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## **Noise-sensitive but more precise subcortical representations co-exist with robust cortical encoding of natural vocalizations**

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7 **robust cortical encoding of natural vocalizations**  
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12

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44

**Abstract**

45

46 Humans and animals maintain accurate sound discrimination in the presence of loud sources  
47 of background noise. It is commonly assumed that this ability relies on the robustness of  
48 auditory cortex responses. However, only a few attempts have been made to characterize  
49 neural discrimination of communication sounds masked by noise at each stage of the auditory  
50 system and to quantify the noise effects on the neuronal discrimination in terms of alterations  
51 in amplitude modulations. Here, we measured neural discrimination between communication  
52 sounds masked by a vocalization-shaped stationary noise from multiunit responses recorded  
53 in the cochlear nucleus, inferior colliculus, auditory thalamus, primary and secondary auditory  
54 cortex at several signal-to-noise ratios (SNR) in anesthetized male or female guinea pigs.  
55 Masking noise decreased sound discrimination of neuronal populations in each auditory  
56 structure, but collicular and thalamic populations showed better performance than cortical  
57 populations at each SNR. In contrast, in each auditory structure, discrimination by neuronal  
58 populations was slightly decreased when tone-vocoded vocalizations were tested. These  
59 results shed new light on the specific contributions of subcortical structures to robust sound  
60 encoding, and suggest that the distortion of slow amplitude modulation cues conveyed by  
61 communication sounds is one of the factors constraining the neuronal discrimination in  
62 subcortical and cortical levels.

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**Significance statement**

66 Dissecting how auditory neurons discriminate communication sounds in noise is a major goal  
67 in auditory neuroscience. Robust sound coding in noise is often viewed as a specific property  
68 of cortical networks although this remains to be demonstrated. Here, we tested the  
69 discrimination performance of neuronal populations at five levels of the auditory system in  
70 response to conspecific vocalizations masked by noise. In each acoustic condition, subcortical  
71 neurons better discriminated target vocalizations than cortical ones and in each structure, the  
72 reduction in discrimination performance was related to the reduction in slow amplitude  
73 modulation cues.

74

## Introduction

75  
76  
77 Understanding the neural mechanisms used by the auditory system to extract and represent  
78 relevant information for discriminating communication sounds in a variety of acoustic  
79 environments is a major goal in auditory neurosciences.

80 Several studies have prompted the view that the perceptual robustness mainly relies on the  
81 capacity of cortical neurons to extract invariant acoustic features (Narayan et al., 2007;  
82 Schneider and Woolley, 2013; Carruthers et al., 2015; Ni et al., 2017; Town et al., 2018), and  
83 it was proposed that this capacity is due to a larger adaptation of cortical cells to the noise  
84 statistics compared with subcortical cells (Rabinowitz et al., 2013). Indeed, in the cortical  
85 field L - the analogous of primary auditory cortex (A1) in bird - the percentage of correct  
86 neuronal discrimination between zebra-finch songs embedded in different types of acoustic  
87 maskers decreases proportionally to the target-to-masker ratio and parallels behavioral  
88 performance (Narayan et al., 2007). Also, consistent to behavioral data (for review see Verhey  
89 et al., 2003), the co-modulation of different frequency bands in background noise improved  
90 tone detection in noise of auditory cortical, thalamic and collicular neurons (Nelken et al.,  
91 1999; Las et al., 2005). Moreover, between-vowels discrimination performance of neuronal  
92 populations located in A1 resists to a large range of acoustic alterations (including changes in  
93 fundamental frequency, spatial location or level) and is similar to behavioral performance  
94 (Town et al., 2018).

95 The goal of the present study was to challenge this view by identifying the auditory structures  
96 responsible for this robust neural discrimination. Background noise has three disruptive  
97 effects on communication sounds (Noordhoek and Drullman, 1997; Dubbelboer and Houtgast,  
98 2007): it attenuates the power of their amplitude modulation components (AM, also called  
99 “temporal-envelope”; Houtgast and Steeneken, 1985; Ewert and Dau, 2000; Biberger and  
100 Ewert, 2017), corrupts their frequency modulation components (FM, also called “temporal  
101 fine structure”; Shamma and Lorenzi, 2013; Varnet et al., 2017) and introduces stochastic  
102 fluctuations in AM power which generate temporal irregularities (from bin to bin) in the  
103 signal temporal envelopes (Ewert and Dau, 2000). Here, electrophysiological recordings were  
104 collected from the cochlear nucleus up to a secondary auditory cortical area in anesthetized  
105 guinea pigs and the discrimination performance of neuronal populations was assessed for four  
106 utterances of the same vocalization category (the whistle, e.g. the guinea pig alarm call)  
107 presented against a vocalization-shaped stationary noise at three signal-to-noise ratios (SNRs:  
108 +10, 0, -10 dB). An increased discrimination performance may result from the specialization

109 of cortical responses for detecting crucial vocalization features (Wang et al., 1995; Wang and  
110 Kadia, 2001; Schneider and Woolley, 2013), whereas a decreased discrimination performance  
111 may result from the loss of spectro-temporal details promoting the categorization of sounds  
112 into auditory objects (Nelken and Bar-Yosef, 2008; Chechik and Nelken, 2012). Mutual  
113 information was used to determine if the temporal patterns of neuronal responses to the four  
114 vocalizations sufficiently differed to assign each response to a particular vocalization. The  
115 results obtained in noise were compared to the effects of a deterministic signal-processing  
116 scheme, namely a tone vocoder, which markedly altered the FM cues and progressively  
117 attenuated the AM cues (within 38 to 10 frequency bands). The AM spectra were computed at  
118 the output of simulated guinea pig auditory filters for each acoustic alteration. Our results  
119 suggest that, the attenuation of slow AM cues is one of the factors explaining the decrease in  
120 discrimination performance in cortical and subcortical structures. In addition, this study  
121 revealed that, for each acoustic distortion tested, the highest level of discrimination was found  
122 in subcortical structures, either at the collicular level (in masking-noise conditions) or at the  
123 thalamic level (in vocoder conditions).

124

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## Materials and Methods

### 128 **Subjects**

129 These experiments were performed under the national license A-91-557 (project 2014-25,  
130 authorization 05202.02) and using the procedures N° 32-2011 and 34-2012 validated by the  
131 Ethic committee N°59 (CEEA Paris Centre et Sud). All surgical procedures were performed  
132 in accordance with the guidelines established by the European Communities Council  
133 Directive (2010/63/EU Council Directive Decree).

134 Extracellular recordings were obtained from 47 adult pigmented guinea pigs (aged 3 to 16  
135 months, 36 males, 11 females) at five different levels of the auditory system: the cochlear  
136 nucleus (CN), the inferior colliculus (IC), the medial geniculate body (MGB), the primary  
137 (AI) and secondary (area VRB) auditory cortex. Animals, weighting from 515 to 1100 g  
138 (mean 856 g), came from our own colony housed in a humidity (50-55%) and temperature  
139 (22-24°C)-controlled facility on a 12 h/12 h light/dark cycle (light on at 7:30 A.M.) with free  
140 access to food and water.

141 Two to three days before each experiment, the animal's pure-tone audiogram was determined  
142 by testing auditory brainstem responses (ABR) under isoflurane anaesthesia (2.5 %) as  
143 described in Gourévitch et colleagues (2009). The ABR was obtained by differential  
144 recordings between two subdermal electrodes (SC25-NeuroService) placed at the vertex and  
145 behind the mastoid bone. A software (RTLab, Echodia, Clermont-Ferrand, France) allowed  
146 averaging 500 responses during the presentation of nine pure-tone frequencies (between 0.5  
147 and 32 kHz) delivered by a speaker (Knowles Electronics) placed in the animal right ear. The  
148 auditory threshold of each ABR was the lowest intensity where a small ABR wave can still be  
149 detected (usually wave III). For each frequency, the threshold was determined by gradually  
150 decreasing the sound intensity (from 80 dB down to -10 dB SPL). All animals used in this  
151 study had normal pure-tone audiograms (Gourévitch et al., 2009; Gourévitch and Edeline,  
152 2011; Aushana et al., 2018).

### 153 **Surgical procedures**

154 All animals were anesthetized by an initial injection of urethane (1.2 g/kg, i.p.) supplemented  
155 by additional doses of urethane (0.5 g/kg, i.p.) when reflex movements were observed after  
156 pinching the hind paw (usually 2-4 times during the recording session). A single dose of

157 atropine sulphate (0.06mg/kg, s.c.) was given to reduce bronchial secretions and a small dose  
158 of buprenorphine was administrated (0.05mg/kg, s.c.) as urethane has no antalgic properties.  
159 After placing the animal in a stereotaxic frame, a craniotomy was performed and a local  
160 anesthetic (Xylocain 2%) was liberally injected in the wound.

161 For auditory cortex recordings (area A1 and VRB), a craniotomy was performed above the  
162 left temporal cortex. The opening was 8 mm wide starting at the intersection point between  
163 parietal and temporal bones and 8-10 mm height. The dura above the auditory cortex was  
164 removed under binocular control and the cerebrospinal fluid was drained through the cisterna  
165 to prevent the occurrence of oedema.

166 For the recordings in MGB, a craniotomy was performed above the most posterior part of the  
167 MGB (8 mm posterior to Bregma) to reach the left auditory thalamus at a location where the  
168 MGB is mainly composed of its ventral, tonotopic, division (Redies et al., 1989; Edeline et  
169 al.; 1999, 2000; Anderson et al., 2007; Wallace et al., 2007).

170 For IC recordings, a craniotomy was performed above the IC and portions of the cortex were  
171 aspirated to expose the surface of the left IC. For CN recordings, after opening the skull above  
172 the right cerebellum, portions of the cerebellum were aspirated to expose the surface of the  
173 right CN (Paraouty et al., 2018).

174 After all surgeries, a pedestal in dental acrylic cement was built to allow an atraumatic  
175 fixation of the animal's head during the recording session. The stereotaxic frame supporting  
176 the animal was placed in a sound-attenuating chamber (IAC, model AC1). At the end of the  
177 recording session, a lethal dose of Exagon (pentobarbital >200 mg/kg, i.p.) was administered  
178 to the animal.

#### 179 **Recording procedures**

180 Data from multi-unit recordings were collected in 5 auditory structures, the non-primary  
181 cortical area VRB, the primary cortical area A1, the medial geniculate body (MGB), the  
182 inferior colliculus (IC) and the cochlear nucleus (CN). In a given animal, neuronal recordings  
183 were only collected in one auditory structure. Cortical extracellular recordings were obtained  
184 from arrays of 16 tungsten electrodes ( $\varnothing$ : 33  $\mu\text{m}$ ,  $<1 \text{ M}\Omega$ ) composed of two rows of 8  
185 electrodes separated by 1000  $\mu\text{m}$  (350  $\mu\text{m}$  between electrodes of the same row). A silver wire,  
186 used as ground, was inserted between the temporal bone and the dura matter on the  
187 contralateral side. The location of the primary auditory cortex was estimated based on the  
188 pattern of vasculature observed in previous studies (Edeline and Weinberger, 1993; Manunta



189 and Edeline, 1999; Edeline et al., 2001; Wallace et al., 2000). The non-primary cortical area  
190 VRB was located ventral to A1 and distinguished because of its long latencies to pure tones  
191 (Grimsley et al., 2012; Rutkowski et al., 2002). For each experiment, the position of the  
192 electrode array was set in such a way that the two rows of eight electrodes sample neurons  
193 responding from low to high frequency when progressing in the rostral-caudal direction [see  
194 examples of tonotopic gradients recorded with such arrays in figure 1 of Gaucher and  
195 colleagues (2012) and in figure 6A of Occelli and colleagues (2016)].

196 All the remaining extracellular recordings (in MGB, IC and CN) were obtained using 16  
197 channel multi-electrode arrays (NeuroNexus) composed of one shank (10 mm) of 16  
198 electrodes spaced by 110  $\mu\text{m}$  and with conductive site areas of  $177\mu\text{m}^2$ . The electrodes were  
199 advanced vertically (for MGB and IC) or with a  $40^\circ$  angle (for CN) until evoked responses to  
200 pure tones could be detected on at least 10 electrodes.

201 All thalamic recordings were from the ventral part of MGB (see above surgical procedures)  
202 and all displayed latencies  $< 9\text{ms}$ . At the collicular level, we distinguished the lemniscal and  
203 non-lemniscal divisions of IC based on depth and on the latencies of pure tone responses. We  
204 excluded the most superficial recordings (until a depth of  $1500\mu\text{m}$ ) and those exhibiting  
205 latency  $\geq 20\text{ms}$  in an attempt to select recordings from the central nucleus of IC (CNIC). At  
206 the level of the cochlear nucleus, the recordings were collected from both the dorsal and  
207 ventral divisions.

208 The raw signal was amplified 10,000 times (TDT Medusa). It was then processed by an RX5  
209 multichannel data acquisition system (TDT). The signal collected from each electrode was  
210 filtered (610-10000 Hz) to extract multi-unit activity (MUA). The trigger level was set for  
211 each electrode to select the largest action potentials from the signal. On-line and off-line  
212 examination of the waveforms suggests that the MUA collected here was made of action  
213 potentials generated by a few neurons at the vicinity of the electrode. However, as we did not  
214 use tetrodes, the result of several clustering algorithms (Pouzat et al., 2002; Quiroga et al.,  
215 2004; Franke et al., 2015) based on spike waveform analyses were not reliable enough to  
216 isolate single units with good confidence. Although these are not direct proofs, the fact that  
217 the electrodes were of similar impedance (0.5-1M $\Omega$ ) and that the spike amplitudes had  
218 similar values (100-300 $\mu\text{V}$ ) for the cortical and the subcortical recordings, were two  
219 indications suggesting that the cluster recordings obtained in each structure included a similar  
220 number of neurons.

221

222 **Acoustic stimuli**

223 Acoustic stimuli were generated using MATLAB (The Mathworks, Natick, MA), transferred  
224 to a RP2.1-based sound delivery system (TDT) and sent to a Fostex speaker (FE87E). The  
225 speaker was placed at 2 cm from the guinea pig's right ear, a distance at which the speaker  
226 produced a flat spectrum ( $\pm 3$  dB) between 140 Hz and 36 kHz. The stimulation was not  
227 purely monaural, but the animal's head and body largely attenuated binaural cues. Calibration  
228 of the speaker was made using noise and pure tones recorded by a Bruel & Kjaer microphone  
229 4133 coupled to a preamplifier B&K 2169 and a digital recorder Marantz PMD671.

230 The Time-Frequency Response Profiles (TFRP) were determined using 129 pure-tones  
231 frequencies covering eight octaves (0.14-36 kHz) and presented at 75 dB SPL. The tones had  
232 a gamma envelop given by  $\gamma(t) = \left(\frac{t}{4}\right)^2 e^{-\frac{t}{4}}$ , where  $t$  is time in ms. At a given level, each  
233 frequency was repeated eight times at a rate of 2.35 Hz in pseudorandom order. The duration  
234 of these tones over half-peak amplitude was 15 ms and the total duration of the tone was 50  
235 ms, so there was no overlap between tones.

236 A set of four conspecific vocalizations was used to assess the neuronal responses to  
237 communication sounds. These vocalizations were recorded from animals of our colony. Pairs  
238 of animals were placed in the acoustic chamber and their vocalizations were recorded by a  
239 Bruel & Kjaer microphone 4133 coupled to a preamplifier B&K 2169 and a digital recorder  
240 Marantz PMD671. A large set of whistle calls was loaded in the Audition software (Adobe  
241 Audition 3) and four representative examples of whistle were selected. As shown in figure  
242 1A, despite the fact the maximal energy of the four selected whistles was in the same  
243 frequency range (typically between 4 and 26 kHz), these calls displayed slight differences in  
244 their spectrogram and spectrum (Fig. 1A-B). In addition, their global temporal envelopes  
245 clearly differed (Fig. 1C). The four selected whistles were processed by three tone vocoders  
246 (Gnansia et al., 2009, 2010). In the following figures, the unprocessed whistles will be  
247 referred to as the original versions, and the vocoded versions as Voc38 (Voc20, Voc10  
248 respectively) for the 38-band (20-band, 10-band, respectively) vocoded whistles. In contrast  
249 to previous studies that used noise-excited vocoders (Nagarajan et al., 2002; Ranasinghe et  
250 al., 2012; Ter-Mikaelian et al., 2013), a tone vocoder was used here, because noise vocoders  
251 introduce random (i.e., non-informative) intrinsic temporal-envelope fluctuations distorting  
252 the crucial spectro-temporal modulation features of communication sounds (Shamma and  
253 Lorenzi, 2013; Kates, 2011; Stone et al., 2011).

254 Figure 1D displays the spectrograms of the 38-band vocoded (first column), the 20-band  
255 vocoded (second column) and the 10-band vocoded (third column) of the four whistles. The  
256 three vocoders differed only in terms of the number of frequency bands (i.e., analysis filters)  
257 used to decompose the whistles (38, 20 or 10 bands). The 38-band vocoding process is briefly  
258 described below, but the same principles apply to the 20-band or the 10-band vocoders. Each  
259 digitized signal was passed through a bank of 38 fourth-order Gammatone filters (Patterson,  
260 1987) with center frequencies uniformly spaced along a guinea-pig adapted ERB (Equivalent  
261 Rectangular Bandwidth) scale ranging from 20 to 35505 Hz (Sayles and Winter, 2010). In  
262 each frequency band, the temporal envelope was extracted using full-wave rectification and  
263 lowpass filtering at 64 Hz with a zero-phase, sixth-order Butterworth filter. The resulting  
264 envelopes were used to amplitude modulate sine-wave carriers with frequencies at the center  
265 frequency of the Gammatone filters, and with random starting phase. Impulse responses were  
266 peak-aligned for the envelope (using a group delay of 16 ms) and the temporal fine structure  
267 across frequency channels (Hohmann, 2002). The modulated signals were finally weighted  
268 and summed over the 38 frequency bands. The weighting compensated for imperfect  
269 superposition of the bands' impulse responses at the desired group delay. The weights were  
270 optimized numerically to achieve a flat frequency response. Figure 1E shows the long-term  
271 power spectrum of the 38-band, 20-band and 10-band vocoded whistles, and figure 1F shows  
272 their global temporal envelopes (which were relatively well preserved by the vocoding  
273 process).

274 The four whistles were also presented in a frozen noise ranging from 10 to 24,000 Hz. To  
275 generate this noise, recordings were performed in the colony room where a large group of  
276 guinea pigs were housed (30-40; 2-4 animals/cage). Several 4-seconds of audio recordings  
277 were added up to generate a "chorus noise", which power spectrum was computed using the  
278 Fourier transform. This spectrum was then used to shape the spectrum of a white Gaussian  
279 noise. The resulting vocalization-shaped stationary noise therefore matched the "chorus-  
280 noise" audio spectrum, which explains why some frequency bands were over-represented in  
281 the vocalization-shaped stationary noise. Figure 1G displays the spectrograms of the four  
282 whistles in the vocalization-shaped stationary noise with a SNR of +10 dB SPL, 0 dB SPL, -  
283 10 dB SPL. Figure 1H shows the long-term power spectrum of the four whistles at the +10  
284 dB, 0 dB and -10 dB SNR, and figure 1I shows their global temporal envelopes (which were  
285 severely altered at the 0 dB and -10 dB SNR).

286 Amplitude-modulation (AM) spectra were computed for the original, vocoded and noisy  
287 versions of each vocalization by decomposing each sound with the same bank of 50

288 gammatone filters than for the vocoding (spanning the range 0.1-50 kHz). The AM  
289 component (envelope) thus corresponds to the magnitude of the analytic signal, whereas the  
290 TFS corresponds to its unwrapped instantaneous phase.

291 For the AM spectrum, we analyzed the temporal envelope in each frequency band through a  
292 bank of AM filters using a method adapted from the human study by Varnet and colleagues  
293 (2017) for the guinea pigs' hearing range (1/3-octave wide first-order Butterworth bandpass  
294 filters overlapping at -3 dB, with center frequencies between 0.1 Hz and 410 Hz). The root-  
295 mean-square amplitude of the filtered output was multiplied by a factor of  $\sqrt{2}$ . For each AM  
296 filter, a modulation index was calculated by dividing the output by the mean amplitude of the  
297 AM component for the vocalization sample in the corresponding gammatone filter.

### 298 **Experimental protocol**

299 As inserting an array of 16 electrodes in a brain structure almost systematically induces a  
300 deformation of this structure, a 30-minutes recovering time lapse was allowed for the  
301 structure to return to its initial shape, then the array was slowly lowered. Tests based on  
302 measures of time-frequency response profiles (TFRPs) were used to assess the quality of our  
303 recordings and to adjust the electrodes' depth. For auditory cortex recordings (AI and VRB),  
304 the recording depth was 500-1000  $\mu\text{m}$ , which corresponds to layer III and the upper part of  
305 layer IV according to Wallace and Palmer (2008). For thalamic recordings, the NeuroNexus  
306 probe was lowered about 7mm below pia before the first responses to pure tones were  
307 detected.

308 When a clear frequency tuning was obtained for at least 10 of the 16 electrodes, the stability  
309 of the tuning was assessed: we required that the recorded neurons displayed at least three  
310 successive similar TFRPs (each lasting 6 minutes) before starting the protocol. When the  
311 stability was satisfactory, the protocol was started by presenting the acoustic stimuli in the  
312 following order: We first presented the 4 original whistles in their natural versions, followed  
313 by the vocoded versions with 38, 20 and 10 bands at 75 dB SPL. The same set of original  
314 whistles was then presented in the vocalization-shaped stationary noise presented at 65, 75  
315 and 85 dB SPL. Thus, the level of the original vocalizations was kept constant (75 dB SPL),  
316 and the noise level was increased (65, 75 and 85 dB SPL). In all cases, each vocalization was  
317 repeated 20 times. Presentation of this entire stimulus set lasted 45 minutes. The protocol was  
318 re-started either after moving the electrode arrays on the cortical map or after lowering the  
319 electrode at least by 300  $\mu\text{m}$  for subcortical structures.

320 **Data analysis**321 *Quantification of responses to pure tones*

322 The TFRP were obtained by constructing post-stimulus time histograms (PSTH) for each  
 323 frequency with 1 ms time bins. The firing rate evoked by each frequency was quantified by  
 324 summing all the action potentials from the tone onset up to 100 ms after this onset. Thus,  
 325 TFRP are matrices of 100 bins in abscissa (time) multiplied by 129 bins in ordinate  
 326 (frequency). All TFRPs were smoothed with a uniform 5x5 bin window.

327 For each TFRP, the Best Frequency (BF) was defined as the frequency at which the highest  
 328 firing rate was recorded. Peaks of significant excitatory response were automatically  
 329 identified using the following procedure: An excitatory peak in the TFRP was defined as a  
 330 contour of firing rate above spontaneous activity plus six times the standard deviation of the  
 331 spontaneous activity. Recordings without significant excitatory peak of responses or with only  
 332 inhibitory responses were excluded from the data analyses. The bandwidth (BW) was defined  
 333 as the sum of all peak widths in octaves. The response duration was the time difference  
 334 between the first and last spikes of the significant peaks. The response  
 335 strength was the total number of spikes falling in the significant peaks.

336 *Quantification of responses evoked by vocalizations*

337 The responses to vocalizations were quantified using two parameters: (i) The firing rate of the  
 338 evoked response, which corresponds to the total number of action potentials occurring during  
 339 the presentation of the stimulus minus spontaneous activity; (ii) the trial-to-trial temporal  
 340 reliability coefficient (named CorrCoef as in our previous studies: Gaucher et al., 2013a;  
 341 Huetz et al., 2014; Gaucher and Edeline, 2015; Aushana et al., 2018) which quantifies the  
 342 trial-to-trial reliability of the responses over the 20 repetitions of the same stimulus. This  
 343 index was computed for each vocalization: it corresponds to the normalized covariance  
 344 between each pair of spike trains recorded at presentation of this vocalization and was  
 345 calculated as follows:

$$346 \text{CorrCoef} = \frac{1}{N(N-1)} \sum_{i=1}^{N-1} \sum_{j=i+1}^N \frac{\sigma_{x_i x_j}}{\sigma_{x_i} \sigma_{x_j}}$$

347 where N is the number of trials and  $\sigma_{x_i x_j}$  is the normalized covariance at zero lag between  
 348 spike trains  $x_i$  and  $x_j$  where i and j are the trial numbers. Spike trains  $x_i$  and  $x_j$  were previously  
 349 convolved with a 10-msec width Gaussian window. Based upon computer simulations, we

350 have previously shown that this CorrCoef index is not a function of the neurons' firing rate  
 351 (Gaucher et al., 2013a).

352 *Quantification of mutual information from the responses to vocalizations*

353 The method developed by Schnupp and colleagues (2006) was used to quantify the amount of  
 354 information (Shannon, 1948) contained in the responses to vocalizations obtained with natural  
 355 vocoded and noise stimuli. This method allows quantifying how well the vocalization's  
 356 identity can be inferred from neuronal responses. Here, "neuronal responses" refer either to (i)  
 357 the spike trains obtained from a small group of neurons below one electrode (for the  
 358 computation of the individual Mutual Information,  $MI_{\text{Individual}}$ ), or to (ii) a concatenation of  
 359 spike trains simultaneously recorded under several electrodes (for the computation of the  
 360 population,  $MI_{\text{Population}}$ ). In both cases, the following computation steps were the same.  
 361 Neuronal responses were represented using different time scales ranging from the duration of  
 362 the whole response (firing rate) to a 1-ms precision (precise temporal patterns), which allows  
 363 analyzing how much the spike timing contributes to the information. As this method is  
 364 exhaustively described in Schnupp and colleagues (2006) and in Gaucher and colleagues  
 365 (2013a), we only present below the main principles.

366 The method relies on a pattern-recognition algorithm that is designed to "guess which  
 367 stimulus evoked a particular response pattern" (Schnupp et al., 2006) by going through the  
 368 following steps: From all the responses of a cortical site to the different stimuli, a single  
 369 response (test pattern) is extracted and represented as a PSTH with a given bin size (different  
 370 sizes were considered as indicated in the Results section). Then, a mean response pattern is  
 371 computed from the remaining responses (training set) for each stimulus class. The test pattern  
 372 is then assigned to the stimulus class of the closest mean response pattern. This operation is  
 373 repeated for all the responses, generating a confusion matrix where each response is assigned  
 374 to a given stimulus class. From this confusion matrix, the Mutual Information (MI) is given  
 375 by Shannon's formula:

$$376 \quad MI = \sum_{x,y} p(x,y) \times \log_2 \left( \frac{p(x,y)}{p(x) \times p(y)} \right)$$

377 where  $x$  and  $y$  are the rows and columns of the confusion matrix, or in other words, the values  
 378 taken by the random variables "presented stimulus class" and "assigned stimulus class".

379 In our case, we used responses to the 4 whistles and selected the first 280 ms of these  
 380 responses to work on spike trains of exactly the same duration (the shortest whistle being 280



381 ms long). In a scenario where the responses do not carry information, the assignments of each  
382 response to a mean response pattern is equivalent to chance level (here 0.25 because we used  
383 4 different stimuli and each stimulus was presented the same number of times) and the MI  
384 would be close to zero. In the opposite case, when responses are very different between  
385 stimulus classes and very similar within a stimulus class, the confusion matrix would be  
386 diagonal and the mutual information would tend to  $\log_2(4) = 2$  bits.

387 This algorithm was applied with different bin sizes ranging from 1 to 280 ms (see figure 2B  
388 for the evolution of MI with temporal precisions ranging from 1 to 40 ms).

389 The MI estimates are subject to non-negligible positive sampling biases. Therefore, as in  
390 Schnupp and colleagues (2006), we estimated the expected size of this bias by calculating MI  
391 values for “shuffled” data, in which the response patterns were randomly reassigned to  
392 stimulus classes. The shuffling was repeated 100 times, resulting in 100 MI estimates of the  
393 bias ( $MI_{\text{bias}}$ ). These  $MI_{\text{bias}}$  estimates are then used as estimators for the computation of the  
394 statistical significance of the MI estimate for the real (unshuffled) datasets: the real estimate is  
395 considered as significant if its value is statistically different from the distribution of  $MI_{\text{bias}}$   
396 shuffled estimates. Significant MI estimates were computed for MI calculated from neuronal  
397 responses under one electrode. The range of  $MI_{\text{bias}}$  values was very similar between auditory  
398 structures: depending on the conditions (original, vocoded, noisy vocalizations), it was from  
399 0.102 to 0.107 in the CN, from 0.107 to 0.110 in the IC, from 0.105 to 0.114 in the MGB,  
400 0.107 to 0.111 in A1 and from 0.106 to 0.116 in VRB. There was no significant difference  
401 between the mean  $MI_{\text{bias}}$  values in the different structures (unpaired t-test, all  $p > 0.25$ ).

402 The information carried by a group of recordings was estimated by the population MI  
403 ( $MI_{\text{Population}}$ ), using the same method described above: responses of several simultaneous  
404 multiunit recordings were concatenated and considered as a single pattern. To assess the  
405 influence of the group size of simultaneous multiunit recordings on the information carried by  
406 that group ( $MI_{\text{Population}}$ ), the number of sites used for computing  $MI_{\text{Population}}$  varied from 2 to  
407 the maximal possible size (which is equal to 16 minus the non-responsive sites). As the  
408 number of possible combinations could be extremely large ( $C_n^k$ , where  $k$  is the group size and  
409  $n$  the number of responsive sites in a recording session), a threshold was fixed to save  
410 computation time: when the number of possible combinations exceeded one hundred, 100  
411 combinations were randomly chosen, and the mean of all combinations was taken as the  
412  $MI_{\text{Population}}$  for this group size.

413 For the  $MI_{\text{Population}}$ , the values of bias were also computed: on average and for all sets of 9  
414 simultaneous recordings, it was 0.104 in the CN, 0.111 in the IC, 0.114 in the MGB, 0.107 in

415 AI and 0.106 in VRB. There was no significant difference between the mean  $MI_{\text{Population}}$  bias  
416 values in the different structures (unpaired t-test, all  $p > 0.20$ ).

417

418

419 *Statistics*

420 To assess the significance of the multiple comparisons (vocoding process: four levels;  
421 masking noise conditions: three levels; auditory structure: five levels), we used an analysis of  
422 variance (ANOVA) for multiple factors to analyze the whole data set. Post-hoc pair-wise tests  
423 were performed between the original condition and the vocoding or noisy conditions. They  
424 were corrected for multiple comparisons using Bonferroni corrections and were considered as  
425 significant if their p value was below 0.05. All data are presented as mean values  $\pm$  standard  
426 error (s.e.m.).

427

428



429

## Results

430 From a database of 2334 recordings collected in the five auditory structures, two criteria were  
431 used to include neuronal recordings in our analyses. A recording had to show significant  
432 responses to pure tones (see Methods) and an evoked firing rate significantly above  
433 spontaneous firing rate (200 ms before each original vocalization) for at least one of the four  
434 original vocalizations. Applying these two criteria led to the inclusion of 499 recordings in  
435 CN, 386 recordings in CNIC, 262 recordings in MGv, 354 recordings in A1 and 95 recordings  
436 in VRB. Table 1 summarizes the range of best frequencies, mean bandwidth, response  
437 duration and response strength obtained when testing pure tone responses in each auditory  
438 structure. In the following sections, the neuronal responses to the original vocalizations  
439 presented in quiet are compared across brain structures and the discrimination performance  
440 are described at the individual and population levels. The neuronal discrimination tested with  
441 tone-vocoded vocalizations and vocalizations presented against different levels of masking  
442 noise are described and compared next.

443

### 444 **Determination of optimal parameters for temporal analyses of spike trains in the five** 445 **auditory structures**

446

447 Before quantifying the neuronal discrimination performance in the five investigated  
448 structures, we first looked for the optimal parameters for analyzing the temporal patterns of  
449 spike trains in the five structures.

450 First, the CorrCoef index which quantifies the trial-to-trial temporal reliability, was computed  
451 with a Gaussian window ranging from 1 to 50 ms. As a general rule, the largest the Gaussian  
452 window, the largest the CorrCoef mean value whatever the structure was. We questioned if  
453 selecting a particular value for the Gaussian window influenced the between-structure  
454 differences in CorrCoef mean values. Based upon the responses to the original vocalizations,  
455 figure 2A shows that the relative ranking between auditory structures remained unchanged  
456 whatever the width of the Gaussian window was. Therefore, we kept the value of 10 ms for  
457 the Gaussian window (dashed line in Fig. 2A) as it was used in previous cortical studies  
458 (Huetz et al., 2009; Gaucher et al., 2013a; Gaucher and Edeline, 2015; Aushana et al., 2018).

459 Second, at the cortical level, it was previously showed that the maximal value of mutual  
460 information (MI) based on temporal patterns was obtained, on average, with a bin size of 8ms  
461 (Schnupp et al., 2006; Gaucher et al., 2013a). However, it has never been demonstrated that  
462 the same bin size was optimal at all levels of the auditory system. Figure 2B shows the

463 evolution of MI as a function of temporal precision ranging from 1 to 40 ms based on the  
464 responses to the original vocalizations. In our experimental conditions, and with our set of  
465 acoustic stimuli, the 8-ms temporal precision was found to be optimal for all auditory  
466 structures, in the original (dashed line in Fig. 2B), vocoded and noisy conditions (data not  
467 shown). Therefore, the MI value obtained for a temporal precision of 8 ms was subsequently  
468 used in our analyses.

469

#### 470 **Subcortical structures better discriminate the original vocalizations**

471

472 Figure 3A displays neuronal responses of two simultaneous multiunit recordings obtained at  
473 five levels of the auditory pathway (CN, CNIC, MGv, AI and VRB). The neuronal responses  
474 were strong and sustained in the CN and CNIC, more transient in MGv, phasic in AI and  
475 more diffuse in VRB. For most of the recordings, temporal patterns of response were clearly  
476 reproducible from trial-to-trial, but they differed from one vocalization to another both at the  
477 cortical and subcortical level. The PSTHs displayed in figure 3B show that at each level of the  
478 auditory system, the four whistles triggered distinct temporal patterns of responses.

479 Quantifications of evoked responses to original vocalizations over all the recordings are  
480 presented on figures 3C-F for each auditory structure. These analyses clearly pointed out large  
481 differences between the mean values of evoked firing rate, CorrCoef and MI quantified at the  
482 cortical vs. at the subcortical level. First, the evoked firing rate was significantly higher in the  
483 subcortical structures than in the cortex (unpaired t-test, lowest p value  $p < 0.001$ ). It was also  
484 higher in CN compared to the other subcortical structures (Fig. 3C). Second, the CorrCoef  
485 values were significantly higher in CNIC and MGv compared to AI and VRB (Fig. 3D),  
486 indicating that the trial-to-trial reliability of evoked responses was stronger in these structures  
487 than in CN, AI and VRB. Third, the  $MI_{\text{Individual}}$  values obtained at the subcortical level were  
488 significantly higher than at the cortical level (unpaired t-test, highest  $p < 0.001$  between the  
489 cortex and the other structures; Fig. 3E). At the subcortical level, the  $MI_{\text{Individual}}$  values were  
490 significantly higher in MGv than in CNIC and in CN (unpaired t-test,  $p < 0.01$ ) with the CN  
491 exhibiting the lowest MI values at the subcortical level. The  $MI_{\text{Individual}}$  values were also  
492 significantly lower in VRB than in AI ( $p = 0.037$ ). Recordings in MGv displayed the highest  
493  $MI_{\text{Individual}}$  mean values, suggesting that, on average, thalamic neurons discriminate better the  
494 four original whistles than the other auditory structures. As shown in figure 3G, in each  
495 auditory structure, high  $MI_{\text{Individual}}$  values were strongly correlated with high values of trial-to-  
496 trial temporal reliability (indexed by the CorrCoef value;  $0.77 < r < 0.88$ ;  $p < 0.001$ ). Finally,

497 MI was also computed based on the temporal patterns obtained from two to sixteen  
498 simultaneous multiunit recordings to determine whether the discrimination performance of  
499 neural networks confirm the results obtained at the individual (i.e., single recording) level.  
500  $MI_{Population}$  quantifies how well the four whistles can be discriminated based on temporal  
501 patterns expressed by neuronal populations distributed on the tonotopic map. The  $MI_{Population}$   
502 computed from 9 simultaneous multiunit recordings shows that neural populations in  
503 subcortical structures discriminate the four original whistles better than the cortical  
504 populations (unpaired t-test, highest p value  $p < 0.002$  between CN and VRB) without any  
505 statistical difference between the three subcortical structures (Fig. 3F).

506 We next investigated the diversity of the  $MI_{Individual}$  and  $MI_{Population}$  values obtained in the  
507 different structures. The distributions of  $MI_{Individual}$  values were plotted as a function of  
508 temporal precision for each structure (Fig. 4 A1-A5). It showed that whatever the temporal  
509 precision, there were more curves with high  $MI_{Individual}$  values in the subcortical structures  
510 than in the cortical areas (see red curves on Fig. 4 A1-A5). The examination of the evolution  
511 of the  $MI_{Population}$  as a function of the number of simultaneous multiunit recordings in the  
512 different structures revealed that the growth functions rapidly reached high values in all  
513 subcortical structures, whereas there were only a few of such curves in AI and VRB whatever  
514 the number of recordings considered (Fig. 4 B1-B5).

515 With a temporal resolution of 8 ms, we presented the cumulative percentages of neurons for  
516 the  $MI_{Individual}$  (Fig. 5A) and the  $MI_{Population}$  values (Fig. 5B) in each structure. Above a value  
517 of 1.5 bits (indicating that at least 3 stimuli can be discriminated), there were 39% of MGv  
518 neurons, 18% and 14% of the neurons in CNIC and CN respectively; but only 3.5% and 2%  
519 of the neurons in A1 and VRB respectively. This proportion was significantly higher in MGv  
520 than in CN and CNIC ( $p = 0.017$  and  $p = 0.04$ ) and was also significantly higher in subcortical  
521 structures compared with the cortical ones (all p values  $< 0.01$ ). The same conclusions were  
522 reached for the  $MI_{Population}$  values: More than 90% of the MGv neuronal populations were  
523 above 1.5 bits, 83 % and 75% of the populations in CNIC and CN respectively, whereas these  
524 populations represented less than 40% at the cortical level (36 % and 34% in A1 and VRB  
525 respectively).

526 Thus, both at the level of individual recordings, and at the population of simultaneous  
527 multiunit recordings, subcortical neurons are more accurate in discriminating the four original  
528 whistles than cortical ones.

529  
530

531

532 **Modest effects of tone vocoding**

533

534 Figure 6A displays rasters of recordings obtained in the five structures in response to the  
535 original and tone-vocoded vocalizations using 38 (Voc38), 20 (Voc20) and 10 (Voc10)  
536 frequency bands. As illustrated by the rasters and the PSTHs presented in figure 6B, in all  
537 structures, neurons still vigorously responded to the vocoded stimuli even for 10-band  
538 vocoded stimuli.

539 Figure 6C-F summarizes the vocoding effects on the four parameters quantifying neuronal  
540 responses. Compared to the responses to the original vocalizations, the evoked firing rate  
541 obtained in all structures in response to vocoded stimuli only showed modest variations (Fig.  
542 6C): apart from an increase in firing rate in the CN with the 38-band vocoded stimuli, a  
543 significant decrease in evoked firing rate in response to the 10-band vocoded vocalizations  
544 was only found at the subcortical level (for all subcortical structures, one-way ANOVA:  
545  $F_{CN(3,1995)}=22.6$ ;  $F_{CNIC(3,1543)}=8.85$ ;  $F_{MGv(3,1047)}=6.55$ ,  $p<0.001$ ; with post-hoc paired t tests,  
546  $p<0.05$ ), whereas there was no decrease in either AI or VRB. Vocoding also decreased the  
547 CorrCoef mean values in every structure except in VRB (Fig. 6D). This decrease was  
548 significant with the 10-band vocoded vocalizations in CN, MGv and in AI (one-way  
549 ANOVA:  $F_{CN(3,1930)}=26.48$ ;  $F_{MGv(3,889)}=7.7$ ;  $F_{AI(3,1125)}=3.42$ , highest p value,  $p<0.02$ ; with  
550 post-hoc paired t tests,  $p<0.05$ ). The decrease in CorrCoef value was already significant with  
551 20-band vocoded vocalizations in the CNIC (one-way ANOVA:  $F_{(3,1391)}=26.19$ ,  $p<0.001$ ; with  
552 post-hoc paired t tests,  $p<0.05$ ).

553 Similarly, vocoding decreased the  $MI_{Individual}$  values in each structure except in VRB (Fig.  
554 6E). Here too, the decrease was significant with the 10-band vocoded vocalizations in CN,  
555 MGv and AI (one-way ANOVA:  $F_{CN(3,1445)}=12.23$ ,  $F_{MGv(3,810)}=3.75$ ,  $F_{AI(3,720)}=3.59$ , highest p  
556 value,  $p<0.02$ ; with post-hoc paired t tests,  $p<0.05$ ) and it was already significant with 20-  
557 band vocoded vocalizations in the CNIC (one-way ANOVA:  $F_{CNIC(3,1231)}=13.17$ ,  $p<0.001$ ;  
558 with post-hoc paired t tests,  $p<0.05$ ). At the population level ( $MI_{Population}$ ), compared to the  
559 values obtained in response to the original vocalizations, the  $MI_{Population}$  values computed with  
560 the 10-band vocoded vocalizations were significantly lower in the subcortical structures (one-  
561 way ANOVA:  $F_{CN(3,127)}=6.46$ ,  $F_{CNIC(3,115)}=6.28$ ,  $F_{MGv(3,67)}=4.62$ , highest p value,  $p<0.005$ ; with  
562 post-hoc paired t tests,  $p<0.05$ ) but not at the cortical level (Fig. 6F). The evolution of  
563  $MI_{Population}$  as a function of the number of simultaneous multiunit recordings (Fig. 7 A-E)  
564 showed that in each subcortical structure, the curves rapidly reached high  $MI_{Population}$  values

565 (close to the maximal value of 2 bits) in each vocoding conditions, whereas in AI and VRB  
566 the curves slowly reached the maximum  $MI_{Population}$  values.

567 In conclusion, for the five auditory structures, the neuronal responses to 10-band vocoded  
568 vocalizations were slightly weaker, temporally less accurate and less discriminative than the  
569 responses to the original vocalizations. Nonetheless, on average, subcortical neurons still  
570 maintained the highest discrimination performance between tone-vocoded vocalizations, both  
571 at the level of individual recordings and at the population level.

572

### 573 **Pronounced effects of masking noise on neuronal discrimination**

574

575 The rasters presented in figure 8A illustrate the effects induced by presenting the original  
576 vocalizations against a vocalization-shaped stationary noise at three SNRs (+10, 0 and -10  
577 dB). As illustrated by the rasters and the PSTHs presented in figure 8B, masking noise  
578 attenuated neuronal responses at each level of the auditory system. However, the auditory  
579 structures were differentially affected by noise. The responses in the CNIC did not change up  
580 to a 0 dB SNR, decreasing only at a -10 dB SNR. This was not the case in the other auditory  
581 structures where the responses decreased either at a +10 dB SNR (MGv and CN) or at a 0 dB  
582 SNR (AI and VRB).

583 Figure 8C-F summarizes the effects of masking noise on the different parameters quantifying  
584 neuronal responses. Masking noise significantly reduced the evoked firing rate in each  
585 auditory structure already at the +10 dB SNR (Fig. 8C, one-way ANOVA:  $F_{CN(3,1995)}=309.33$ ,  
586  $F_{CNIC(3,1543)}=220.64$ ,  $F_{MGv(3,1047)}=155.07$ ,  $F_{AI(3,1415)}=96.27$ ,  $p<0.001$ ; with post-hoc paired t  
587 tests,  $p<0.05$ ), except in VRB.

588 At the subcortical level, masking noise strongly reduced the CorrCoef values in CN and MGv  
589 at the highest SNR (+10 dB) tested here (Fig. 8D; one-way ANOVA:  $F_{CN(3,1884)}=382.22$ ,  
590  $F_{MGv(3,791)}=155.82$ ,  $p<0.001$ ; with post-hoc paired t tests,  $p<0.05$ ) whereas in the CNIC, this  
591 reduction was significant only at the 0 dB SNR (one-way ANOVA:  $F_{CNIC(3,1357)}=154.12$ ,  
592  $p<0.001$ ; with post-hoc paired t tests,  $p<0.05$ ). At the cortical level, the CorrCoef values were  
593 significantly reduced in AI at the +10 dB SNR and in VRB at the 0 dB SNR (one-way  
594 ANOVA:  $F_{AI(3,1093)}=60.83$ ,  $F_{VRB(3,335)}=29.56$ ,  $p<0.001$ ; with post-hoc paired t tests,  $p<0.05$ ).

595 At the subcortical level, noise reduced the  $MI_{Individual}$  values but again, there was a marked  
596 difference between the CNIC and the other subcortical structures: the  $MI_{Individual}$  mean value  
597 in CN and MGv was significantly reduced at the +10 dB SNR (Fig. 8E; one-way ANOVA:  
598  $F_{CN(3,819)}=56.75$ ,  $F_{MGv(3,621)}=63.61$ ,  $p<0.001$ ; with post-hoc paired t tests,  $p<0.05$ ), whereas the

599  $MI_{\text{Individual}}$  value in the CNIC was only significantly reduced at the 0 dB SNR (one-way  
600 ANOVA:  $F_{(3,1078)}=32.08$ ,  $p<0.001$ ; with post-hoc paired t tests,  $p<0.05$ ). At the cortical level,  
601 noise significantly reduced the average  $MI_{\text{Individual}}$  in AI only at the -10 dB SNR (one-way  
602 ANOVA:  $F_{(3,649)}=9.49$ ,  $p<0.001$ ; with post-hoc paired t tests,  $p<0.05$ ) whereas the average  
603  $MI_{\text{Individual}}$  in VRB remained unchanged (Fig 8E).

604 The effects of masking noise on the network discrimination performance were quantified with  
605 the  $MI_{\text{Population}}$  (Fig. 8F). At the cortical level, there was a significant reduction of  $MI_{\text{Population}}$   
606 values only at the -10 dB SNR (one-way ANOVA:  $F_{A1(3,111)}=16.63$ ,  $F_{VRB(3,23)}=11.41$ ,  $p<0.001$ ;  
607 with post-hoc paired t tests,  $p<0.05$ ) whereas there was a significant decrease in CN already at  
608 the +10 dB SNR (one-way ANOVA:  $F_{CN(3,127)}=51.49$ ,  $p<0.001$ ; with post-hoc paired t tests,  
609  $p<0.05$ ). In MGv and CNIC, neuronal populations still displayed the highest discrimination  
610 performance although the decrease in  $MI_{\text{Population}}$  value was significant at the 0 dB SNR (one-  
611 way ANOVA:  $F_{MGv(3,67)}=41.59$ ,  $F_{CNIC(3,115)}=22.59$ ,  $p<0.001$ ; with post-hoc paired t tests,  
612  $p<0.05$ ).

613 Note that, in VRB, the CorrCoef and  $MI_{\text{Population}}$  were much more decreased in the noise  
614 conditions than in the vocoding conditions, suggesting that the lack of significant decreases in  
615 vocoding conditions was not a “floor effect” due to the low initial values.

616 The evolution of the  $MI_{\text{Population}}$  as a function of the number of simultaneous multiunit  
617 recordings in the different structures (Fig. 9A-E) revealed that regardless of the number of  
618 neurons considered, noise effects were similar up to the 0 dB SNR: the population curves in  
619 CNIC and MGv grew up relatively rapidly and reached higher values than the curves obtained  
620 in CN and in the two cortical areas. At the -10 dB SNR, the  $MI_{\text{Population}}$  from the CNIC  
621 remained higher (regardless of the number of neurons considered) than in the other structures;  
622 whereas there was no increase of the  $MI_{\text{Population}}$  with the number of neurons in VRB.

623 One puzzling result came from the fact that on average, the values of  $MI_{\text{Individual}}$  and  
624  $MI_{\text{Population}}$  decreased more for CN recordings than for the two subsequent subcortical relays.  
625 However, at least 20% of the CN recordings at the +10 dB SNR maintained  $MI_{\text{Individual}}$  values  
626 above 1 bit (Fig. 10A, red curves) and  $MI_{\text{Population}}$  values above 1.5 bits (Fig. 10C, red curves),  
627 suggesting that a sub-population of CN neurons were still able to send information about the  
628 vocalization identity at higher brainstem centers. This also suggests that the discrimination  
629 performed by a group of a fixed number of neurons deteriorates with noise faster in the CN  
630 and consequently, more CN neurons are necessary to obtain an equivalent amount of  
631 information observed in CNIC.



632 The distributions of the TFRP parameters (best frequency, bandwidth, response duration,  
633 response strength) from this specific sub-population of CN neurons did not differ from the  
634 neurons exhibiting  $MI_{\text{Individual}}$  values below 1 bit at the +10 dB SNR in terms of best  
635 frequency and bandwidth but significantly differ in terms of response duration and response  
636 strength (chi-square tests;  $p < 0.05$ , Fig. 10B). More precisely, the CN recordings exhibiting  
637 higher  $MI_{\text{Individual}}$  values at +10 dB SNR had longer duration responses and stronger evoked  
638 firing rate to pure tones.

639 A more general question is to evaluate whether the TFRP characteristics in the different  
640 auditory structures (see examples in Fig. 11A) influenced the noise effects quantified by the  
641  $MI_{\text{Individual}}$  values (Fig. 11B-C). As indicated in figure 11, there was no relationship between  
642 the best frequency values and the changes in  $MI_{\text{Individual}}$  values (Fig. 11B) and no relationship  
643 between the frequency bandwidth and the changes in  $MI_{\text{Individual}}$  values (Fig. 11C). Thus, in all  
644 structures, the noise-induced alterations in  $MI_{\text{Individual}}$  values seem to be independent from the  
645 characteristics of pure tone responses.

646 To summarize, masking noise differently impacted the neurons' discrimination performance  
647 at the subcortical and cortical levels. Although cortical neurons were more resistant to  
648 changes in noise level, the thalamic and collicular neurons maintained higher MI values, with  
649 the CNIC neurons displaying the highest discrimination performance both at the individual  
650 and population level in the most challenging condition (i.e., at the -10 dB SNR).

651

### 652 **Alteration of slow amplitude modulations as one of the factors explaining the changes in** 653 **neuronal discrimination**

654

655 Masking noise produced spectro-temporal degradations: it reduced the AM cues in the  
656 different audio-frequency bands, introduced irrelevant envelope fluctuations and altered the  
657 temporal fine structure (TFS) of the sound. Tone vocoding removed almost all the TFS but  
658 also progressively filtered out the fast AM. As a vast literature demonstrated that slow AM  
659 cues are crucial for speech understanding in normal and degraded conditions (Houtgast and  
660 Steeneken, 1985; Drullman et al., 1994, 1995; Shannon et al., 1995; Dubbelboer and  
661 Houtgast, 2007; Jorgensen and Dau, 2011), we quantified the alterations of AM cues (due to  
662 masking noise and to vocoding) and looked for potential relationships with the alterations in  
663 neural discrimination ( $MI_{\text{Population}}$ ) in the five structures.

664 The AM spectra obtained in vocoding and noise conditions showed that the AM cues were  
665 attenuated compared to the original condition (Fig. 12A). The +10 dB SNR condition

666 produced a flattening of the AM modulation spectrum, which was further accentuated in the 0  
667 dB and -10 dB SNR conditions. In these two most degraded conditions, noise also introduced  
668 non-relevant fluctuations at high rates. In contrast, vocoding preserved the general shape of  
669 the AM spectra while progressively filtering out the AM fluctuations.

670 We investigated the relationships between these degradations of AM cues and neural  
671 discrimination ( $MI_{\text{Population}}$ ) in the five structures for each experimental condition (Fig. 12B).  
672 More precisely, for all conditions, figure 12B shows the changes in  $MI_{\text{Population}}$  for each  
673 auditory structure as a function of the attenuation of AM cues (computed as the mean  
674 modulation index between 1 and 20 Hz). Figure 12B reveals that in all structures other than  
675 the CN,  $MI_{\text{Population}}$  is barely affected as long as the reduction of the AM index ( $\Delta$ modulation  
676 index) remains lower than 25%; beyond this limit, the  $MI_{\text{Population}}$  is reduced (i.e., at the 0 dB  
677 and -10 dB SNR). The straightforward conclusion is that the reduction of slow AM cues is  
678 one of the factors controlling the decrease in  $MI_{\text{Population}}$  at the cortical and subcortical levels.  
679 In the cochlear nucleus, the decrease on the  $MI_{\text{Population}}$  is much larger than in the other  
680 structures, suggesting that the alteration of AM cues has more impact on the  $MI_{\text{Population}}$  at the  
681 most peripheral level. Alternatively, one should keep in mind that the neuronal discrimination  
682 in noise can be based upon other acoustic cues such as the FM cues (in particular pitch cues),  
683 spectral regularity and harmonicity cues, and the simultaneous rising slope of energy across  
684 channels. Thus, in the cochlear nucleus, but also in the other structures, the strong decrease in  
685  $MI_{\text{Population}}$  can potentially result from alterations of one, or several, of these parameters.

686 Dissecting the contributions of each of these parameters to neuronal discrimination and its  
687 decrease in degraded conditions will require manipulations of controlled stimuli in  
688 independent conditions. Confirming that the slow AM cues are the main factor for  
689 discrimination in degraded conditions could theoretically be achieved by keeping the exact  
690 same AM cues and modifying only one of the acoustic parameter listed above. Using a  
691 computational model of the peripheral auditory system will help to estimate the respective  
692 representations of the envelope and temporal fine structure after acoustic degradations (Moon  
693 et al., 2014; Wirtzfeld et al., 2017). For example, the search for "equivalent" experimental  
694 conditions in terms of amounts of neural degradation of AM and FM cues could be performed  
695 by using the FAME vocoder (Zeng et al., 2005) to alter systematically AM and FM  
696 parameters (i.e., cutoff frequency, modulation strength, modulation phase) of the  
697 vocalizations used as stimuli. The results of this type of experiments should also be  
698 generalized with other categories of guinea pig calls, other types of communication sounds  
699 from other species and should included in other types of masking noises.



## Discussion

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702 Here, we demonstrated that for each acoustic distortion, subcortical neurons displayed the  
703 highest level of discrimination performance of natural vocalizations, either at the collicular  
704 level (in masking noise conditions) or at the thalamic level (in vocoder conditions). More  
705 precisely, background noise markedly reduces neural discrimination performance in all  
706 auditory structures with larger effects in the cochlear nucleus, whereas the vocoder induced  
707 little effect in each auditory structure. Interestingly, the discrimination performance of cortical  
708 neurons was less impacted making these neurons more robust to all acoustic alterations.  
709 Moreover, comparison of neural data collected in response to noisy versus vocoded  
710 vocalizations suggests that the transmission of slow ( $< 20$  Hz) amplitude modulation  
711 information is one of the factors contributing to the neural discrimination decrease in noise at  
712 the cortical and subcortical levels.

713

714 **Subcortical structures represent natural vocalizations more precisely than primary and**  
715 **non-primary cortical areas**

716

717 In contrast with previous cortical studies, which have quantified the discrimination between  
718 calls that belong to different categories making the discrimination easy for cortical neurons  
719 (Narayan et al., 2006, 2007; Ter-Mikaelian et al., 2013; Ni et al., 2017), we used four  
720 vocalizations that belong to the same category making the discrimination more difficult for  
721 cortical neurons. We showed that on average subcortical populations discriminated the  
722 original vocalizations better than cortical populations. Moreover, smaller populations of  
723 subcortical neurons compared to cortical ones were sufficient to discriminate between the  
724 stimuli used in this study. These results corroborate the finding by Chechik and colleagues  
725 (2006) that the MGB and AI responses contain 2-to-4 fold less information than the responses  
726 of IC neurons. Here, the discrimination performance in MGv was closer than the ones  
727 displayed by the other subcortical structures. A potential explanation is that Chechik and  
728 colleagues (2006) recorded from all MGB divisions, including the medial and dorsal  
729 divisions, whereas our thalamic recordings were limited to MGv and exhibited tonic  
730 responses to vocalizations similar to those observed in the CNIC and the CN (Fig. 3A and  
731 5A). The stimulus sets also differ, as we used four utterances of the same category (the  
732 Whistle), whereas Chechik and colleagues (2006) used three birds' chirps and variants of  
733 these stimuli leading potentially to an easier classification between groups of stimuli

734 compared to our protocol. An interesting result was that the optimal bin size for computing  
735 MI was similar for all structures (8 ms bin, Fig. 2B). Importantly, with a smaller or a larger  
736 bin, the mutual information would have been underestimated, but this would not have  
737 changed the differences reported here: whatever the bin size, subcortical neurons will still  
738 discriminate better the original vocalizations than the cortical areas (Fig. 2B). Potentially, the  
739 optimal bin size depends more upon the stimuli durations than upon the auditory structure.  
740 When computing mutual information from IC, MGB and A1 neuronal responses, Chechik and  
741 colleagues (2006) usually found an optimal bin size of 4 ms, different from ours, probably  
742 because their stimulus durations are shorter than our stimuli (67-111 ms vs. to 280-363 ms  
743 here). Recently, we also found shorter optimal bin size when computing MI with shorter (12-  
744 65 ms) communication sounds (Royer et al., 2019).

745 Our original stimuli differed in terms of temporal envelope and, as a consequence, the most  
746 efficient way to discriminate them is probably to follow the time course of AM cues. It is well  
747 known that when progressing from the lower to the upper stages of the auditory system, the  
748 neurons' ability to follow AM cues considerably changes (Joris et al, 2004; Escabi and Read,  
749 2005). Brainstem neurons phase-lock on AM modulations up to hundreds of Hertz (Frisina et  
750 al., 1990; Rhode and Greenberg, 1994), whereas thalamic neurons do so for a few tens of  
751 Hertz (Creutzfeldt et al., 1990; Preuss and Müller-Preuss, 1990) and cortical neurons for even  
752 lower rates (Gaese and Ostwald, 1995; Schreiner and Urbas, 1998). As a consequence,  
753 subcortical neurons, (but not cortical ones) can follow the largest and fastest AM cues (7-15  
754 Hz) contained in the original vocalizations (see the peak of the black curve in AM spectra,  
755 Fig. 12A). This likely explains why subcortical neurons better discriminate the original  
756 stimuli both at the individual and population levels. Cortical neurons only follow the weakest  
757 and slowest AM cues (1-5 Hz) of the original vocalizations, which potentially explains why  
758 cortical neurons weakly discriminate the original stimuli and tend to encode them as a single  
759 category (Mesgarani et al., 2014b).

760

761 **Alterations of slow amplitude modulation cues is one of the factors explaining the**  
762 **changes in cortical and subcortical discrimination**

763

764 Previous studies using vocoded vocalizations reported that cortical responses were not  
765 drastically reduced even with two frequency bands (Nagarajan et al., 2002; Ranasinghe et al.,  
766 2012; Ter-Mikaelian et al., 2013; Aushana et al., 2018). At the level of AI, studies have

767 pointed out the relationships between the noise impact on the cortical and behavioral  
768 discrimination performance. In bird field L (homologous to AI), neuronal responses to song  
769 motifs were strongly reduced by three types of masking noises, and the neural discrimination  
770 performance was progressively reduced when the SNR decreased, in parallel with the  
771 behavioral performance (Narayan et al., 2007). Our VRB results are reminiscent of those  
772 obtained in area NCM (homologous to a secondary area) where feed-forward inhibition  
773 allowed the emergence of invariant neural representations of target songs in noise conditions  
774 (Schneider and Woolley, 2013). Similarly to the results by Ranasinghe and colleagues (2012),  
775 our IC neuronal responses were found to be resistant to drastic spectral degradations.  
776 Only one study directly compared the impact of vocoding and masking noise on cortical  
777 responses to vocalizations (Nagarajan et al., 2002). In this study, auditory cortex responses  
778 were robust to spectral degradations even in response to 2-band vocoded vocalizations. Also,  
779 broadband white noise reduced neuronal responses at 0 dB SNR. Last, temporal-envelope  
780 degradations strongly reduced the evoked firing rate and the neural synchronization to the  
781 vocalization envelope. Importantly, band-pass filtering the vocalizations between 2-30 Hz did  
782 not reduce firing rate and neural synchronization to the vocalization envelope. This is in  
783 agreement with the results in our conditions: when the  $\Delta$ modulation index (computed between  
784 1 and 20 Hz) revealed modest AM alterations, there was little effect on the neuronal  
785 discrimination, but when the AM alterations reached about 20-30% or more, the neuronal  
786 discriminations were reduced (Fig. 12B). Thus, our results are consistent with the hypothesis  
787 that one of the factors constraining auditory discrimination at the cortical and subcortical level  
788 is the fidelity of transmission and processing of slow AM cues.

789 When quantifying how different noise levels alter neuronal coding in the auditory system, it  
790 was found that the neural representation of natural sounds becomes progressively independent  
791 of the level of background noise from the auditory nerve to the IC and AI (Rabinowitz et al.,  
792 2013). It was proposed that this tolerance to background noise results from an adaptation to  
793 the noise statistics, which is more pronounced at the cortical than at the subcortical level. In  
794 agreement with this study, we found that populations of cortical neurons (AI and VRB) were  
795 more resistant to noise than subcortical ones. However, we did not observe a monotonic  
796 evolution of resistance to noise in the auditory system: at the subcortical level, the  
797 discrimination performance of CN neuronal populations drastically dropped as early as +10  
798 dB SNR, the populations of CNIC neurons maintained the highest discrimination performance  
799 even at the -10 dB SNR, those of thalamic ones largely decreased at 0 dB SNR, whereas

800 cortical neurons showed the lowest discrimination performance at all SNRs but were more  
801 robust to noise. In the IC, previous work showed that background noise changes the shape of  
802 the temporal modulation transfer function of individual neurons from bandpass to lowpass  
803 (Lesica and Grothe, 2008). The CNIC is a massive hub receiving probably the highest  
804 diversity of inhibitory and excitatory inputs (Malmierca, 2004; Ayala et al., 2016) and  
805 potentially the large diversity of these inputs allows this structure to extract crucial temporal  
806 information about the stimulus temporal envelope, even at relatively low SNR.

807

### 808 **Limitations of the study**

809

810 We previously did not find evidence for higher cortical discrimination in awake animals  
811 compared with anesthetized animals (Huetz et al., 2009): with normal and reversed whistle  
812 stimuli, the percentage of cortical cells with significant MI values was higher in anesthetized  
813 (71%) than in awake animals (44%, Table 1 in Huetz et al., 2009). In addition, the Hmax  
814 value (equivalent of MI) was higher in anesthetized than in awake animals (0.38 vs. 0.24,  
815 Table 2 in Huetz et al., 2009). Last, the trial-to-trial temporal reliability of cortical cells to  
816 whistle calls was not different in anesthetized and awake guinea pigs (anesthetized 0.48 vs.  
817 awake 0.42; Fig. 8 in Huetz et al., 2009). A recent study (Town et al., 2018) revealed that the  
818 cortical discrimination performance between vowels observed in awake animals using  
819 acoustic degradations were similar in anesthetized animals (Bizley et al., 2009). Therefore,  
820 based on these two studies, the cortical discrimination performance can only be slightly lower  
821 or similar in awake compared to anesthetized animals. At the subcortical level, it seems that  
822 there is not a large difference between the phase-locking properties of neurons in anesthetized  
823 and awake animals (Joris et al., 2004). Temporal properties of IC neurons are only mildly  
824 affected by anesthesia (Ter-Mikaelian et al., 2007), indicating that collicular neurons will still  
825 be far better than cortical ones to follow the 10-20 Hz temporal cues contained in the four  
826 vocalizations. Together, these studies suggest that the hierarchy between cortical and  
827 subcortical structures in discriminating communication sounds should be more pronounced or  
828 should remained the same in awake animals.

829 Another limitation of the present study lies in the use of a limited set of stimuli that is  
830 restricted to the four same whistles. However, the four whistles used here were clearly  
831 representative of our whole database of whistles in terms of frequency range, duration, range  
832 of frequency and amplitude modulations. Changing the four whistles from one recording to  
833 another can help generalizing the results, but the main advantage of using exactly the same  
834 four whistles is that from one recording to the next, and from one structure to another, we

835 were sure that the same acoustic cues were available for the neural discrimination. However,  
836 the whistles are a subset of the guinea pig repertoire, and therefore the present results may not  
837 generalize to other communication sounds, and larger sets of stimuli should be used to  
838 confirm that the slow AM cues control the neural discrimination. Even if amplitude  
839 modulations seem the main cues for speech understanding (Drullman et al., 1994; Shannon et  
840 al., 1995), other factors (the pitch, the frequency modulation, the harmonicity cues) can also  
841 be involved.

842 As our results are based on multiunit recordings, we do not know whether the same number of  
843 neurons were present in the cluster recordings from the different structures, and whether the  
844 individual discrimination performance of the cell types found in each structure are equivalent.  
845 On the other hand, the MI evaluated here is the reflection of a local computation performed  
846 by a small population of individual neurons, which gives us a good estimation of the whole  
847 discrimination performance of a given structure.

848

#### 849 **Functional implications**

850 In humans, speech sounds (such as phonemes) showing similar acoustic properties trigger  
851 similar responses and are represented as a single category in the superior temporal gyrus  
852 (Mesgarani et al., 2014b). As already proposed by Chechick and Nelken (2012), auditory  
853 cortex neurons extract abstract auditory entities rather than detailed spectro-temporal features.  
854 Obviously, this urges to define the acoustic features that form a category of auditory objects.  
855 It is relatively easy to delimit broad categories such as environmental sounds, animal  
856 vocalizations, music and speech (Gygi and Shafiro, 2013; Gygi et al., 2004, 2007; Woolley et  
857 al., 2005; Singh and Theunissen, 2003) in terms of modulation cues, but within these  
858 categories, defining invariant features is a difficult task. Here, the use of vocalizations  
859 belonging to the same category of the guinea pig repertoire, i.e. “whistles”, may explain both  
860 the relatively poor discrimination abilities of cortical neurons compared to subcortical ones  
861 and the robustness of cortical responses to vocoding and background noise.

862 From the present study, it appears that the subcortical structures engage significantly more  
863 neurons (20-40%) with high discrimination performance than the cortical areas (2-3% see Fig.  
864 5A), confirming that the neural code is rather sparse at the cortical level (Hromádka et al.,  
865 2008), which might not be the case at the subcortical level. However, it is also possible that  
866 top-down projections coming from auditory cortex and reaching the thalamus, inferior  
867 colliculus and cochlear nucleus (Jacomme et al., 2003; Malmierca and Ryugo, 2011)

868 influence the neural discrimination at the subcortical level, especially in awake, behaving,  
869 animals. Thus, we can envision that in behaving animals, learning-induced cortical plasticity  
870 also contributes to enhancing the subcortical neural discrimination via the corticofugal  
871 projections. Further studies are required to determine to what extent these subcortical  
872 representations influence auditory abilities in animals and humans.  
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	CN	Lemniscal pathway			Non-lemniscal pathway
		CNIC	MGv	A1	VRB
Number of animals	10	11	10	11	5
Number of recordings tested	672	478	448	544	192
TFRP only	560	421	285	455	126
TFRP and significant response to at least one vocalization	499	386	262	354	95
TFRP quantifications					
BF Range (kHz): min-max	0.18 - 18	0.34 - 36	0.33 - 33	0.14 - 36	0.67 - 36
Mean bandwidth (octave)	3.91	2.88	4.16	2.07	1.79
Mean response duration (ms)	26.83	35.37	17.31	43.73	44.83
Response strength (AP/sec)	77.23	82.25	41.61	37.69	19.97

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**Table 1.** Summary of the number of animals, number of selected recordings and TFRP quantifications in each structure.

## Figure Legends

1100

1101

1102 **Figure 1. Spectrograms, spectra and temporal envelopes of the acoustic stimuli. A-C.**  
 1103 Spectrograms (A), spectra (B) and temporal envelopes (C) of the four original whistles used  
 1104 in this study. **D-F.** From left to right, spectrograms (D), spectra (E) and temporal envelopes  
 1105 (F) of the four vocoded whistles using 38, 20 and 10 frequency bands. **G-I.** From left to right,  
 1106 spectrograms (G), spectra (H) and temporal envelopes (I) of the four original whistles  
 1107 embedded in a vocalization-shaped stationary noise at three SNRs (+10, 0 and -10 dB).

1108

1109 **Figure 2. Evolution of the CorrCoef and MI mean values as a function of temporal**  
 1110 **precision in each structure. A.** The trial-to-trial temporal reliability, quantified by the  
 1111 CorrCoef, was calculated from responses to original vocalizations with a width Gaussian  
 1112 window varying from 1 to 50 ms in CN (in black), CNIC (in green), MGv (in orange), A1 (in  
 1113 blue) and VRB (in purple). In our study, a 10-ms width Gaussian window (dashed black line)  
 1114 was selected for the data analysis in each structure. **B.** Mutual information (in bits) was  
 1115 calculated from neuronal responses to original vocalizations with a bin size varying from 1 to  
 1116 40 ms in CN (in black), CNIC (in green), MGv (in orange), A1 (in blue) and VRB (in purple).  
 1117 In this study, the value of 8 ms was selected for the data analysis because in each structure,  
 1118 the MI value was maximal (dashed black line). This hold true also in the different conditions  
 1119 of acoustic alterations, both in noise and vocoded conditions (data not shown).

1120

1121 **Figure 3. Subcortical neurons discriminate better the original vocalizations than cortical**  
 1122 **neurons. A.** From bottom to top, neuronal responses were recorded in CN, CNIC, MGv, A1  
 1123 and VRB simultaneously under 16 electrodes but only two are represented here, with  
 1124 alternated black and red colors. Each dot represents the emission of an action potential and  
 1125 each line corresponds to each presentation of one of four original whistles. The grey part of  
 1126 rasters corresponds to evoked activity. For each example, the values of the best frequency (BF  
 1127 in kHz) and of the bandwidth (BW in octave) obtained when testing the responses to pure  
 1128 tones are indicated in the left side. The waveforms of the four original whistles are displayed  
 1129 under the rasters. **B.** Peristimulus time histograms (PSTHs) of each neuronal response  
 1130 presented in A. For each neuronal recording, the four PSTHs of the four original whistles  
 1131 have been overlaid.

1132 **C-F.** The panels show the mean values of **(C)** the evoked firing rate (spikes/sec), **(D)** the trial-  
 1133 to-trial temporal reliability quantified by the CorrCoef value, **(E)** the neuronal discrimination  
 1134 assessed by the mutual information (MI) computed at the level of the individual recording  
 1135 ( $MI_{\text{Individual}}$ , bits) and **(F)** the neuronal discrimination at the population level ( $MI_{\text{Population}}$ , bits)  
 1136 with populations of 9 simultaneous multiunit recordings obtained with the four original  
 1137 vocalizations in CN (in black), CNIC (in green), MGv (in orange), A1 (in blue) and VRB (in  
 1138 purple). The evoked firing rate corresponds to the total number of action potentials occurring  
 1139 during the presentation of the stimulus minus spontaneous activity (200 ms before each  
 1140 acoustic stimulus). In each structure, error bars represent the SEM of the mean values and  
 1141 black lines represent significant differences between the mean values (unpaired  $t$  test,  
 1142  $p < 0.05$ ). The evoked firing rate decreases from the CN to VRB but both the trial-to-trial  
 1143 temporal reliability (CorrCoef) and the discrimination performance (MI) reach a maximal  
 1144 value in MGv. Note also that at the population level, all the subcortical structures discriminate  
 1145 better the original vocalizations than cortical areas. **G.** Scatter plots showing in each structure,  
 1146 the strong correlations ( $0.77 < r < 0.88$ ) between the CorrCoef and the  $MI_{\text{Individual}}$  (bits) values  
 1147 obtained in original conditions.

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1150 **Figure 4. Diversity of neuronal discrimination performance in quiet for each structure**  
 1151 **at the individual and population level.**

1152 **A. Neural discrimination performance in response to original vocalizations in each**  
 1153 **auditory structure.** Waterfall plots show the mutual information (MI, *bits*) as a function of  
 1154 temporal resolution (1 to 256 ms) for the selected recordings in CN (*A1*), CNIC (*A2*), MGv  
 1155 (*A3*), A1 (*A4*) and VRB (*A5*). In each structure, the units are ranked by the mean MI value  
 1156 obtained for all bin sizes. Note that there was a larger proportion of neurons with high values  
 1157 of MI (close from the maximal value of 2 bits) in MGv, CNIC and CN (*red curves*) compared  
 1158 to a much lower proportion in the cortical areas AI and VRB.

1159 **B. Population information quickly reaches high values with simultaneous multiunit**  
 1160 **recordings at the subcortical but not cortical level.** For each auditory structure, each thin  
 1161 line represents a particular case of simultaneous recording with a maximum number of  
 1162 electrodes (maximum 16 simultaneous multiunit recordings) and each thick line represents the  
 1163 mean value of  $MI_{Population}$  in CN (*B1, in black*), CNIC (*B2, in green*), MGv (*B3, in orange*), A1  
 1164 (*B4, in blue*) and VRB (*B5, in purple*). Note that the mean  $MI_{Population}$  value quickly reaches  
 1165 high values close from the maximum value of 2 bits in the subcortical structures (CN, CNIC  
 1166 and MGv) compared to the two cortical areas (A1 and VRB).  
 1167

1168 **Figure 5. High discrimination performance neurons are more numerous in subcortical**  
 1169 **structures than in auditory cortex in original conditions. A.** Cumulative percentage of the  
 1170 neuronal discrimination performance obtained in original vocalizations assessed by the  
 1171 mutual information (MI) computed at the level of the individual recordings ( $MI_{Individual}$ , bits)  
 1172 and (**B**) at the population level ( $MI_{Population}$ , bits) with populations of 9 simultaneous multiunit  
 1173 recordings in CN (*in black*), CNIC (*in green*), MGv (*in orange*), A1 (*in blue*) and VRB (*in*  
 1174 *purple*).  
 1175

1176 **Figure 6. Vocoding slightly alters neuronal responses at each stage of the auditory**  
 1177 **system. A.** From left to right, examples of raster plots representing the responses to the four  
 1178 original whistles (*Original*) and their vocoded versions (*Voc38, Voc20 and Voc10*). The grey  
 1179 part of rasters corresponds to evoked activity. From bottom to top, neuronal responses were  
 1180 recorded in CN, CNIC, MGv, A1 and VRB. For each example, the values of the best  
 1181 frequency (BF in kHz) and of the bandwidth (BW in octave) obtained when testing the  
 1182 responses to pure tones are indicated in the left side. For each example, the mean evoked  
 1183 firing rate (spikes/sec) obtained in each condition is indicated below the rasters. **B.**  
 1184 Peristimulus time histograms (PSTHs) of each neuronal response presented in A. For each  
 1185 neuronal recording, the four PSTHs of the original and vocoded conditions have been  
 1186 overlaid. The grey part of the PSTHs corresponds to evoked activity. **C-F.** The mean values  
 1187 ( $\pm$ SEM) represent the vocoding effects on (**C**) the evoked firing rate (spikes/sec), (**D**) the  
 1188 temporal reliability represented by the CorrCoef value, (**E**) the neuronal discrimination  
 1189 assessed by the mutual information (MI) computed at the level of the individual recordings  
 1190 ( $MI_{Individual}$ , bits) and (**F**) the neuronal discrimination at the population level ( $MI_{Population}$ , bits)  
 1191 with populations of 9 simultaneous multiunit recordings in CN (*in black*), CNIC (*in green*),  
 1192 MGv (*in orange*), A1 (*in blue*) and VRB (*in purple*) (*one-way ANOVA, P < 0.05*; with post-  
 1193 hoc paired t tests,  $*P < 0.05$ ). The evoked firing rate corresponds to the total number of action  
 1194 potentials occurring during the presentation of the stimulus minus spontaneous activity (200  
 1195 ms before each acoustic stimulus). At the population level, the discrimination performance  
 1196 significantly decreased only for 10 frequency bands in subcortical structures and did not  
 1197 decrease in cortical areas.

1198

1199

1200 **Figure 7. Vocoding effects on the  $MI_{Population}$  growth functions in each auditory**  
 1201 **structure.** The curves display the average growth functions of the  $MI_{Population}$  for each  
 1202 structure in each vocoding condition (indicated by a gradient colors) in CN (**A**, in black).  
 1203 CNIC (**B**, in green), MGv (**C**, in orange), A1 (**D**, in blue) and VRB (**E**, in purple). In each  
 1204 structure, the vocoding slightly reduced the  $MI_{Population}$  values. At the cortical level, the  
 1205 reduction induced by vocoding was similar at 38 and 20 bands, then a stronger reduction was  
 1206 observed at 10 bands. At the thalamic level, there was almost no change in the growth  
 1207 function of the  $MI_{Population}$  with 38 and 20 bands vocalizations, but there was a large decrease  
 1208 in  $MI_{Population}$  with the 10-band vocoded stimuli. In the CNIC, the vocoding only induced a  
 1209 reduction of the  $MI_{Population}$  for 20 and 10 bands; a similar scenario was observed at the CN  
 1210 level.

1211  
 1212 **Figure 8. Noise strongly reduces neuronal responses in all structures but to a lesser**  
 1213 **extent in the central nucleus of the inferior colliculus. A.** From left to right, raster plots of  
 1214 responses of four original whistles (*Original*) and their noisy versions embedded in the  
 1215 vocalization-shaped stationary noise at three SNRs: +10, 0 and -10 dB. The grey part of  
 1216 rasters corresponds to evoked activity. From bottom to top, neuronal responses were recorded  
 1217 in CN, CNIC, MGv, A1 and VRB. For each example, the values of the best frequency (BF in  
 1218 kHz) and of the bandwidth (BW in octave) obtained when testing the responses to pure tones  
 1219 are indicated in the left side. For each example, the mean evoked firing rate (spikes/sec)  
 1220 obtained in each condition is indicated below the rasters. The green dashed box indicates a  
 1221 typical example of CNIC neuronal responses that are resistant to the noise addition. **B.**  
 1222 Peristimulus time histograms (PSTHs) of each neuronal response presented in A. For each  
 1223 neuronal recording, the four PSTHs of the original and noisy conditions have been overlaid.  
 1224 The grey part of the PSTHs corresponds to evoked activity. **C-F.** The mean values ( $\pm$ SEM)  
 1225 represent the noise effects on (**C**) the evoked firing rate (spikes/sec), (**D**) the temporal  
 1226 reliability represented by the CorrCoef value, (**E**) the neuronal discrimination assessed by the  
 1227 mutual information (MI) computed at the level of the individual recordings ( $MI_{Individual}$ , bits)  
 1228 and (**F**) the neuronal discrimination at the population level ( $MI_{Population}$ , bits) with populations  
 1229 of 9 simultaneous multiunit recordings in CN (in black), CNIC (in green), MGv (in orange),  
 1230 A1 (in blue) and VRB (in purple) (one-way ANOVA,  $P < 0.05$ ; with post-hoc paired t tests,  $*P$   
 1231  $< 0.05$ ). The evoked firing rate corresponds to the total number of action potentials occurring  
 1232 during the presentation of the stimulus minus spontaneous activity (200 ms before each  
 1233 acoustic stimulus). At the population level, the discrimination performance significantly  
 1234 decreased in all structures when the SNR decreased, with on average the CNIC populations  
 1235 still able to discriminate 2 out of 4 stimuli ( $MI_{Population}$  value  $> 1$ bit).

1236

1237 **Figure 9. Noise effects on the  $MI_{Population}$  growth functions in each auditory structure.**  
 1238 The curves display the noise effects on the  $MI_{Population}$  growth functions for each structure and  
 1239 at each SNR (indicated by a gradient colors) in CN (**A**, in black), CNIC (**B**, in green), MGv  
 1240 (**C**, in orange), A1 (**D**, in blue) and VRB (**E**, in purple). In general, background noise largely  
 1241 altered the growth functions of the  $MI_{Population}$  in each structure (but to a lesser extent in the  
 1242 CNIC). In the CN, noise induced a stronger reduction of the  $MI_{Population}$ , which was clearly a  
 1243 function of SNR. In the CNIC, noise induced SNR-dependent reduction in the  $MI_{Population}$   
 1244 values, the reduction being modest at a +10 and 0 dB SNR but more important at a -10 dB  
 1245 SNR. In the MGv, noise progressively lowered the curves of the  $MI_{Population}$ . In the cortex, the  
 1246  $MI_{Population}$  growth functions were not strongly impacted except at the -10 dB SNR.

1247

1248 **Figure 10. A subpopulation of CN neurons maintains good neuronal discrimination**  
 1249 **performance at a +10 dB SNR.**

1250 **A.** Waterfall plot shows the mutual information ( $MI_{\text{Individual}}$ , bits) as a function of temporal  
 1251 resolution (1 to 256 ms) for the CN recordings at +10 dB SNR. The recordings are ranked by  
 1252 the mean MI value obtained for all bin sizes. Note that at this particular SNR, 20% of the CN  
 1253 recordings still maintained  $MI_{\text{Individual}}$  values above 1 bit, indicating that some CN neurons  
 1254 still send information about the vocalization identity at higher brainstem centers such as the  
 1255 CNIC. **B.** Distributions of the Time-Frequency Response Profile (TFRP) parameters (best  
 1256 frequency, bandwidth, response duration and response strength) for the two neuronal  
 1257 populations in CN depending of the MI value (*in grey*,  $MI \geq 1$  bit and *in black*,  $MI < 1$  bit). Note  
 1258 that, there were significant differences in terms of response duration and the response  
 1259 strength. **C.** The curves display the individual and average growth functions of the  $MI_{\text{Population}}$   
 1260 for the simultaneous CN recordings at the +10 dB SNR. Note that despite the fact that the  
 1261 mean  $MI_{\text{Population}}$  value was much lower than in the original condition (see figure 4B1), about  
 1262 20% of the simultaneously recorded populations reached a value of 1.5 bits with 9 neurons or  
 1263 less (*red curve lines*).

1264

1265 **Figure 11. No relationship between the mutual information and the parameters of**  
 1266 **TFRPs (the best frequency, BF and the bandwidth, BW) at each stage of the auditory**  
 1267 **system.**

1268 **A.** Typical examples of Time-Frequency Response Profile (TFRP) recorded in VRB, AI,  
 1269 MGv, CNIC and CN. These TFRPs are examples of responses to pure tones and the first  
 1270 column also corresponds to the same neurons as those presented in figures 3, 5 and 7. *From*  
 1271 *left to right*, the maximal firing rate (in spikes/sec) was 100 and 220 in VRB, 195 and 200 in  
 1272 AI, 460 and 420 in MGv, 315 and 250 in CNIC and 340 and 330 in CN. From these TFRPs,  
 1273 we extracted parameters such as the best frequency (in kHz), the bandwidth (in octave), the  
 1274 response duration (in ms) and the response strength (in spikes/sec). **B.** Noise effect on  
 1275 neuronal discrimination ( $MI_{\text{Individual}}$ , bits) according to the best frequency (BF). Scattergrams  
 1276 of the  $MI_{\text{Individual}}$  values obtained at the +10 dB SNR as a function of the  $MI_{\text{Individual}}$  values  
 1277 obtained with the original vocalizations based on neuronal responses recorded in CN, CNIC,  
 1278 MGv, AI and VRB. We separated the recordings in three groups according to the best  
 1279 frequency:  $BF < 5$  kHz (in red),  $5 \leq BF \leq 15$  kHz (in blue) and  $BF > 15$  kHz (in green).  
 1280  $MI_{\text{Individual}}$  mean values are represented with a black cross. **C.** Noise effect on neuronal  
 1281 discrimination ( $MI_{\text{Individual}}$ , bits) according to the bandwidth (BW). Scattergrams of the  
 1282  $MI_{\text{Individual}}$  values obtained at the +10 dB SNR as a function of the  $MI_{\text{Individual}}$  values obtained  
 1283 with the original vocalizations based on neuronal responses recorded in CN, CNIC, MGv, AI  
 1284 and VRB. We separated the recordings in three groups according to the bandwidth:  $BW \leq 2$   
 1285 octaves (in red),  $2 \leq BW \leq 4$  octaves (in blue) and  $BW \geq 4$  octaves (in green).  $MI_{\text{Individual}}$   
 1286 mean values are represented with a black cross. Note that, in all structures, the decrease in  
 1287  $MI_{\text{Individual}}$  value from the original conditions to the +10 dB SNR occurred whatever the BF  
 1288 and the BW values.

1289

1290 **Figure 12. Reduction of slow AM cues as one of the factors explaining the neuronal**  
 1291 **discrimination performance at the subcortical and cortical levels. A.** Vocoding and noise

1292 effects on the amplitude-modulation (AM) spectra. The plot represents the averaged  
 1293 modulation spectra of the four original vocalizations (*in black*), vocoded vocalizations  
 1294 (Voc38, Voc20 and Voc10: *red, green and blue respectively, solid lines*) and vocalizations in  
 1295 noise at three SNRs (+10, 0 and -10 dB: *red, green and blue respectively, dashed lines*).



1296 Vertical black dashed line corresponds to the maximum frequency (20 Hz) selected for the  
1297 data analysis.  
1298 **B.** Percentage of  $\Delta MI_{\text{Population}}$  as a function of  $\Delta$ modulation index computed for each structure  
1299 from mean  $MI_{\text{Population}}$  or mean modulation-index values obtained in all adverse conditions and  
1300 mean values in the original condition. Each dot represents neuronal data ( $\Delta MI_{\text{Population}}$ ) in CN  
1301 (*in black*), CNIC (*in green*), MGv (*in orange*), A1 (*in blue*) and VRB (*in purple*). Polynomial  
1302 curves fitting all acoustic conditions have been generated (*color lines*). In all conditions  
1303 (vocoding or noise), there is a limit of AM reduction from which the  $\Delta MI_{\text{Population}}$  decreases in  
1304 cortical and subcortical structures.  
1305  
1306

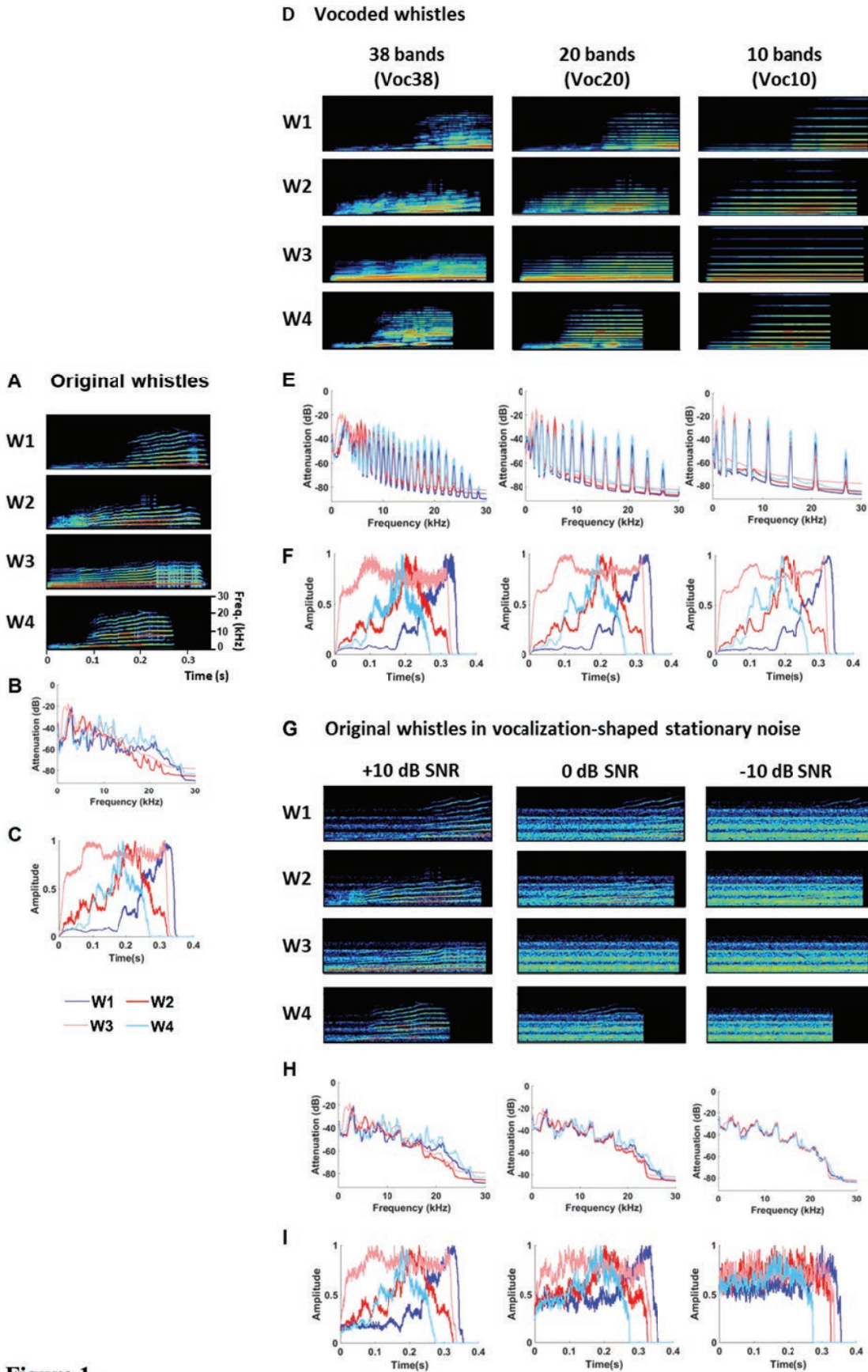


Figure 1.

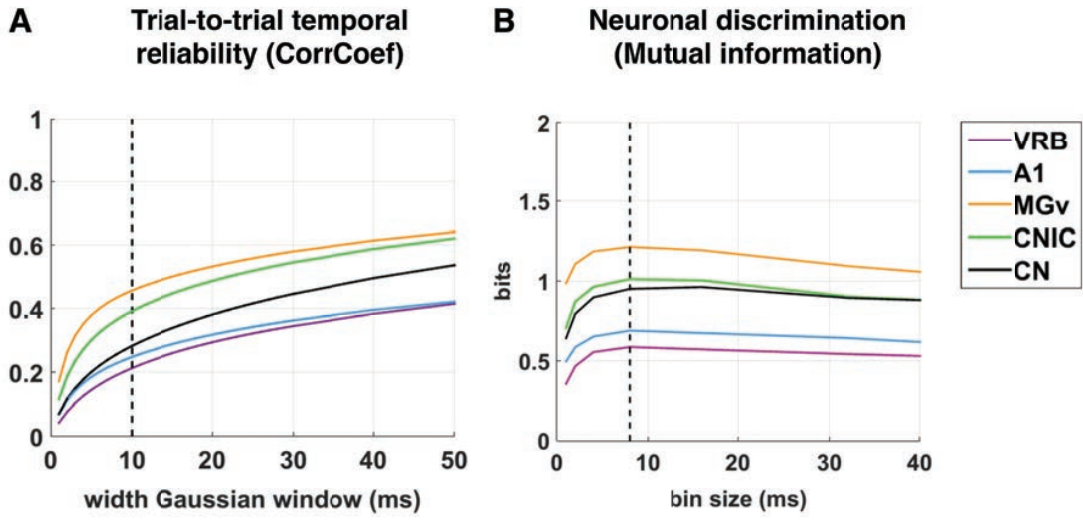


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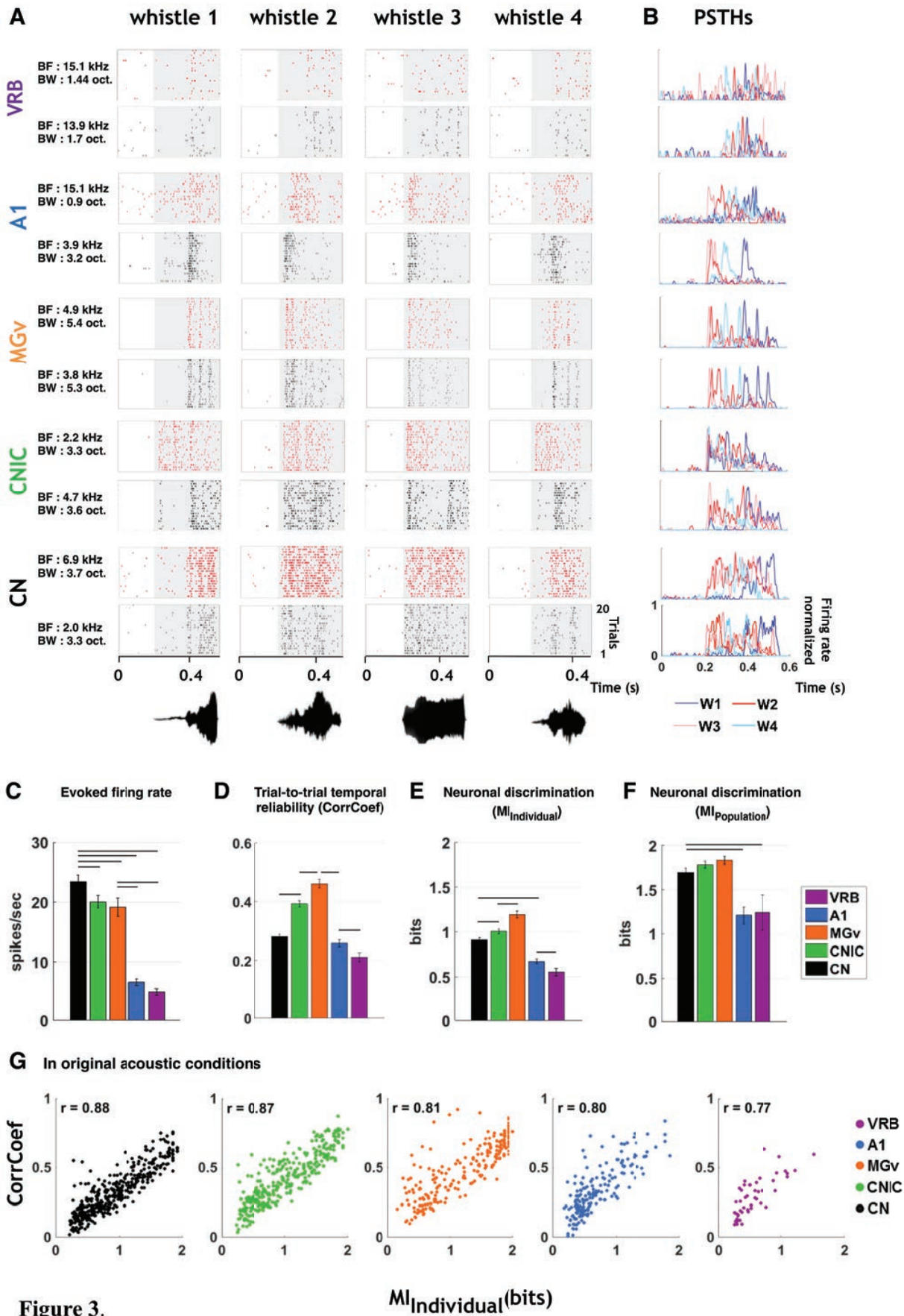


Figure 3.



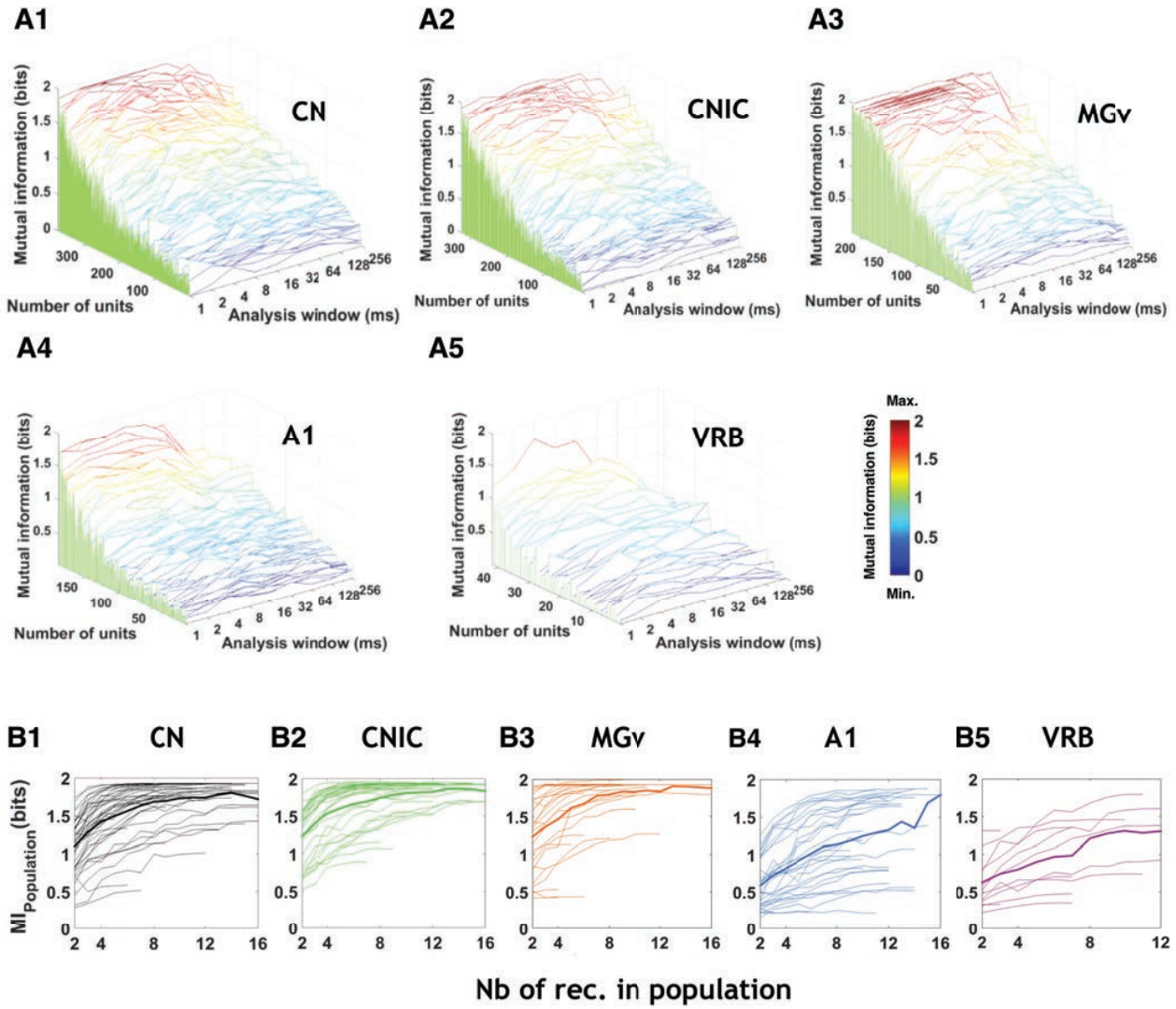


Figure 4.

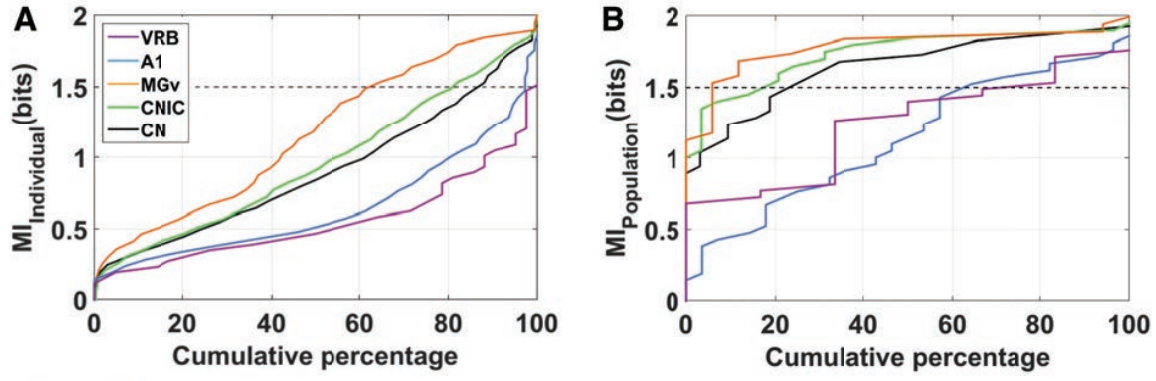


Figure 5.



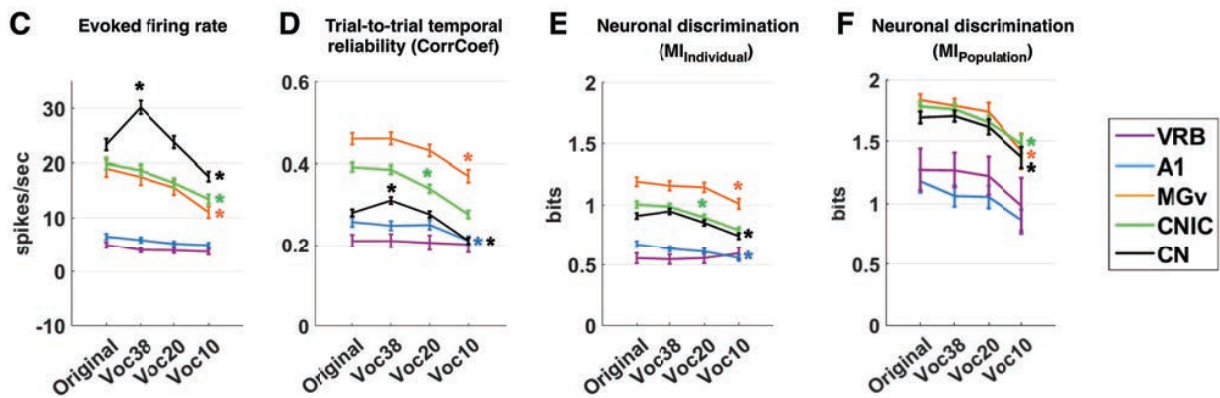
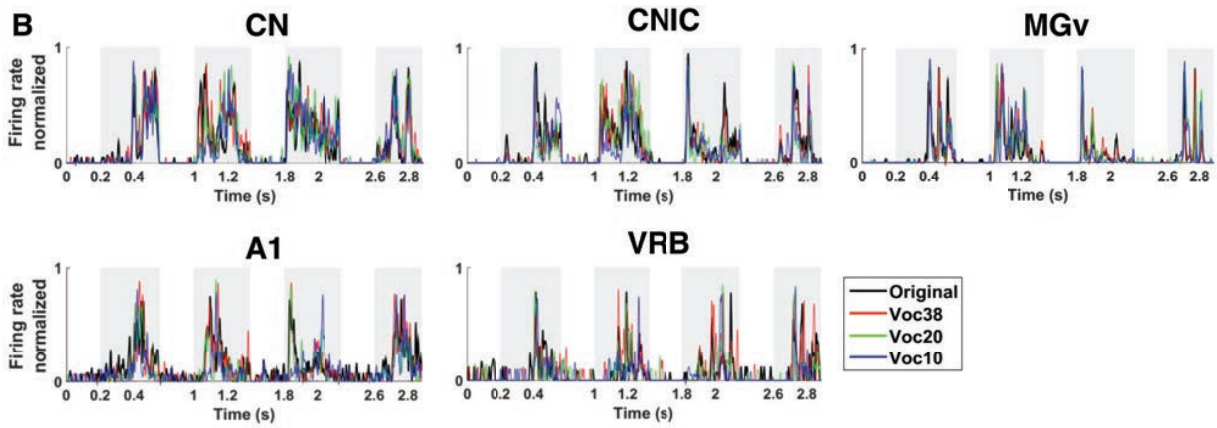
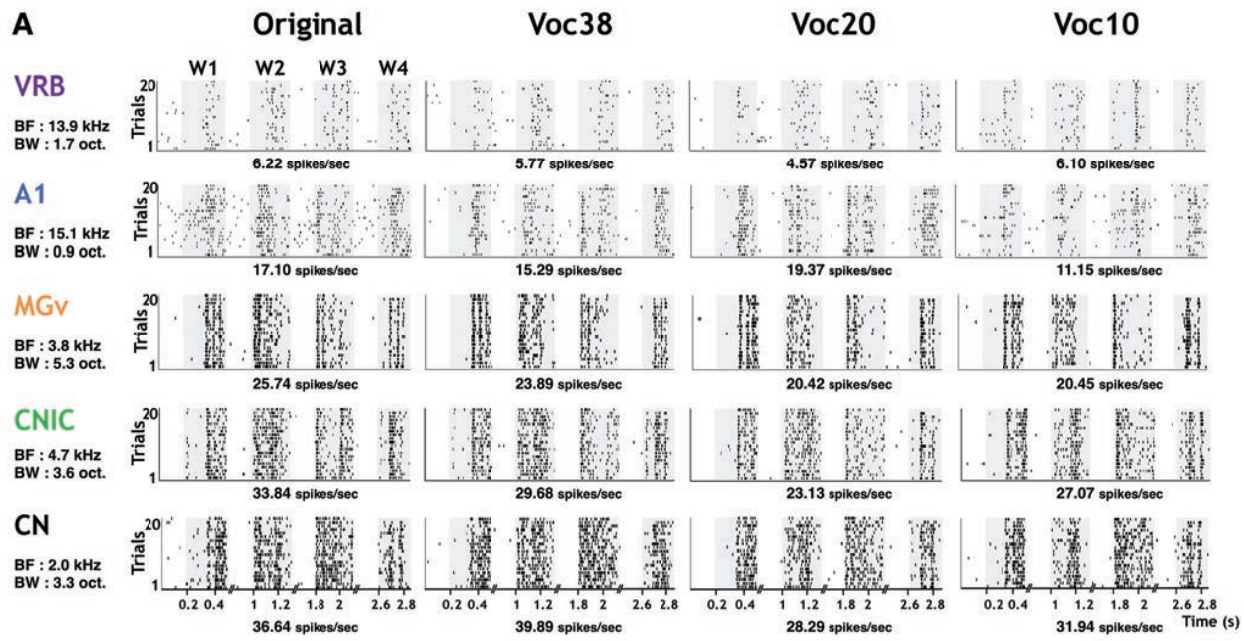


Figure 6.

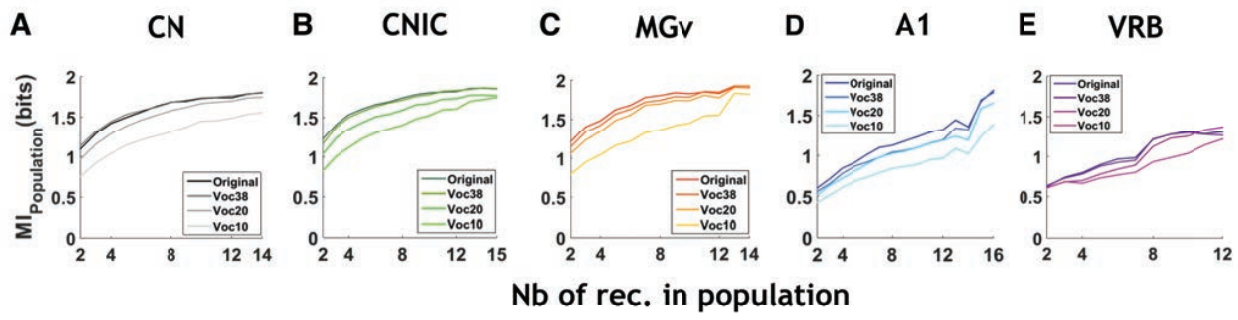


Figure 7.

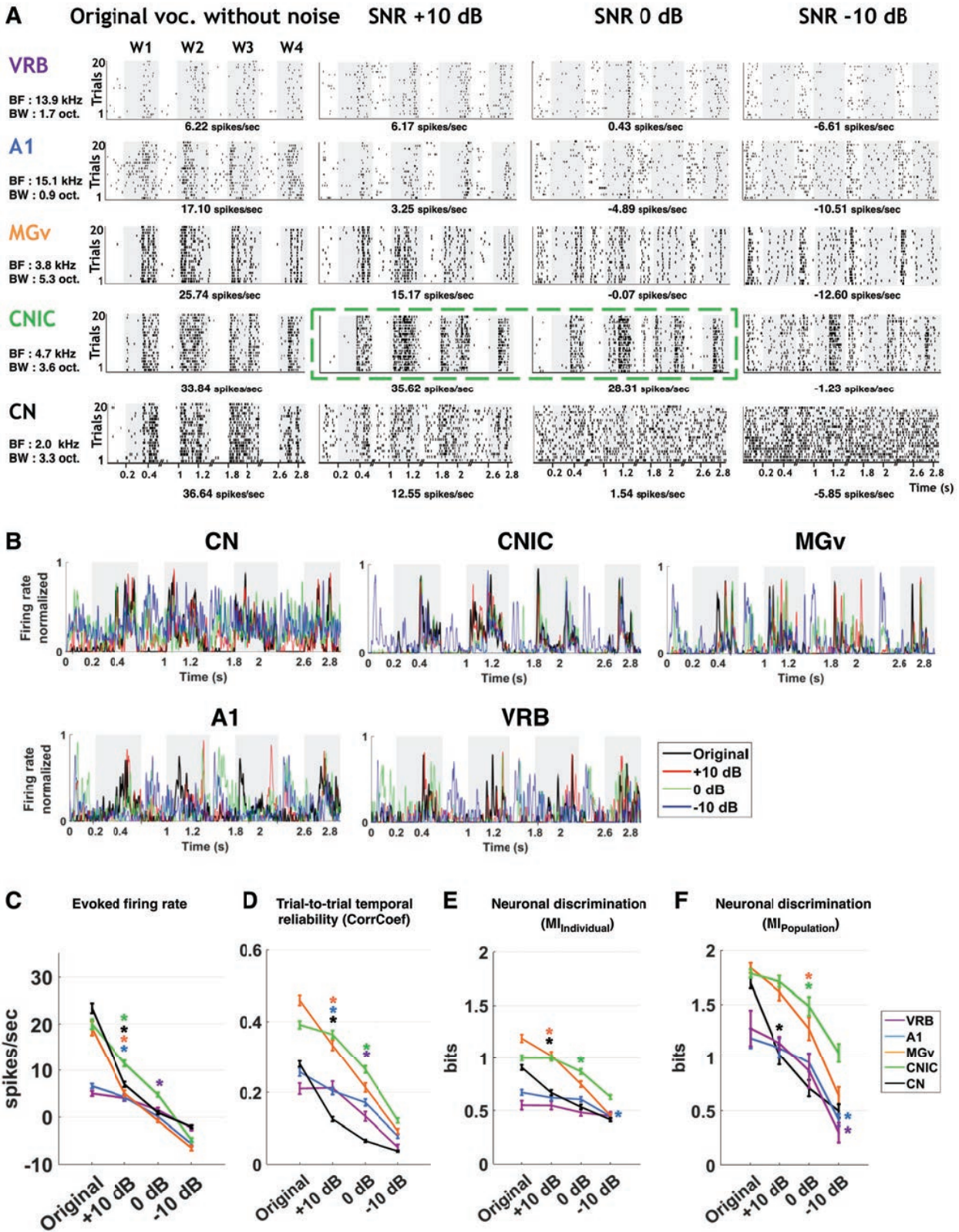


Figure 8.



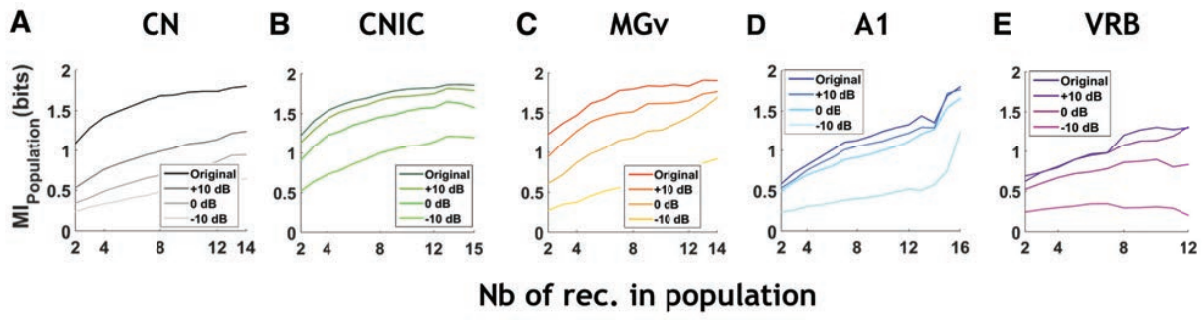


Figure 9.

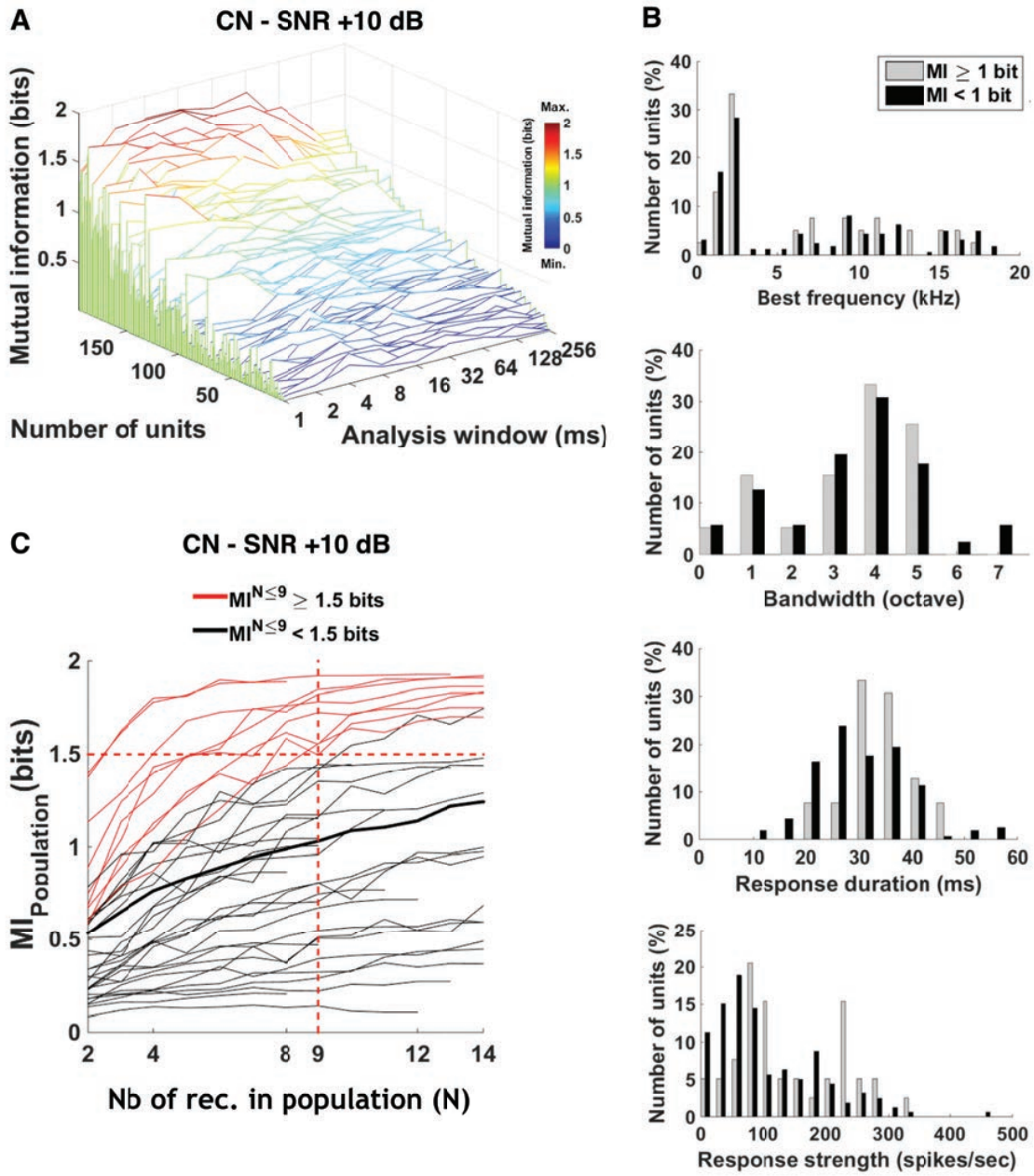


Figure 10.

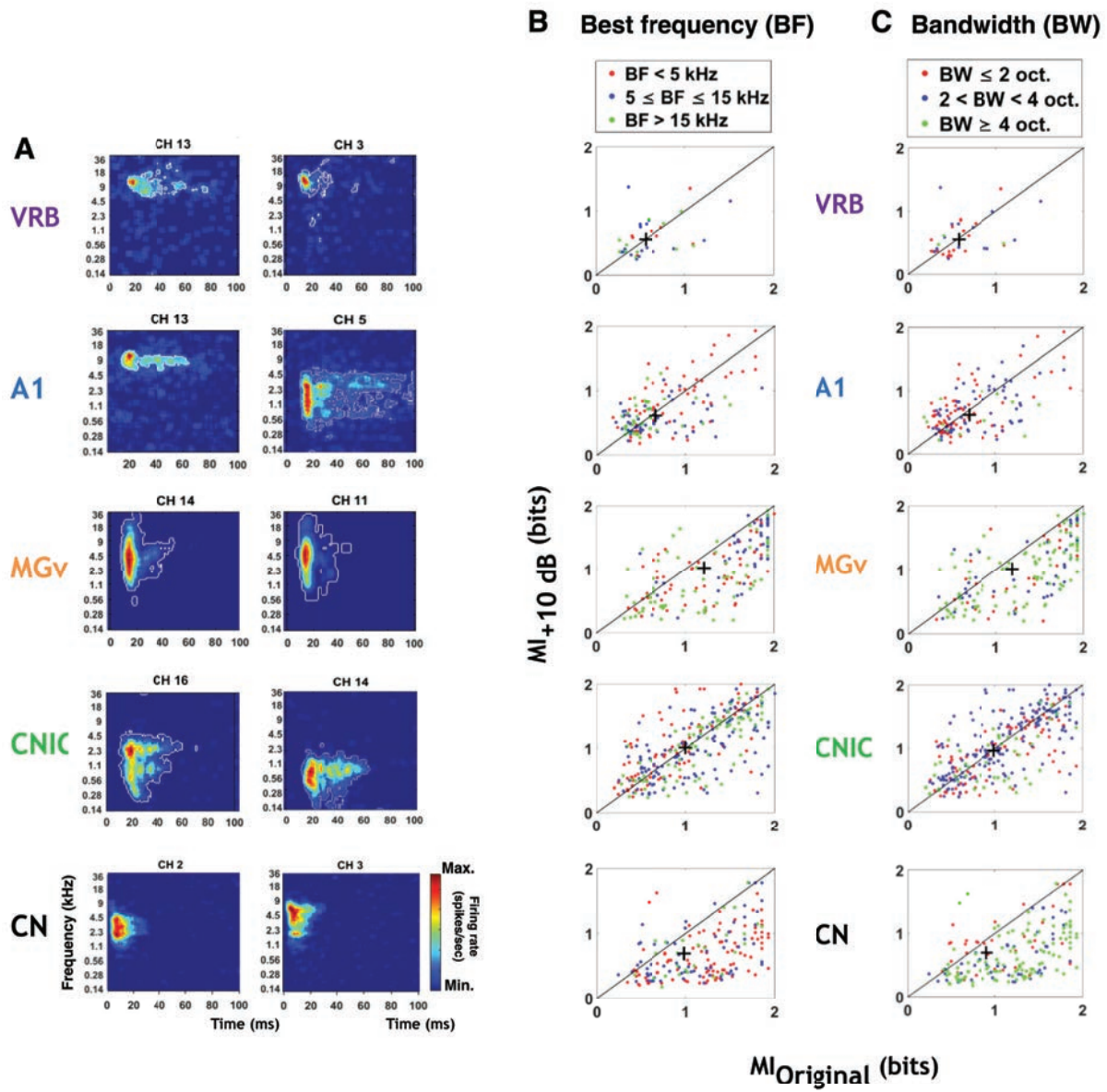


Figure 11.



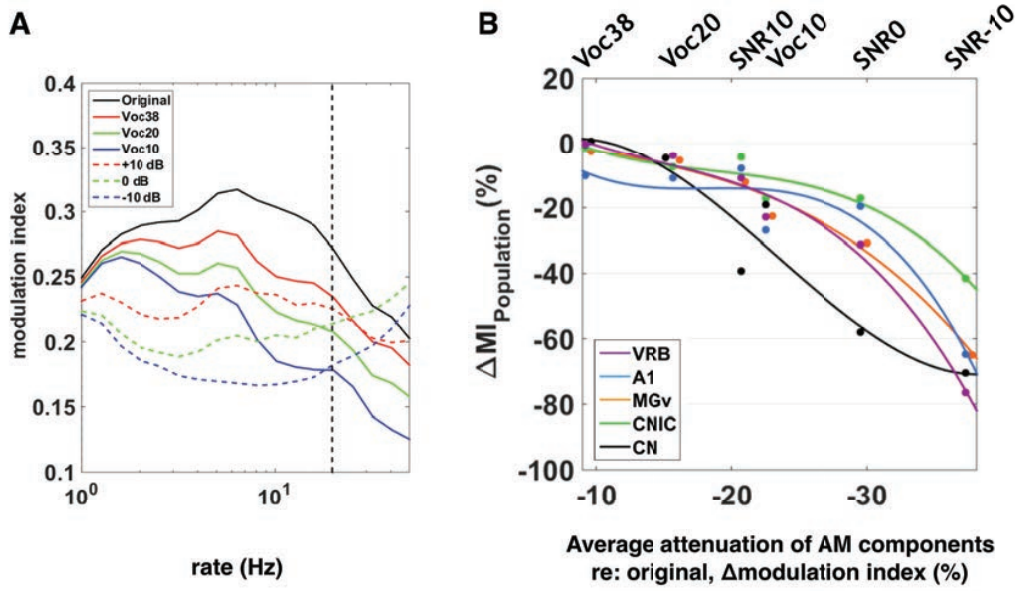


Figure 12.