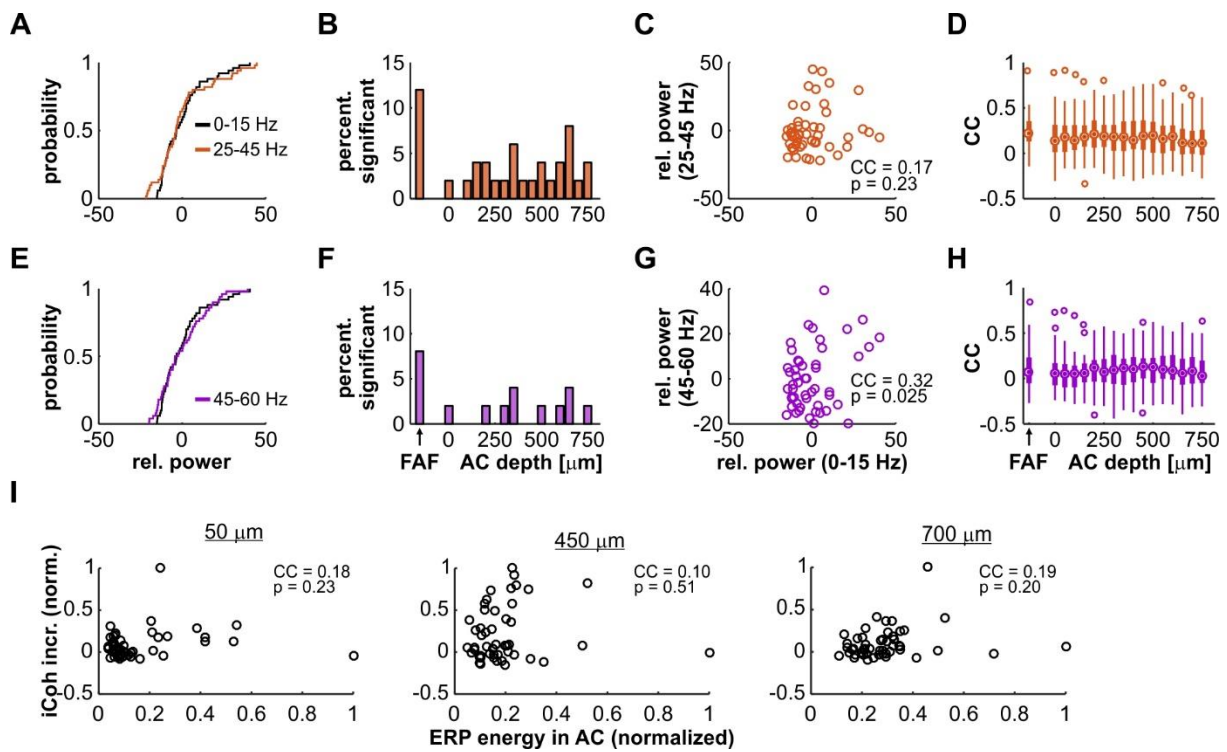
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1239 **Fig. 6. Onset related power increase in AC and FAF.** (A) Representative LFP recordings of one
 1240 penetration pair (FAF, top; AC at 450 μm , bottom), depicting 6 single trials for illustrative
 1241 purposes (thin lines) and the average across all 50 trials. The time segments of *pre*, *onset*, *late*,
 1242 and *full*, used for analyses (see main text), are indicated in the graphs. First and second syllable
 1243 presentations of the 5.28 Hz train are indicated with vertical, red dashed lines. (B) Power spectral
 1244 density (PSD) of the *pre* (red), *onset* (green), *late* (blue) and *full* (black, dashed) periods from the
 1245 data depicted in **A** (average over the 50 trials), in the FAF (top) and AC (bottom). (C) Percentage
 1246 of penetrations (after a total of 50) for which the power (at several frequency bands, indicated in
 1247 the figure) was significantly different during the *late* period than during the *pre* period. (D)
 1248 Time-frequency analysis illustrating the percentage of penetrations in FAF and AC (at three
 1249 representative depths: 50, 450 and 700 μm) in which the power at a given time window was
 1250 significantly higher than the power at a window preceding the stimulus onset.

1251



1252

1253 **Fig. 7. Power distributions of gamma-band and low-frequency LFPs in AC and FAF. (A)**

1254 Distributions of the relative power of low-frequency (0-15 Hz; black) and gamma-band activity
1255 (25-45 Hz; orange) across trials, recorded from a single representative penetration in the FAF.

1256 These distributions were not significantly different from each other (2-sample Kolmogorov-
1257 Smirnov test, $p = 0.84$). (B) Percentage from the total number of penetrations ($n = 50$) for which

1258 the distributions of low-frequency and gamma (25-45 Hz) power were significantly different
1259 from each other at an alpha of 0.01, in FAF and at different depths of the AC. (C) Scatter plot

1260 and correlation coefficient (CC) of the trial-by-trial relationship between low-frequency and
1261 gamma band (25-45 Hz) power ($n = 50$ trials), for the same representative penetration shown in

1262 A. The CC was of 0.17, and it was not significant: $p = 0.23$. (D) Distribution, in FAF and at all
1263 AC depths, of CCs between gamma-band (25-45 Hz) and low-frequency power. The median in

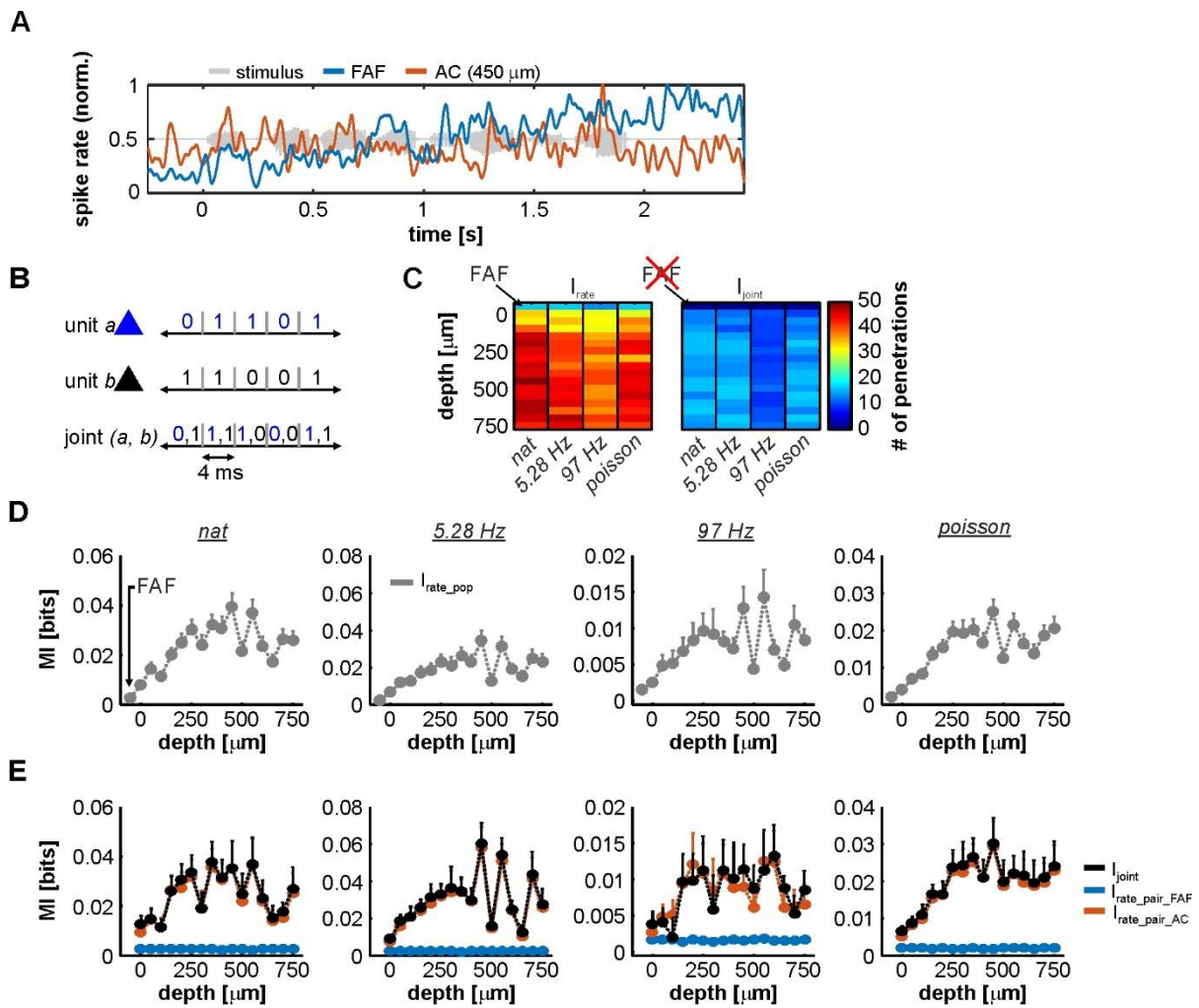
1264 the AC across depths was of 0.17, whereas the median in the FAF was of 0.22. (E-H) Similar to
1265 A-D, but the gamma range considered was of 45-60 Hz (signaled in purple). In panel E, both

1266 distributions were also not significant from each other (2-sample Kolmogorov-Smirnov test, $p =$
1267 0.84). The CC in G was of 0.32, and it was not significant at an alpha of 0.01 ($p = 0.025$). In

1268 panel H, the median across depths in the AC was of 0.08, whereas the median CC in the FAF
1269 was of 0.07. (I) Correlations between evoked-potential (ERP) energy in AC and gamma-band

1270 coherence increase (same as in Fig. 5) for three representative depths in the AC (at 50, 450 and

1271 700 μm ; all depths are shown in **Fig. S3**). Values are normalized for clarity. There were no
1272 significant correlations at any of the depths shown ($p \geq 0.2$).
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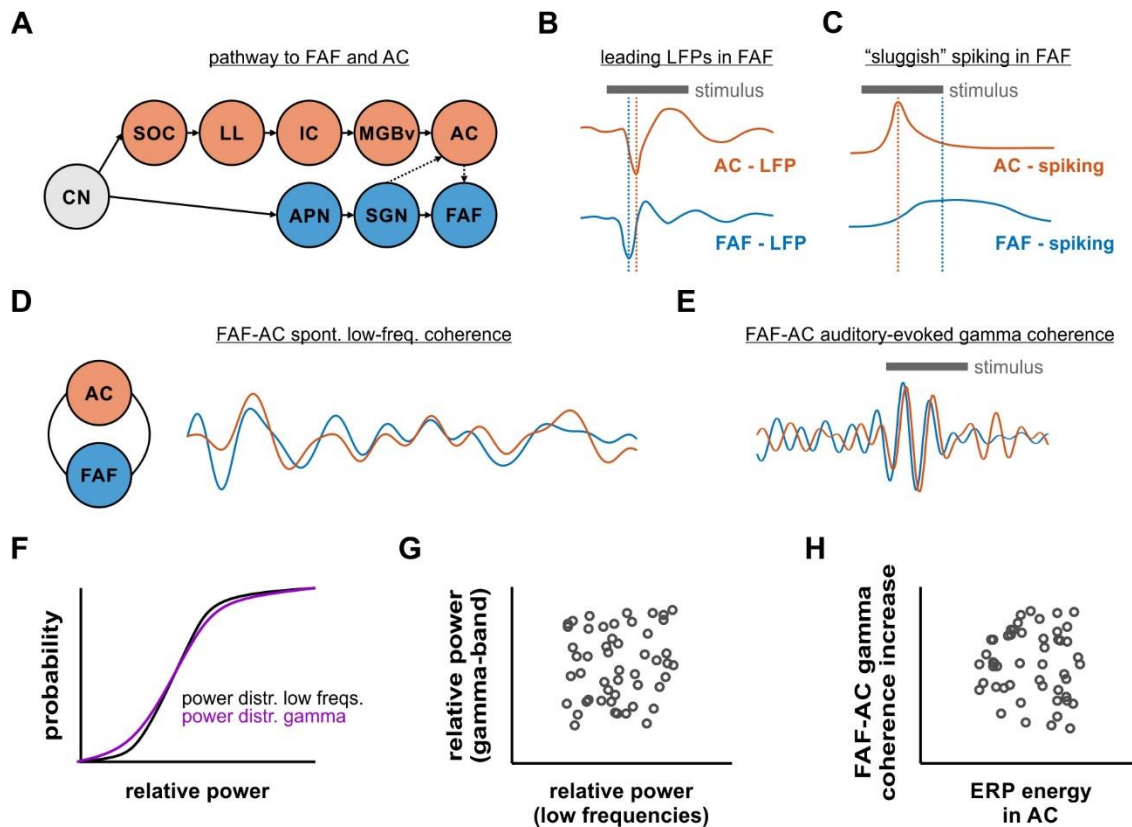


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1275 **Fig. 8. Information in rate codes of the FAF-AC circuit.** (A) Spiking activity in an exemplary
 1276 simultaneous recording from the FAF (blue) and the AC (at 450 μm , red). Note the difference in
 1277 the response patterns between the two structures. (B) Schematic representation of the joint code
 1278 used for information theoretic calculations. (C) Number of units used to calculate I_{rate} (left
 1279 heatmap; 1 unit per penetration), for each stimulus (natural call, syllable train at 5.28 Hz, syllable
 1280 train at 97 Hz, and Poisson syllable train) and depth in the AC (note that the first row in the heatmap
 1281 corresponds to the FAF). Only units that had at least 0.1 bit/s of information were considered. The
 1282 right heatmap depicts similar information, showing the number of pairs (FAF-AC spiking; 1 pair
 1283 per penetration) used to calculate I_{rate} per stimulus and AC depth. In this case, FAF is missing
 1284 because it is already part of each a pair. (D) Population I_{rate} in the FAF and across AC depths (note
 1285 that the leftmost values correspond to the FAF), for each of the four stimuli presented (left to right).
 1286 (E) I_{joint} (black) shown together with I_{rate} from AC (orange) and FAF (blue) units that conformed
 1287 the pairs, across stimuli (i.e. $I_{\text{rate_pair_AC}}$ and $I_{\text{rate_pair_FAF}}$). There were no consistent significant

1288 differences between I_{joint} and I_{rate} , when the latter was calculated for AC units (Wilcoxon signed
1289 rank tests, $p > 0.05$).

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1292 **Fig. 9. Functional coupling dynamics in the FAF-AC circuit of *C. perspicillata*.** (A) Representation
 1293 of the auditory pathway to the FAF and the AC (CN, cochlear nucleus; SOC, superior olivary
 1294 complex; LL, lateral lemniscus; IC, inferior colliculus; MGBv, ventral division of the medial
 1295 geniculate body of the thalamus; AC, auditory cortex; APN, anterolateral periolivary nucleus;
 1296 SGN, supragenulate nucleus of the thalamus; FAF, frontal auditory field). (B) Schematic
 1297 representation illustrating that stimulus-related LFPs in FAF lead relative to those in the AC (see
 1298 **Fig. 1**). (C) Fast LFP responses in FAF do not necessarily elicit fast spiking responses (schematic).
 1299 Neurons in the frontal region typically respond more "sluggishly" than their auditory cortical
 1300 counterparts. (D) FAF and AC were coherent in low-frequencies during spontaneous activity (i.e.
 1301 in the absence of sound stimulation). (E) During acoustic processing in passive listening animals,
 1302 low-frequency coherence was unaltered in the FAF-AC circuit, although there was an emergence
 1303 of auditory-evoked gamma band coherence in the network. Traces in panels D and E are based on
 1304 data shown in **Figs. 3** and **4**. Note that, for illustrative purposes, the temporal scales and amplitudes
 1305 in **D** and **E** are not comparable. (F) Distributions of power in low and gamma-band frequencies
 1306 were typically not significantly different from each other. However, there was very weak trial-by-
 1307 trial correlation between low-frequency and gamma power (**G**), as well as very low correlations

1308 between event-related potential (ERP) energy and gamma coherence increase across penetrations
1309 **(H)**.

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