1   Full title: Deviance detection in subthalamic neural population

2   responses to natural stimuli in bats

3   Short title: Subthalamic deviance detection to natural stimuli in bats

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Abstract

Deviance detection describes an increase of neural response strength caused by a stimulus with a low probability of occurrence. This ubiquitous phenomenon has been reported for multiple species, from subthalamic areas to auditory cortex. While cortical deviance detection has been well characterised by a range of studies covering neural activity at population level (mismatch negativity, MMN) as well as at cellular level (stimulus-specific adaptation, SSA), subcortical deviance detection has been studied mainly on cellular level in the form of SSA. Here, we aim to bridge this gap by using noninvasively recorded auditory brainstem responses (ABRs) to investigate deviance detection at population level in the lower stations of the auditory system of a hearing specialist: the bat *Carollia perspicillata*. Our present approach uses behaviourally relevant vocalisation stimuli that are closer to the animals' natural soundscape than artificial stimuli used in previous studies that focussed on subcortical areas. We show that deviance detection in ABRs is significantly stronger for echolocation pulses than for social communication calls or artificial sounds, indicating that subthalamic deviance detection depends on the behavioural meaning of a stimulus. Additionally, complex physical sound features like frequency- and amplitude-modulation affected the strength of deviance detection in the ABR. In summary, our results suggest that at population level, the bat brain can detect different types of deviants already in the brainstem. This shows that subthalamic brain structures exhibit more advanced forms of deviance detection than previously known.

1. Introduction

Like all echolocating bats, *Carollia perspicillata* navigates in the dark by emitting stereotypical acoustic pulses and listening to the echoes reflected off objects in its environment. In addition, this bat species has a large variety of social communication calls[1,2], which is a consequence of its social lifestyle, with groups of more than 100 individuals sharing the same roost[3]. This has led to the development of a broad variety of social communication calls. Echolocation pulses and social communication calls differ from each other in their carrier frequencies and durations, with echolocation pulses being higher in frequency and shorter in time (see Fig. 1a for an example echolocation pulse and social communication call). Those two vocalisation types represent fundamentally different behaviours (navigation and social communication) and can alternate in rapid succession for freely behaving bats. This raises a question that has puzzled neuroethologists for years: How does the bat brain process echolocation and social sounds in a fast and energy-efficient way, when they occur in the same acoustic stream? A theoretical model that explains how the brain efficiently deals with the tremendous amount of input it receives is the predictive coding framework and, in relation to this, the ability of deviance detection[4,5]. According to the predictive coding theory, the brain is constantly creating predictions about the incoming stimuli[6]. When the system encounters an unexpected signal, expectations are updated which is represented by a prediction error component in the electrophysiological response. This makes the identification of regularities and deviants in the incoming stream of signals (i.e., deviance detection) crucial for the predictive coding framework. The present study investigates deviance detection to naturally occurring sounds – echolocation pulses and social communication calls – in the bat species *C. perspicillata*. We focussed on studying deviance detection in subthalamic neural populations of the auditory pathway by combining a naturalistic oddball stimulation paradigm (Fig. 1b) with noninvasively recorded auditory brainstem potentials (ABRs). Two experiments were performed: In experiment 1, an

71 echolocation pulse and a social communication call (Fig. 1a) were presented in an oddball

72 paradigm (Fig. 1b). Additionally, by using two control paradigms (the "Many-Standards"

73 (MS) and the 50 % control, Fig. 1c), we aimed to shed light on the possible underlying neural

74 mechanisms responsible for deviance detection, namely deviant enhancement and repetition

75 suppression of the standard response. These neural mechanisms are affected by both controls

76 in different ways, allowing a more detailed characterisation of the effects than by only using

77 an oddball paradigm. In experiment 2, the effect of different acoustic parameters (e.g., carrier

78 frequency and temporal structure) and the behavioural meaning of the auditory input on

79 subthalamic deviance detection was evaluated by performing a cross-comparison of the

80 responses to different stimuli. The stimuli considered ranged from natural vocalisations on

81 one end, to artificially generated vocalisation-mimics, noise bursts that resemble the

82 vocalisations in their frequency range and duration but not in their temporal structure, on the

83 other end (Fig. 1d).

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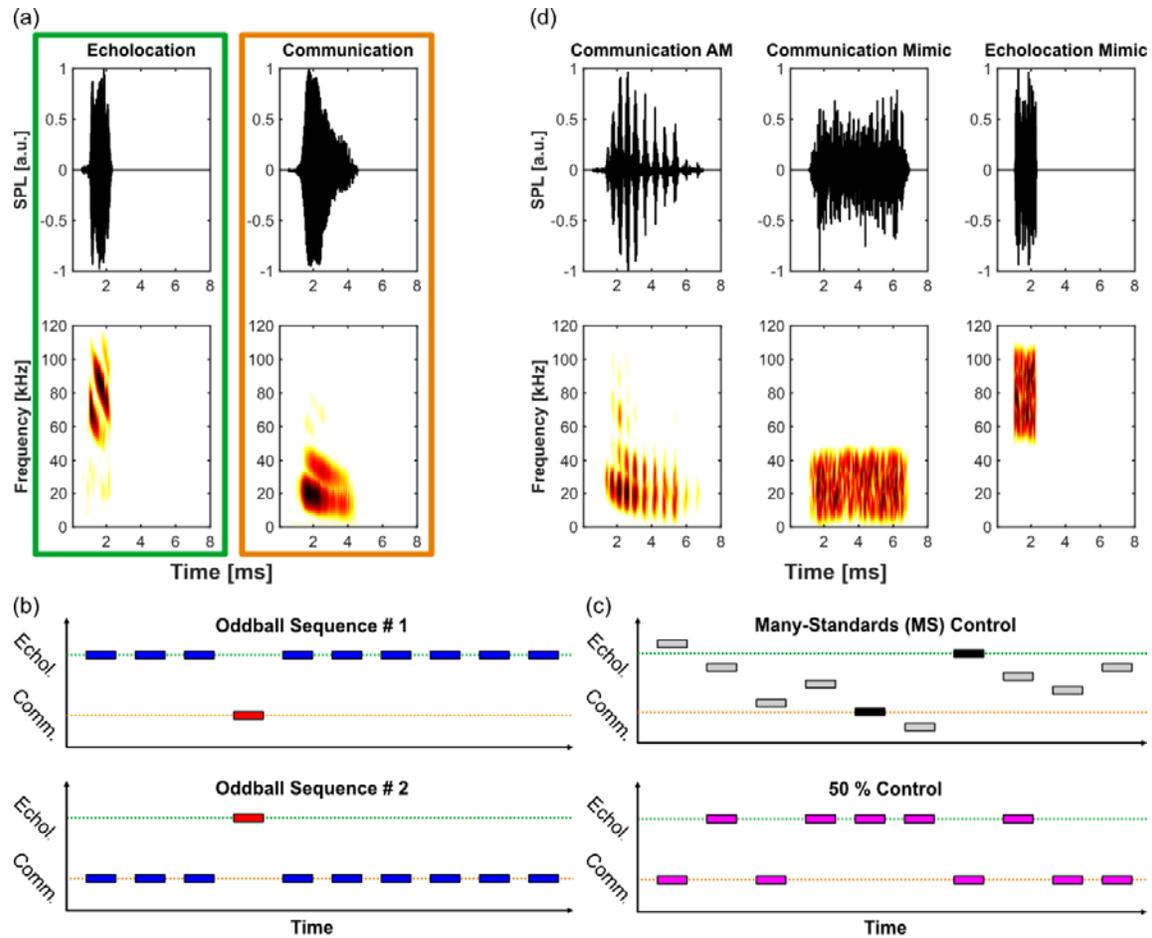
Figure 1: Used stimuli and stimulation protocols. (a) Oscillograms (top) and spectrograms (bottom) of an echolocation pulse (green frame) and a social communication call (orange frame) of C. perspicillata that were used as stimuli in this study. The communication signal is a syllable of a so-called distress call. (b) Schematic representation of the oddball paradigm; blue: standard, red: deviant. (c) Schematic representation of the two control sequences used; Many-Standards control (top) and 50 % control (bottom). (d) Additional stimuli used for a cross-comparison with the vocalisations in (a) to evaluate the importance of the frequency-versus-time structure of the stimuli for deviance detection. The amplitude-modulation of the communication AM call was produced by the animal itself and the call represents another example of a natural distress call of C. perspicillata. Both vocalisation mimics are artificially generated. They resemble the natural vocalisations in their frequency range and duration but not in their temporal structure.

2. Results and Discussion

Deviance detection in broadband filtered ABRs differs between echolocation and social communication sounds

In experiment 1, an echolocation pulse and a social communication call were presented in the oddball paradigm to investigate differences of deviance detection between both vocalisation types with the following results: ABRs to the echolocation pulse were significantly larger when the stimulus was perceived as a low-probability deviant (Fig. 2a, red ABR) than when it was a high-probability standard (blue ABR). This difference is present across the whole response, however, most prominently it appears in the last peak of the ABR, a slow wave that only becomes visible when the responses are broadband filtered between 0.1 and 2500 Hz. This filtering method is different from the usual narrowband filters between 300-2500 Hz that are used in many ABR studies and that will be discussed later. The strong effect of deviance detection in this late part of the response is in line with previous studies that investigated deviance detection in broadband filtered ABRs with pure tones[7,8]. This confirms that this slow, most likely inferior colliculus-generated[9] wave plays a key role in ABR-based deviance detection. It has been proposed that deviance detection is driven by two mechanisms at the neural level: repetition suppression and deviant enhancement. To disentangle which mechanism underlies the neural responses, the MS control has been suggested[10] (Fig. 1c, top). In this control, the target stimuli (Fig. 1a) are pseudo randomly presented together with multiple other stimuli (here: 8 stimuli; Fig. 1d; Supp. Fig. 1), which makes it impossible for the brain to detect regularities or deviations in the acoustic input. This results in responses that are unaffected by repetition suppression and deviant enhancement. A reduction of response strength to the standard relative to the MS response indicates repetition suppression while a stronger deviant than MS response is evidence for deviant enhancement. The echolocation response that was recorded in the MS control was significantly smaller than the deviant

120   response and not significantly different from the standard response (Fig. 2a, top). This

121   observation shows that the neural mechanism driving deviance detection for echolocation is a

122   deviant-related enhancement of the response (i.e., a prediction error response in the predictive

123   coding framework) and not a repetition suppression effect on the standard response. Possibly,

124   deviant stimuli cause the brainstem neurons to respond more synchronously than standard or

125   MS stimuli, resulting in larger deviant ABR amplitudes. In line with this hypothesis, former

126   studies have demonstrated the importance of synchronisation and phase locking of brainstem

127   neurons for speech[11] and music[12,13] perception in humans. Interestingly, the slow wave

128   of the MS response has an earlier peak and offset latency compared to the deviant and

129   standard ABR. This could indicate that additional neural mechanisms become active and

130   modify the ABRs when the natural acoustic input becomes more complex, as occurs in the

131   MS control compared to the oddball sequence. To further investigate deviance detection in the

132   ABR, we used another common control paradigm, the so-called 50 % control. Here, both

133   target stimuli are presented in a sequence with equal probability of 50 %. The analysis yielded

134   a similar result to the MS control, that is the deviant response being significantly enlarged and

135   no difference between control and standard response (Fig. 2a, bottom). The fact that deviant

136   enhancement and not repetition suppression is driving low-level deviance detection for

137   echolocation calls is interesting since previous studies have suggested repetition suppression

138   to be the dominant mechanism causing deviance detection in subcortical nuclei[4,5].

139   However, those studies used pure tones to stimulate individual neurons instead of measuring

140   vocalisation-related summed potentials like we did here. It is possible that echolocation pulses

141   evoke stronger deviant responses and less repetition suppression due to their high behavioural

142   relevance compared to simple tone pips.

143   As opposed to echolocation, the social communication sounds did not elicit deviance

144   detection in this experiment (Fig. 2b). While deviant and standard responses were not

145   significantly different from each other, the MS response was attenuated in comparison to the

146   deviant response (Fig. 2b, top). This is surprising since, as explained above, the MS control is

147   expected to generate a baseline response that is affected by neither deviant enhancement nor

148   repetition suppression and hence should be positioned between deviant and standard response.

149   Likely, the attenuation of the MS communication response is the result of the same

150   mechanisms that modified the timing of the MS echolocation response. Those mechanisms

151   seem to get active only when the acoustic input becomes more variable and appear to have

152   complex, nonlinear effects on ABRs. Interestingly, they are restricted to natural stimuli, as a

153   previous study by Wetekam et al.[8] in the same species did not find similar effects in the MS

154   ABRs to pure tones. However, the 50 % control was very similar to the deviant and standard

155   response, confirming that probability encoding did not affect the ABR size to the social

156   communication call (Fig. 2b, bottom).

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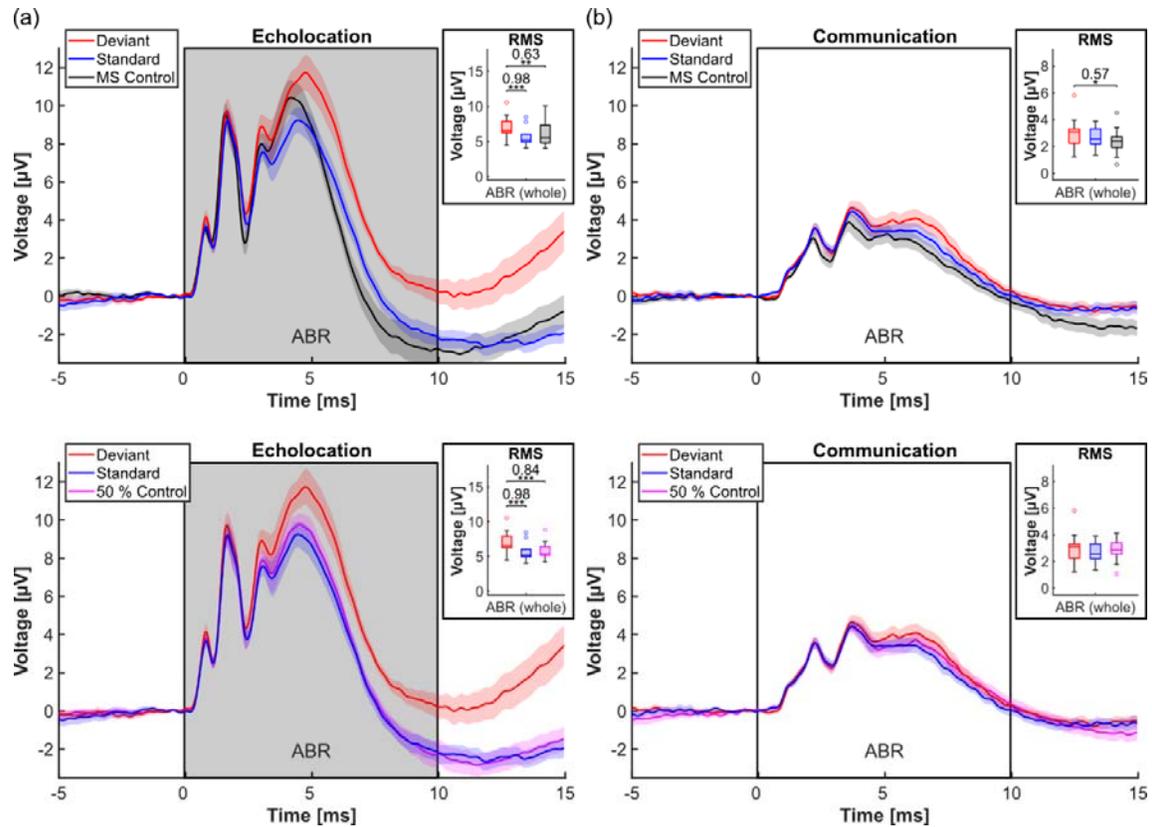
Figure 2: Deviance detection in broadband filtered ABRs differs between echolocation and social communication sounds (n = 13 animals). (a) Grand averages of ABRs to an echolocation pulse presented as deviant (red) and standard (blue) as well as in the MS control (black, top) and the 50 % control (magenta, bottom). The boxes framing the responses represent the time window taken for RMS calculation, covering the whole ABR response (0-10 ms post stimulus onset). The grey colour of the boxes indicates a significant difference between deviant and standard response. Shaded areas around the ABRs depict the standard error of the mean. The inset on the right shows the RMS values calculated for each animal and condition as an estimation of response strength. (b) As in (a) but the stimulus was a social communication call. The white colour of the boxes framing the responses indicates that there was no significant difference between deviant and standard response.

For echolocation, deviance detection is measurable very early in narrowband filtered ABRs

To further characterise the effects of deviance detection on the echolocation response, the data were narrowband filtered (bandpass Butterworth, 300-2500 Hz, 4th order) to analyse the fast ABR components in more detail (Fig 3). ABR wave ii/iii as well as wave iv of the deviant response were significantly larger than the respective components of the standard response. Given that wave ii and iii represent neural activity in the cochlear nucleus and superior olivary complex, respectively[14], this finding strongly supports the hypothesis that auditory

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176   probability encoding at population level is happening already below the inferior colliculus, as

177   it has been suggested in former studies[8,15]. In fact, effects of novelty detection have

178   recently been described for an even lower auditory structure, the cochlea[16,17]. In these

179   reports, the authors propose that the medial olivocochlear reflex is responsible for those

180   effects by suppressing outer hair cell activity, mediated by feedback from the cortex. Since

181   the ABRs presented here are averaged over many trials, it is possible that similar cortical

182   feedback mechanisms are responsible for the very early effects seen in our ABR data.
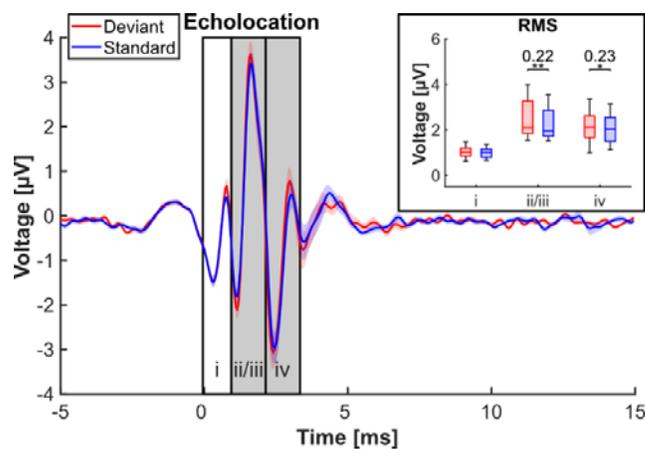
Figure 3: For echolocation, deviance detection is measurable very early in narrowband filtered ABRs (n = 13 animals). Grand averages of ABRs to an echolocation pulse presented as deviant (red) and standard (blue), with a social communication call as context. The boxes framing the responses represent the time window taken for RMS calculation, covering the typical ABR peaks i, ii/iii and iv. The colour of the boxes indicates whether a significant difference between deviant and standard response could be measured (grey: yes, white: no). Shaded areas around the graphs depict the standard error of the mean. The inset on the right shows the RMS values calculated for each animal, condition and time window as an estimation of response strength.

192   **Behavioural meaning and complex sound features of a stimulus affect deviance detection**

193   **in broadband filtered ABRs**

194   The second experiment of this paper tackles the question of how low-level deviance detection

195   is affected by individual stimulus parameters and possible behavioural meaning of the stimuli.

196   Therefore, in addition to the previously used echolocation pulse and social communication

197   call (Fig. 1a), an *amplitude-modulated* communication call (another distress vocalisation of *C.*

198   *perspicillata*) and two artificial vocalisation-mimics that resembled the natural vocalisations

199   in their frequency range and duration but not in their temporal structure (Fig. 1d) served as

200   stimuli. The aim was to assess the relevance of the frequency-versus-time structure of a signal

201   for producing deviance detection in broadband filtered ABRs. In addition, it was tested

202   whether the AM property of a communication call influenced deviance detection, as

203   amplitude modulation appears in natural communication calls[2,18] and could bear additional

204   meaning for the animal. To answer these questions, the five different stimuli were presented

205   to the animals in all possible parings of the oddball paradigm.

206   When the echolocation pulse or the echolocation mimic served as target stimulus,

207   significantly larger deviant than standard responses could be measured when any

208   communication stimulus was the context (Fig. 4, Supp. Fig. 2 for statistics). Interestingly,

209   deviance detection could also be recorded for the responses to the echolocation pulse when

210   the echolocation mimic was the context, but not vice versa. This indicates that differences in

211   auditory input beyond simple frequency deviations – e.g., the frequency modulation of the

212   echolocation pulse that is absent in the mimic – have a direct influence on subthalamic

213   deviance detection in the bat brain. The fact that this effect is not present in the echolocation

214   mimic responses when the echolocation pulse was context supports the claim that the

215   behavioural meaning of a stimulus plays a key role in low-level population-based deviance

216   detection. Modulatory effects of the behavioural meaning of a stimulus on the strength of

217   deviance detection has previously been known for cortical areas[19], but not for the

218   brainstem. Both natural communication calls – whether amplitude modulated or not – did not

219   reveal significant deviance detection in any oddball combination except when presented with

220   the echolocation mimic. This exception could be due to the very different physical properties

221   of both call-types where the artificial nature of the mimic increases the contrast even further.

222   On the other hand, as in experiment 1, the natural echolocation pulse as context did not cause

223   deviance detection in the responses to either of the natural communication calls. Evidence for

224   differences in the processing of novelty detection between echolocation and communication

225   stimuli in *C. perspicillata* has been reported before[20,21] and is in line with the current data.

226   A possible reason for this phenomenon is the fact that both natural communication calls used

227   in this study are distress calls that the animal emits when it is under physical duress[1,2].

228   Those distress calls might always elicit the strongest possible neural response in the brains of

229   conspecifics due to the relevance and importance their perception has for the behavioural

230   response, independent of their probability of occurrence. In contrast, ABRs to the

231   communication mimic did reveal strong deviance detection with significantly enlarged

232   deviant responses when the AM communication call, the echolocation pulse or the

233   echolocation mimic was the context. Only when the unmodulated communication call was the

234   context, no significant difference between deviant and standard response could be measured.

235   Together, these results indicate that the AM of the communication stimulus contributed to the

236   differentiation between the true call and an artificial sound while it did not have a significant

237   impact on the distinction between two different natural communication calls at subthalamic

238   level.

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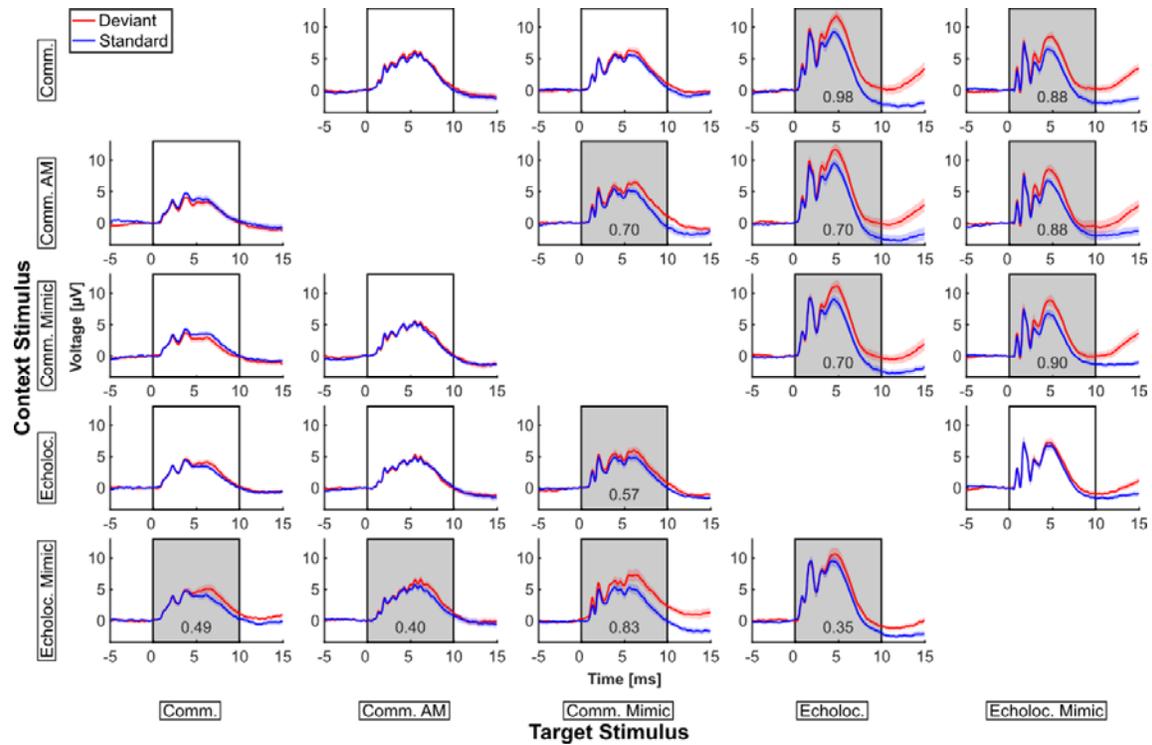
Figure 4: Behavioural meaning and complex sound features of a stimulus affect deviance detection in broadband filtered ABRs (n = 13 animals). All possible parings of the oddball paradigm. Each column contains the recorded responses to the target stimulus of the oddball sequence while each row represents one context stimulus (the second stimulus of the oddball paradigm that served as context for the target stimulus). The stimuli tested were: communication call (Comm.), AM communication call (Comm. AM), communication-mimic (Comm. Mimic), echolocation pulse (Echoloc.) and echolocation mimic (Echoloc. Mimic). Response plots like in Fig. 2. The colour of the boxes indicates whether a significant difference between deviant and standard response could be measured (grey: yes, white: no). If deviant and standard response differed significantly, Cohen's D is provided as a measure of effect size (number in the grey boxes).

Conclusion

In this study, noninvasively recorded ABRs revealed that deviance detection responses to

vocalisations that have different behavioural meanings for bats – navigation and

communication – are processed in a complex and asymmetric way already at the earliest

stations of the ascending auditory pathway. In fact, the results show that when considering the

population response, subthalamic deviance detection is sensitive to physical (carrier

frequency, FM and AM) as well as abstract stimulus features (behavioural meaning of a

vocalisation). By this, population-based subthalamic deviance detection showed a higher

complexity than what has been reported for cellular SSA of neurons in the same brain areas.

260   ## 3. Material and Methods

261   **Animals**

262   For the experiments of this study, 13 adult bats (7 males, 6 females) of the species *Carollia*

263   *perspicillata* from the breeding colony of Goethe University Frankfurt were used. After being

264   caught for the first time, all animals were held separately from the colony until the end of the

265   study. Before every recording session, the animal was anaesthetised by a mixture of ketamine

266   (Ketavet © 10 %, Medistar GmbH Ascheberg, Germany; 7.5 mg per kg bodyweight) and

267   xylazine (Rompun © 2 %, Bayer HealthCare AG, Mohnheim, Germany; 16.5 mg per kg

268   bodyweight) and the anaesthesia was maintained by follow-up injections of the same mixture

269   with reduced volume every 1-1.5 h, for up to 4 h total. A DC-powered heating pad that was

270   attached to the animal holder was used to maintain the animal's body temperature of 37 °C.

271   Two consecutive recording sessions in the same animal were at least five days apart. This

272   study was approved by the Regierungspräsidium Darmstadt (permits: FR/1010 and FR/2007)

273   and was performed in full compliance with current German laws.

274

275   **Stimulation and recording procedure**

276   Custom written MATLAB (MathWorks Inc., US) scripts were used for stimulation and data

277   acquisition. The digital stimulus signal was D/A-converted by a 384 kHz Adi-2 Pro soundcard

278   (RME, Haimhausen, Germany) before it was fed into a HiFi-amplifier (Power Amplifier RB-

279   1050, Rotel, Hongkong, China) and presented to the animal by a Fountek NeoPro 5i Ribbon

280   Tweeter (Fountek Electronics Co.,Ltd, Jiaxing, China). The speaker was positioned 15 cm

281   away from the animal and pointed directly towards the left ear in a 45 ° azimuth angle relative

282   to the head. To ensure a constant distance and angle between ear and speaker, the animal was

283   head-fixed by a mouth-holder. All stimuli were natural vocalisations of *C. perspicillata* or

284   vocalisation mimics with durations between about 2 to 10 ms (Fig 1, Supp. Fig. 1). The social

285   communication call that was used as target tone in experiment 1 (Fig. 1a) is a distress call, a

286   social vocalisation that is emitted by the animal when under physical duress. Like all calls

287   used in this study, it was recorded from a freely behaving bat. The echolocation and

288   communication mimics are noise bursts covering very similar frequency ranges as their

289   natural counterparts. They also resemble the vocalisations in their durations and rise/fall-

290   times, with only the temporal structure of the natural and artificial stimuli being

291   fundamentally different from each other. All stimuli had an intensity of 60 dB SPL and were

292   presented at a rate of 20 Hz, equivalent to a stimulus-onset asynchrony of 50 ms.

293   The oddball paradigm that was used to study effects of deviance detection in the ABR

294   consisted of 2 sequences of stimuli. In the first sequence, stimulus 1 was presented as standard

295   (high probability, 90 %) and stimulus 2 as deviant (low probability, 10 %). The second

296   sequence was presented consecutively and resembled the first one but with opposite roles of

297   the stimuli, where now stimulus 1 was the deviant and stimulus 2 the standard (Fig. 1b). In

298   total, a sequence contained 1000 stimuli (900 standards, 100 deviants). To characterise the

299   measured deviance detection effects in more detail, two control sequences were used. The

300   first was the MS control[10], presenting the target stimuli (echolocation pulse and social

301   communication call) in a pseudo randomly arranged sequence together with eight additional

302   stimuli, all having a probability of occurrence of 10 %. The other eight stimuli were the two

303   vocalisation mimics, an AM communication (distress) call (Fig. 1d) and 5 other social

304   communications of *C. perspicillata* that are related to different behaviours (Supp. Fig. 1). The

305   MS control is expected to generate responses that are unaffected by any modulatory effects of

306   probability encoding (repetition suppression or deviant enhancement) since the stimuli are

307   perceived neither as deviant nor standard. As a second control, the echolocation pulse and

308   social communication call were presented in another sequence where their probability of

15

309   occurrence was 50 %, respectively. Like in the oddball paradigm, the sequences of both

310   controls consisted of 1000 stimuli each.

311   ABRs were differentially recorded by two electrodes – chlorinated silver wires (AG-10T,

312   diameter: 0.25 mm; uninsulated and chlorinated tip of 3 mm) – that were placed

313   subcutaneously at the vertex of the animal's skull and close to the bulla of the left ear. A

314   ground electrode was clipped to the animal's right thumb. The recorded responses were

315   hardware filtered (0.1-3000 Hz, 20 dB/decade roll-offs) and amplified by a factor of 20k by a

316   Dagan EX1 differential amplifier (Science Products GmbH, Hofheim, Germany) before they

317   were A/D-converted by the soundcard and sent to the computer. Blocks of 20 consecutive

318   points of the input signal were averaged in order to down-sample the signal to 19.2 kHz.

319

320   **Data processing and statistical evaluation**

321   All processing and statistical evaluation of the data was conducted in MATLAB. The

322   recorded ABRs were bandpass filtered by a Butterworth filter (4th order) in two different

323   ways, dependent on the analysis. For the broadband filtered responses, low- and high-cut

324   frequencies of 0.1 Hz and 2500 Hz, respectively, were used, which did remove high

325   frequency noise from the signal but left the ABRs otherwise almost unchanged. On the other

326   hand, the narrowband filter removed frequencies below 300 Hz and above 2500 Hz,

327   abolishing all slow components of the response and allowing a more detailed inspection of the

328   fast ABR waves i-iv. Before averaging, each trial was baseline corrected by calculating the

329   mean voltage in a time window 1 ms pre stimulus onset. This value was subtracted from the

330   whole trail resulting in a pre-stimulus activity of 0 µV. Subsequently, the averaging procedure

331   was restricted to those deviant responses that followed a standard response and, vice versa,

332   those standard responses that preceded a deviant response. This method allows to use the

333   same number of trials to calculate the deviant and standard average of each animal (here

334 between 89 and 92 trials) and, at the same time, maximises the effects of deviance detection

335 in the responses[8]. In the case of the 50 % control, the same number of trials that was used to

336 calculate the deviant and standard average for a given animal was used to randomly choose

337 trials out of the 500 available responses to each stimulus. The MS average was calculated

338 based on all responses to a given stimulus in the MS sequence (between 85 and 110 trials;

339 mean difference to oddball responses: + 2.4 trials). All responses were corrected for the

340 sound-travelling delay caused by the distance between speaker and ear. In each graph, the

341 time point of 0 ms represents the moment when the sound reached the bat's ear.

342 To evaluate the response strength of each ABR, time windows were defined within which the

343 response's RMS value was calculated. This has been done successfully in the same species

344 before[8,22]. For all broadband filtered responses, this time window spanned from 0 ms to 10

345 ms, covering the whole ABR with all its fast and slow components. The detailed wave-by-

346 wave analysis of the narrowband filtered responses was done using three consecutive time

347 windows, each containing a different component of the ABR. Those windows had borders of

348 0 ms – 1 ms (wave i), 1 ms – 2.2 ms (wave ii/iii) and 2.2 ms – 3.4 ms (wave iv) which are

349 similar to previously reported ABR-wave latencies of other bat species[23–25].

350 To compare response strengths between conditions with each other, paired one-tailed t-tests

351 (deviant vs. standard responses) and repeated measure ANOVAs (deviant vs. standard vs.

352 control responses) with subsequent Bonferroni-corrected post-hoc tests were used to evaluate

353 differences between the calculated RMS values. Additionally, the effect size measure Cohen's

354 D was calculated for all significant comparisons which allows an estimation of strength of the

355 measured deviance detection effects[26].

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357

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363   Author contributions

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366   Experiments, analysis, and original draft of the manuscript: Johannes Wetekam

367   Review and editing of the original draft: Johannes Wetekam, Julio Hechavarría, Luciana

368   López-Jury, Eugenia González-Palomares, Manfred Kössl

369

370   Conflicts of interest

371   The authors declare no competing interests.

372

373   Abbreviations

374   ABR: Auditory brainstem response

375   AM: Amplitude modulation

376   ANOVA: Analysis of variance

377   FM: Frequency modulation

378   MMN: Mismatch negativity

379   MS: Many-standards

380   RMS: Root Mean Square

381   SSA: Stimulus-specific adaptation

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