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**Citation** (please note it is advisable to refer to the publisher's version if you intend to cite from this work)

**Lameira, AR, Hardus, ME, Mielke, A, Wich, SA and Shumaker, RW (2016)  
Vocal fold control beyond the species-specific repertoire in an orang-utan.  
Scientific Reports, 6. ISSN 2045-2322**

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1 **Vocal fold control beyond the species-specific repertoire in an orang-utan**

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27 **KEYWORDS:** Voice, vocal behavior, call repertoire, great ape vocalization, learned call,  
28 vocal learning, social learning, speech evolution

29 **ABSTRACT**

30 Vocal fold control was critical to the evolution of spoken language, much as it today allows us to  
31 learn vowel systems. It has, however, never been demonstrated directly in a non-human primate,  
32 leading to the suggestion that it evolved in the human lineage after divergence from great apes.  
33 Here, we provide the first evidence for real-time, dynamic and interactive vocal fold control in a  
34 great ape during an imitation “do-as-I-do” game with a human demonstrator. Notably, the orang-  
35 utan subject skilfully produced “wookies” – an idiosyncratic vocalization exhibiting a unique  
36 spectral profile among the orang-utan vocal repertoire. The subject instantaneously matched  
37 human-produced wookies as they were randomly modulated in pitch, adjusting his voice  
38 frequency up or down when the human demonstrator did so, readily generating distinct low vs.  
39 high frequency sub-variants. These sub-variants were significantly different from spontaneous  
40 ones (not produced in matching trials). Results indicate a latent capacity for vocal fold exercise  
41 in a great ape (*i*) in real-time, (*ii*) up and down the frequency spectrum, (*iii*) across a register  
42 range beyond the species-repertoire and, (*iv*) in a co-operative turn-taking social setup. Such  
43 ancestral capacity likely provided the neuro-behavioural basis of the more fine-tuned vocal fold  
44 control that is a human hallmark.

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48 **INTRODUCTION**

49 Spoken languages are learned anew with every human generation. Great apes, however, our  
50 closest relatives, are traditionally thought to be incapable of vocal learning<sup>1,2,cf.3,4</sup> – the capacity  
51 to expand their vocal repertoire with new calls learned from others<sup>5</sup>. This apparent paradox has  
52 led to the suggestion that human vocal capacities have no imitative precursor in nonhuman  
53 species<sup>6</sup>. The evolution of speech – the predominant means of expression of human language<sup>5</sup> –  
54 is hence currently hotly debated, as evidence seemingly challenges the importance of shared  
55 ancestry for the emergence of speech within the primate lineage, even though shared ancestry  
56 represents one of the founding pillars of Darwin’s theory of natural selection<sup>6</sup>.

57 Historical “great ape language projects” have trained captive individuals in the attempt to  
58 teach them new word-like utterances<sup>7,8</sup>. Results were, however, virtually null<sup>1,6</sup>. One major  
59 limitation of these landmark studies was the fact that detailed descriptions of the great ape vocal  
60 repertoire were, for the most part, unavailable at that time. Importantly, scientists had no  
61 verifiable catalogue or database to compare and gauge exhibited vocal flexibility. Ultimately,  
62 great apes’ vocal skills were directly compared with humans’, rather than objectively against  
63 their own natural vocal preferences, predispositions, and limitations.

64 This critical drawback has been addressed recently: new databases on the natural vocal  
65 behaviour of great apes have allowed recognizing vocal learning of new voiceless consonant-like  
66 calls<sup>3,9</sup>, notably requiring supralaryngeal control of the vocal tract. A modern-day and informed  
67 approach to great ape vocal repertoire could, therefore also clarify whether (besides  
68 supralaryngeal control) vocal learning can also involve vocal fold control. This capacity would  
69 permit volitional voice modulation<sup>5</sup>, enabling individuals to expand their repertoire with new  
70 voiced vowel-like calls. Together with consonants, vowels represented the building blocks for  
71 spoken language. Being able to socially learn new voiceless *and* voiced calls would have, thus,  
72 effectively set the evolution of an ancestral hominid articulatory system on a course towards a  
73 vocal system fundamentally similar to modern speech. The evolutionary implications of the

74 presence of vocal fold control (or volitional voice modulation<sup>5</sup>) in great apes warrants, therefore,  
75 revisiting the “unsuccessful” protocols of previous historical studies under a new lens.

76 Thus far, great apes have been shown to exercise vocal fold control in some degree in  
77 “species-specific” voiced calls (or “vocalizations”), i.e. that are typically produced by the  
78 species<sup>10–14</sup>. Other studies have shown that a number of individual-specific and population-  
79 specific voiced calls in great apes do not conform to genetic and ecological divergence<sup>9,15,16</sup>,  
80 suggesting that vocal fold control may play indeed an active role in shaping the composition of  
81 the voiced repertoire of great apes. Together, these data confirm that it is imperative for our  
82 understanding on the evolution of spoken language to assess the extent to which human vocal  
83 fold skills elaborated upon those present in great apes<sup>17,18</sup>.

84 Here, we report a novel orang-utan vocalization, coined “wookie,” idiosyncratic to the  
85 vocal repertoire of an adolescent captive male – named Rocky. Our working hypothesis posed  
86 that the study subject produced wookies through volitional control over the vocal folds. If this  
87 hypothesis was in fact correct, the two major predictions followed. First, vocal fold activity and  
88 acoustic profile of the wookie should be clearly different from those of other orang-utan calls.  
89 Second, the study subject should be able to adapt vocal fold action in response to random stimuli  
90 under rigorous controlled experimental settings (e.g. to rule out arousal-based mechanisms). The  
91 calls produced in this fashion should be perceptually distinct according with their respective  
92 stimuli.

93 To test the first prediction and verify the novelty of wookies, we evaluated wookies’  
94 acoustic profile in light of the known orang-utan call repertoire. Specifically, we measured and  
95 assessed parameters describing vocal fold activity and supralaryngeal manoeuvring between  
96 wookies and its most similar call-type in the orang-utan repertoire. To test the second prediction,  
97 we brought the subject’s putative vocal fold control under scrutiny by presenting him with a  
98 imitative “do-as-I-do” game paradigm<sup>19,20</sup>. Under this paradigm, a human demonstrator produced  
99 wookie-approximations with varying acoustic features as an implicit request towards the subject  
100 to produce vocalizations of matching features. Subject’s vocal responses were recorded and  
101 compared with the human models and between themselves. Our results show that a nonhuman  
102 great ape can achieve levels of volitional voice control qualitatively comparable to those  
103 manifested in humans; notably, real-time, dynamic and interactive vocal fold control beyond the  
104 species-specific vocal repertoire.

## 107 **Methods**

### 108 *Orang-utan wookies and the species-specific repertoire*

#### 110 *Data Collection*

111 To test the first prediction of this study and verify the idiosyncrasy of wookies and their novelty  
112 among the known orang-utan repertoire, we recorded spontaneous wookies from Rocky  
113 (studbook ID: 3331) during interactions with the human experimenter (MEH) between April and  
114 May 2012 at the Indianapolis Zoo, where he is currently housed. We used a ZOOM H4Next  
115 Handy recorder via the inbuilt mic standing on a miniature tripod at approximately ~0.5m  
116 distance from the subject. Recordings were collected at a sampling rate of 24bit/48,000kHz and  
117 saved in wav format. These settings obtained high quality audio recording and are standard for  
118 the collection of orang-utan call behaviour in captivity and the wild. The original version of  
119 wookies has been produced by Rocky for at least the last 6.5 years. It was apparent when the

120 experimenters first met Rocky when he was 3.5 years old. It is unclear how he originally learned  
121 the vocalization and no recordings are available from earlier years. Wookies are produced by the  
122 subject to gather attention from caretakers<sup>16,21</sup>. Recordings from the known orang-utan call  
123 repertoire available from previous work<sup>22</sup> were used in order to draw a comparison with  
124 wookies.

#### 125 126 *Data analyses*

127 In order to verify the novelty of wookies in relation to the remaining orang-utan call repertoire,  
128 we assessed the largest database ever assembled of orang-utan calls<sup>22</sup>, currently spanning more  
129 than 12,000 observation hours across 9 wild and 6 captive populations, and comprising more  
130 than 120 individuals. We compared wookies produced spontaneously (i.e. not given in response  
131 to human wookie-versions) with the spectrally most similar vocalization known to be produced  
132 by orang-utans – the grumph<sup>22</sup>. Grumphs were the only vocalization presently described in the  
133 orang-utan repertoire to exhibit a complete overlap in frequency range with wookies (grumphs:  
134 86 – 1723Hz, wookies: 99.6 – 1418Hz). Both calls were the only orang-utan vocalizations to fall  
135 below 100Hz and simultaneously reach above 350Hz<sup>22</sup> (Fig. 1). Wookies were produced with  
136 ingressive air-flow, whereas grumphs were presumably produced with egressive air-flow (as  
137 various other orang-utan calls)<sup>22</sup>. Nevertheless, we decided to conduct a comprehensive acoustic  
138 comparison in order to verify, with confidence, wookies' idiosyncrasy and prevent claims of  
139 novelty strictly based on one immeasurable articulatory feature (i.e. air-flow direction). For this  
140 comparative analysis, grumphs were sampled from wild adolescent males of similar age as  
141 Rocky in order to control for the largest number of potentially confounding factors as possible;  
142 primarily, sex and body size variation. In order to control for potential geographic variation in  
143 grumph acoustics, all wild adolescent males were sampled from the same population (i.e.  
144 Ketambe Forest, Aceh, Sumatra, Indonesia).

145 To acoustically compare wookies with orang-utan grumphs, acoustic measures were  
146 conducted with Praat, using "voice report" standard settings, except for voicing threshold in the  
147 pitch settings, which was set to 0.15. Seven acoustic parameters describing vocal fold oscillation  
148 were measured: duration, median pitch, mean pitch, pitch standard deviation, minimum pitch,  
149 maximum pitch and pitch amplitude. Complementary, three acoustic parameters describing  
150 supralaryngeal action were measured: first, second and third formant. Because these parameters  
151 directly express the position of the tongue and jaw during vocal production, they were used to  
152 assess whether wookies also involved different oral manoeuvres, besides different oscillation  
153 patterns at the vocal folds.

154 Statistical analyses were conducted using nonparametric tests with IBM SPSS Statistics  
155 21 (SPSS, Inc.). To compare the differences between wookies and grumphs, one would typically  
156 use a Mann-Whitey U test for each parameter. However, because different individuals  
157 contributed with several calls to our dataset, this condition violated the assumption of data  
158 independence for conducting Mann-Whitney U tests. As such, we opted to conduct Kruskal  
159 Wallis tests between individuals for each parameter, while correcting for multiple testing using  
160 Bonferroni correction. We expected that Kruskal Wallis test results would show the following.  
161 For each parameter, our study subject should be different from all other individuals, while all  
162 other individuals should not be different between themselves, since wookies only derived from  
163 our study subject whereas grumphs derived from all the remaining individuals. For these  
164 analyses, we included our subject and the other adolescent males for whom a sample size larger

165 than one was available (i.e. 2 individuals with 24 and 12 calls). This operation resulted in the  
166 exclusion of three adolescent males for which one grumph recording was available.

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### 169 *Orang-utan vocal fold action in match trials*

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#### 171 *Data Collection*

172 To test the second prediction of this study, experimental testing was conducted with Rocky  
173 during April and May 2012 at the Indianapolis Zoo. The zoo's committee provided ethical  
174 approval and permission to conduct research, and the methods were carried out in accordance  
175 with the approved guidelines. "Do-as-I-do" paradigm was selected for match trials because this  
176 paradigm has been successfully used previously to invoke voluntary call responses in captive  
177 orang-utans<sup>19,20</sup>. Human demonstrator used protective gloves and a facial mask at all times and  
178 interacted with Rocky always through enclosed mesh. Rocky was rewarded during trial sessions  
179 with customary food snacks (i.e. raisins and dried plums) or drinks, prepared and provided by  
180 full-time orang-utan caretakers at the zoo. Caretakers assured the items used differed in no  
181 noticeable way in terms of the subject's food preferences and food rewards did not vary within  
182 trial sessions.

183 Under the "do-as-I-do" test paradigm, the human demonstrator presented Rocky with  
184 random sequences (Runs test,  $Z = -4.751$ ,  $p < 0.001$ ) of human wookie-versions varying in  
185 frequency (Hz) – low vs. high wookies. 513 trials were presented (272 low, 241 high), divided  
186 through 13 sessions (~49 trials/session, ~472 seconds/session) over the course of 5 days. The  
187 subject typically responded to the model signal within approximately 500ms.

188 Trial sessions were recorded at ~0.5m distance from the subject with a ZOOM H4Next  
189 Handy recorder via the inbuilt mic standing on a miniature tripod. Recordings were collected at a  
190 sampling rate of 24bit/48,000kHz and saved in wav format. These settings obtained high quality  
191 audio recordings. Rocky only joined trial sessions voluntarily and never refused to participate.  
192 Rocky was never food deprived during trials sessions and trial sessions never interfered with  
193 normal feeding times or working schedule at the orang-utan enclosure so as to prevent imposing  
194 any stress. Rocky was tested when he and his cohort (four other orang-utans) were housed in  
195 their individual quarters.

196 During trial sessions, only the first reply immediately after the human model was  
197 considered for analyses, unless the human demonstrator verbally instructed (repeating the call  
198 model or saying the name of the variant to be matched, "low" or "high") the focal to repeat, in  
199 which case we considered the call produced after the last instruction provided by the human  
200 demonstrator, or the last call produced by the focal before the human demonstrator verbally  
201 closed the bout (e.g. by saying "yes" or "very good"). We did not consider calls when overlap  
202 between human model and orang-utan match reply did not allow suitable extraction of acoustic  
203 parameters from both calls (i.e. focal was too quick to reply).

204 We intentionally selected a human demonstrator with no previous voice training or music  
205 experience. Because our main aim was fundamentally evolutionary, we deliberately avoided  
206 using a demonstrator with vocal skills well beyond those potentially present in a human ancestor.  
207 We mandated model calls to be as "raw" and naturally sounding as much as possible. No *a priori*  
208 guidelines were given to the human demonstrator before match trials and no acoustic treatment  
209 was given to her utterances. Moreover, we purposefully did not obstruct the human demonstrator  
210 from deploying her natural behaviour during the interaction (e.g. occasional approximation to the

211 subject, occasional arm movement). Crucially, this decision allowed the demonstrator to keep the  
212 subject engaged and cooperative during the tests. Nevertheless, we were adamant about  
213 providing no training sessions, opportunities or time to the subject before the match trials, and  
214 the subject was presented a human demonstrator with whom he was not familiar. These factors  
215 confidently assured that our subject did not develop conditioned responses.

216

### 217 *Data analyses*

218 In order to compare the acoustic profile and general vocal fold oscillation between human- and  
219 orang-utan-produced wookies, we selected and analyzed call maximum frequency (Hz). This  
220 parameter was also used to compare the subject's wookie sub-variants between each other  
221 (spontaneous, high and low). Maximum frequency is the frequency at which maximum energy  
222 (dB) occurs within a call. For this reason, maximum frequency contributes disproportionately to  
223 pitch and, in the case of wookies, it represented one of the best proxies available for pitch  
224 (Spearman test between maximum frequency and mean pitch,  $r = 0.341$ ,  $N_{\text{spontaneous wookies}} = 124$ ,  $p$   
225  $> 0.001$ ). Moreover, maximum frequency was equal to the fundamental frequency ( $F_0$ ) 93.4% of  
226 500 measured cases. Therefore, maximum frequency provided one of the most reliable measures  
227 of the oscillation rate of the vocal folds and its perception. In order to assess the subject's level of  
228 accuracy during the task, we also conducted the same test but analysing low and high wookies  
229 separately.

230 Besides maximum frequency, we measured duration and maximum power (dB) within  
231 each call. Because all recordings were conducted at a constant distance from the study subject,  
232 maximum power could be used as a proxy of glottal air pressure during call production. This  
233 measure allowed us, thus, to monitor the contribution of abdominal action (generating air current  
234 within the vocal tract) during the production of wookies exhibiting different maximum  
235 frequencies.

236 Maximum frequency, duration and maximum power were extracted from recordings  
237 using Raven Pro software package (version 1.5, Ithaca, NY: The Cornell Lab of Ornithology)  
238 and Hann type spectrogram grip spacing at 2.93Hz. The use of other important parameters  
239 characterizing vocal fold oscillation (e.g. harmonics-to-noise ratio) was hampered because these  
240 parameters are particularly susceptible to recording settings<sup>20</sup>.

241 Nonparametric statistical analyses were conducted using IBM SPSS Statistics 21 (SPSS,  
242 Inc.). Spearman binomial correlation test was used to assess a potential effect of human model  
243 calls on the responses produced by the study subject. Wilcoxon signed ranks test was used to  
244 identify potential differences between wookie subvariants produced by the study subject.  
245 Discriminant function analyses were used to assess whether wookie subvariants produced by the  
246 study subject could be distinguished perceptually. Discriminant function analyses were  
247 conducted both by setting prior probabilities (i.e. chance probability of correct assignment) equal  
248 between all groups and by computing prior probabilities based on group size. Because our data  
249 set for these analyses derived from the same individual, this did not require conducting a  
250 permuted discriminant function analysis. A permuted analysis would have otherwise allowed  
251 controlling for a possible confounding variable. For instance, if several individuals had  
252 contributed wookie subvariants, the permuted analysis would have allowed controlling for  
253 individual variation while assessing the capacity to correctly distinguish wookie subvariants.

254 Because receivers sense acoustic signals holistically instead of attending to one or few  
255 acoustic parameters separately<sup>23</sup>, we tested whether low and high wookies produced by Rocky  
256 were overall perceptually distinct from each other by using automated classification algorithms,

257 combined with artificial neural networks (ANN) and mel frequency cepstral coefficients  
258 (MFCC)<sup>24</sup>, a classification method that scans and analyses signals based on their general acoustic  
259 profile. These analyses allowed assessing the differences between wookie sub-variants while  
260 taking in consideration their complete acoustic profile simultaneously, other than one acoustic  
261 parameter at a time. For both feature extraction and network analyses, Matlab R2012b (The  
262 MathWorks, Inc., Natick, MS, U.S.A.) was used. The MFCCs in this study were computed using  
263 the ‘melcepst’-routine available in the toolbox Voicebox. We optimized both MFCC and ANN  
264 according to published guidelines<sup>24</sup>. To acquire a MFCC, each call was sliced into seven frames  
265 using a Hamming window, two-thirds frame overlap and 16 mel-spaced filters<sup>24</sup>. We used 10  
266 hidden layer neurons and 100 iterations to obtain an optimal ANN<sup>24</sup>. To increase the reliability of  
267 the results, every call was tested against seven neural networks, and the condition proposed by  
268 the majority of the networks was considered final<sup>24</sup>. Calls were tested using a leave-one-out  
269 procedure<sup>24</sup>.

270 Lastly, we conducted Spearman binomial correlation tests between maximum frequency,  
271 duration and maximum power of the subject’s wookies in order to investigate general production  
272 dynamics. With these analyses, we were particularly interested in examining to what extent low  
273 and high wookies could have been produced strictly by means of changes in glottal air pressure  
274 generated by abdominal control (other than by vocal fold control).  
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277

## 277 **Results**

278 *Orang-utan wookies and the species-specific repertoire*  
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281 A number of acoustic parameters was measured characterizing the oscillation pattern of the vocal  
282 folds with high accuracy. Significant differences were detected within our sample comprised by  
283 our study subject ( $n_{\text{wookies}} = 124$ ) and other adolescent males ( $n_{\text{grumphs}} = 36$ ,  $n_{\text{individuals}} = 2$ ,  
284  $n_{\text{grumphs/ind}} = 24$ , 12) with regards to duration (Kruskal Wallis test,  $df = 2$ ,  $X^2 = 62.080$ ,  $p <$   
285  $0.001$ ), median pitch ( $X^2 = 29.404$ ,  $p < 0.001$ ), mean pitch ( $X^2 = 56.899$ ,  $p < 0.001$ ), pitch  
286 standard deviation ( $X^2 = 20.592$ ,  $p < 0.001$ ), minimum pitch ( $X^2 = 26.508$ ,  $p < 0.001$ ), maximum  
287 pitch ( $X^2 = 62.201$ ,  $p < 0.001$ ), and pitch amplitude ( $X^2 = 20.540$ ,  $p < 0.001$ ). Post hoc pairwise  
288 comparisons between individuals revealed that, for all parameters, our study subject was (with  
289 the exception of two out of 14 pairwise comparisons) always significantly different from the  
290 remaining individuals (duration:  $p < 0.001$  and  $p < 0.001$ ; median pitch:  $p < 0.001$  and  $p = 0.002$ ;  
291 mean pitch:  $p < 0.001$  and  $p < 0.001$ ; pitch standard deviation:  $p < 0.001$  and  $p = 0.054$ ; minimum  
292 pitch:  $p < 0.001$  and  $p = 0.004$ ; maximum pitch:  $p < 0.001$  and  $p < 0.001$ ; pitch amplitude:  $p <$   
293  $0.001$  and  $p = 0.133$ ). At the same time, the remaining individuals showed always no significant  
294 differences between each other (duration:  $p = 0.539$ ; median pitch = 1.000; mean pitch: 1.000;  
295 pitch standard deviation: 0.124; minimum pitch:  $p = 1.000$ ; maximum pitch:  $p = 0.884$ ; pitch  
296 amplitude:  $p = 0.051$ ). Overall, wookies were significantly longer and exhibited lower pitch  
297 values than grumphs (Fig. 2 and Table S1 in Supplementary material).

298

299 In addition, we compared in the same way the first, second, and third formant (F1, F2,  
300 F3) between our subject and other adolescent males to assess differences in supralaryngeal  
301 maneuvering during vocal production. Significant differences within our sample of individuals  
302 were found for F1 (Kruskal Wallis test,  $df = 2$ ,  $X^2 = 11.964$ ,  $p < 0.001$ ), but neither for F2 nor F3  
303 ( $X^2 = 0.470$ ,  $p = 0.791$ ;  $X^2 = 2.307$ ,  $p = 0.316$ , respectively). Post hoc pairwise comparisons  
304 between individuals revealed that our study subject was significantly different from the



303 remaining individuals for F1 ( $p = 0.037$  and  $p = 0.019$ ), but the remaining individuals were not  
304 different between each other ( $p = 1.000$ ). Overall, tongue body (F2) and tip (F3) positioning was  
305 relatively similar between the two calls types but wookies (presenting a higher F1) involved a  
306 wider opening of the mouth during call production than that required for grumph production<sup>25</sup>.

307 These analyses encompassed multiple testing. Correction of significance level was  
308 therefore required. Even though Bonferroni correction represents an over-conservative method  
309 ( $0.05/10 = 0.005$ )<sup>26</sup>, this adjustment did not affect our results on vocal focal action, since all our  
310 tests yielding significant differences provided  $p$  values smaller than 0.001. The only significant  
311 difference dissolved by Bonferroni correction concerned F1 between our subject and the  
312 remaining adolescent males. Essentially, this result indicates that differences in vocal fold action  
313 provided the most reliable and consistent way of distinguishing wookies versus grumphs,  
314 whereas differences in supralaryngeal action were less secure.

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### 317 *Orang-utan vocal fold action in match trials*

318

319 Maximum call frequency (Hz) of human-wookies and orang-utan-wookies showed a significant  
320 positive correlation (Spearman,  $r = 0.574$ ,  $N = 513$ ,  $p < 0.001$ ) (Fig. 3). When testing for low and  
321 high wookies separately, a significant correlation between human-wookies and orang-utan-  
322 wookies was also reached for high wookies (Spearman,  $r = 0.141$ ,  $p = 0.029$ ).

323 Maximum frequency differences between low and high wookies produced by Rocky  
324 significantly differed from each other (Wilcoxon Signed Ranks test,  $Z = -10.409$ ,  $p < 0.001$ ),  
325 with low and high wookies exhibiting a median frequency of 126Hz and 161.1Hz, respectively, a  
326 difference nearly equivalent to a four-note interval on a standard musical octave (B–E) (Fig. 4,  
327 Table S2 in Supplementary material). Low and high frequency wookies produced by the subject  
328 also significantly differed in maximum frequency from spontaneous wookies ( $n = 124$ ) (low vs.  
329 spontaneous wookies: Wilcoxon Signed Ranks test,  $Z = -4.405$ ,  $p < 0.001$ ; high vs. spontaneous  
330 wookies:  $Z = -3.101$ ,  $p = 0.002$ ), with spontaneous wookies exhibiting an intermediary median  
331 frequency of 134.8Hz (Fig. 4, Table S2 in Supplementary material). Bonferroni correction of our  
332 significance value ( $0.05:3=0.0167$ ) did not affect our results.

333 Discriminant function analysis, based on maximal frequency alone, attained 50.1% of  
334 corrected assignments between low, high, and spontaneous wookies (49.6% using leave-one-out  
335 procedure), performing significantly above chance (Wilks' Lambda Chi-square,  $X^2 = 47.128$ ,  $df$   
336  $= 2$ ,  $p < 0.001$ ; Binomial test, chance probability = 0.333,  $p < 0.001$ ). Correct assignments  
337 decreased slightly to 48.0% (48.0% using leave-one-out procedure), but remained well above  
338 chance, when computing chance levels according to group size (low wookies: 42.6%; high:  
339 38.0%; spontaneous: 19.4%). Percentage of correct assignments to the three sub-variants  
340 increased to 69.5% (69.3% using leave-one-out procedure) when supplementing duration and  
341 maximum power to the analyses (Fig. 5). In these conditions, maximum frequency (together with  
342 maximum power) held the largest absolute correlation with the first discriminant function, which  
343 explained 79.4% of the total observed variation. Percentage of correct assignments increased to  
344 72.5% (72.1% using leave-one-out procedure) when computing chance levels according to group  
345 size.

346 These results were corroborated when ascribing the classification of low and high  
347 wookies to an automated process scanning the vocalizations' general acoustic profile. The mean  
348 (25%; 75% percentiles) percentage of correct assignments per session was 87.82% (84.82%;

349 95.12%). Altogether, these results confirmed that low and high wookies were perceptually  
350 distinct, and thus, that they could potentially encode biologically pertinent differences.

351 Maximum frequency, duration, and maximum power of Rocky's wookies showed  
352 significant positive correlations (Spearman,  $n = 639$ , maximum frequency x duration:  $r = 0.116$ ,  
353  $p = 0.003$ ; maximum frequency x maximum power:  $r = 0.134$ ,  $p = 0.001$ ). Bonferroni correction  
354 of our significance value ( $0.05:3=0.025$ ) did not affect these results. Graphical examination of  
355 Rocky's phonetogram (Fig. 6) showed that at any given sound pressure level Rocky was capable  
356 of generating a frequency range wider than 100Hz. This effect was particularly visible in high  
357 frequency wookies, with Rocky producing most of the calls around 160 dB but spanning well  
358 above 200Hz. At the same time, Rocky was able to produce any specific frequency tone across a  
359 range of more than 20dB.

360

361

## 362 **DISCUSSION**

### 363 *Orang-utan wookies and the species-specific repertoire*

364

365 Our results validated our first prediction, showing that wookies represent an acoustically distinct  
366 voiced call within the orang-utan call repertoire. Wookies exhibit features of air-flow, vocal fold  
367 action and jaw position unique to Rocky and described here for the first time in the *Pongo* genus.  
368 These results confirm the capacity of orang-utans to learn and acquire new calls into their  
369 individual repertoires, both in the form of voiceless consonant-like calls<sup>3,4,9,15,20</sup> and voiced  
370 vowel-like calls<sup>9,15</sup>.

371 Because our analyses focused on an idiosyncratic vocalization, there were inevitable  
372 limitations in our statistical analyses. However, after conducting procedures that contemplated  
373 the potential of confounding effects, results were always highly significant. Together with the  
374 observation that wookies and their closest counterpart in the known orang-utan repertoire exhibit  
375 opposite air-flow directions, our analyses allow determining with confidence that wookies are a  
376 novel vocalization based on parameters describing vocal fold oscillation.

377 Despite an N of 1, our study allows reevaluating current assumptions on great ape vocal  
378 capacities as well as reformulating some of the basic premises of a general theory of spoken  
379 language evolution. By demonstrating vocal learning beyond the species-specific repertoire in a  
380 great ape, our results unveil a fundamental parallel with human spoken languages. Namely, the  
381 two vocal systems, separated by approximately 10mya<sup>27</sup>, can be assumed homologous regarding  
382 open-endedness and the voiced/voiceless nature of their two building blocks.

383

### 384 *Orang-utan vocal fold action in match trials*

385

386 Our results validated our second prediction, indicating that the subject modulated vocal fold  
387 oscillation according to the model-calls provided by the human demonstrator under controlled  
388 settings. The subject adjusted his voice frequency up or down when the human model did so. For  
389 this, the subject produced significantly different vocal sub-variants that stood in average outside  
390 his normal spectrum of wookie vocalizations. Human demonstrations, thus, effectively guided  
391 the subject's vocal output. Moreover, results suggest that the subject attended, was sensitive to  
392 and coordinated his vocal responses according to the spectral dispersion of sub-variants beyond  
393 the low/high dichotomy and down to a scale of tens of Hz. Manual and automated procedures

394 demonstrated that his low vs. high wookies exhibited clear perceptible differences, allowing  
395 discerning the two with high accuracy.

396 Correlation between wookies' acoustic parameters produced by the subject indicated that  
397 high frequency wookies were simultaneously louder and longer. That is, high wookies were  
398 partly underlined by higher airflow pressure exciting the vocal folds. Accordingly, the  
399 production of wookie sub-variants by our subject resulted from the synchronized exercise of the  
400 vocal folds and the abdominal musculature generating glottal airflow (e.g. diaphragm). The  
401 action of abdominal muscles may have partially alleviated the degree of vocal fold control  
402 required to obtain the observed dynamic production across frequencies during match-trials. This  
403 positive acoustic interdependence between frequency and glottal air pressure also characterizes,  
404 however, overall human vocal production, including people with musical training<sup>28</sup>, and is a  
405 phenomenon predicted to be common among animal vocal communication systems.  
406 Nevertheless, different wookies produced by Rocky with equal frequencies exhibited wide  
407 differences in acoustic power, and vice versa. These observations would have been theoretically  
408 impossible if Rocky had not exercised some degree of direct control over vocal fold oscillation,  
409 and instead had only resorted to abdominal action to produce modulations at the level of vocal  
410 fold oscillation. The subject's phonetogram attests that vocal fold control was effective and  
411 moderately autonomous from abdominal control.

412 Our match trials were conducted in constant settings in one-to-one interactions between  
413 the subject and the human demonstrator. Food rewards were part of the subject's daily diet and  
414 were always kept constant within sessions. Accordingly, we can ascertain that the subject's  
415 performance and vocal output was not affected by the influence of other orang-utans, physical  
416 surroundings or food-driven arousal. Thus, the different wookie sub-variants produced by the  
417 subject were unrelated to specific changes in context and can be considered to have conveyed no  
418 change in function or informational content.

419 Any possible biasing effects deriving from the natural behaviour of the human  
420 demonstrator can also be excluded in light of our results. For example, the demonstrator  
421 occasionally approached the subject and moved her arm during low and high vocal models,  
422 respectively. The subject could have hypothetically used these supplementary visual cues to  
423 know which response was "correct" (instead of directly mimicking the demonstrator's voice  
424 modulation), or these cues could have somehow affected the subject's arousal in a coherent way  
425 with correct responses ("clever Hans effect"). Such interpretations can, however, be dismissed at  
426 least for three reasons. First, the subject neither necessarily gazed directly at the human  
427 demonstrator to produce a correct response, nor did human supplementary cues ensured subject's  
428 correct responses (see supplementary video). Second, the subject never raised his arm in  
429 response to the similar movement by the demonstrator. Thus, he attended to human *acoustic*  
430 signals, not other cues. Third, in case the subject's arousal had been affected, one would expect  
431 an increase in subject's arousal when interacting with a human. However, subject's low calls  
432 were lower than his spontaneous calls. Overall, visual cues or arousal offer no parsimonious  
433 explanation for our results.

434

#### 435 *Implications for spoken language evolution*

436

437 Our findings imply the functional presence of direct pathways between the primary motor cortex  
438 and the nucleus ambiguus (site of the laryngeal motor-neurons in medulla oblongata) in the ape  
439 brain, as observed in an chimpanzee by Kuypers<sup>29</sup>, allowing some degree of vocal fold control

440 autonomous from context and individual's affective state. Specifically, our analyses indicate that  
441 vocal fold control pathways and respective firing in the ape brain integrate with pathways  
442 innervating other musculatures engaged in vocal production (namely, abdominal muscles).  
443 Several motor maneuvers are brought together synergistically to generate a particular acoustic  
444 output.

445 Contrarily to the notion that spoken language emerged abruptly sometime along the  
446 genus *Homo*<sup>30</sup>, our findings amplify the spoken language evolution timeline at least five-fold  
447 (assuming speech evolution onset in *Homo* paleodemes, from 2 mya onwards) and up to 50-fold  
448 (assuming speech emergence in *H. sapiens*, 200kya)<sup>31</sup>. Full articulatory range and excellent  
449 vocal control as observed today in humans may be relatively recent within the human lineage.  
450 However, the presence of learned consonant- and vowel-like calls, potentially as far as 10 mya  
451 within our lineage, allows considering gradual forces and progression in stages towards full-  
452 blown language. This intriguing possibility raises caution in the inference of the vocal capacities  
453 of extinct hominoidae from the fossil record without complementary assessment of the vocal  
454 capacities of extant great apes.

455 Vocal control over laryngeal and supralaryngeal structures at the root of a 10 mya  
456 timeline for spoken language evolution suggests that vocal evolution could have co-evolved with  
457 cognition within the human lineage. Whereas monkey cognitive skills have been hitherto  
458 assumed to surpass their vocal counterparts<sup>32,33</sup>, the possibility that the two skillsets originally  
459 exhibited even levels of sophistication in an ancestral hominid opens new considerations on  
460 speech/language evolution. In this scenario, vocal control would have allowed the immediate  
461 manifestation, or “verbalization,” of advanced cognition. Forces propelling cognitive processes  
462 would have then compelled vocal progress by association, and vice versa. For instance, with the  
463 emergence of theory of mind, individuals would have been able to exploit deceptive calls<sup>34-36</sup>,  
464 effectively launching new communicative and social dynamics within a population where  
465 acoustic deception was previously absent. If vocal and cognitive sophistication developed hand-  
466 in-hand over the course of human evolution during the last 10 mya, then, the processes of speech  
467 evolution and language evolution could be considered to have been one and the same. This  
468 “speech-language co-evolution” hypothesis will require future examination but it may perhaps  
469 expedite, for example, our understanding on the evolution of syntax and semantics. Because  
470 vocal control allows a functional divide between a signal (signifier<sup>35</sup>) and its functional use or  
471 meaning (signified<sup>35</sup>) – as suggested in our results – there would be few articulatory limitations  
472 for the assemblage of vocal sequences and the attribution of their respective informational  
473 content, so long as we had the required cognitive machinery to do so. In other words, in a  
474 condition where vocal evolution kept close pace with cognition, a human ancestor (regardless  
475 his/her position along human evolution timeline) would rarely have cognitive computations for  
476 which there were no matching vocal counterparts.

477

478

## 479 CONCLUSION

480

481 We demonstrate real-time, dynamic and interactive vocal fold control beyond the vocal range of  
482 the orang-utan genus. This study offers a new category of vocal learning in great apes, in  
483 addition to previous cases describing gradual (over the course of months) and directional shift  
484 (exclusively downwards in frequency) of a species-specific vocalization<sup>10</sup>. Orang-utans (and  
485 possibly other great apes) possess a latent capacity for controlled deployment of vocal fold

486 oscillation, allowing the volitional production of novel vowel-like calls. Theoretically, together  
487 with the capacity of great apes to socially learn voiceless consonant-like calls<sup>3,20</sup>, this proto-  
488 linguistic capacity constituted a crucial prerequisite for the onset of spoken language evolution.  
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### 591 **Acknowledgments**

592 ARL was supported by a European Union COFUND/Durham Junior Research Fellowship. We  
593 thank the Indianapolis Zoo for permission to conduct this study and logistical support. We thank  
594 Tecumseh Fitch, Robert Barton and Roger Mundry for helpful comments on earlier versions of  
595 the manuscript. The authors confirm that all data underlying the findings are fully available  
596 without restriction. The majority of relevant data are within the paper. Remaining data is  
597 available upon request to the corresponding author.  
598

### 599 **Competing interests**

600 None of the authors have any competing interests.  
601

### 602 **Author contribution statement**

603 ARL, MEH, SW and RS conceived the study and methodological protocol. ARL and MEH  
604 conducted the experiments. ARL and AM conducted data analyses. ARL, MEH, SW and RS  
605 wrote the manuscript.  
606  
607  
608

609 **Figure legends**

610

611 Fig. 1. Spectrographic representation of two orang-utan grumphs followed by two wookies

612

613 Fig. 2. Boxplot per acoustic parameter of Rocky (producing wookies) and other adolescent males  
614 (producing grumphs) (middle line represents the median, the box represents the interquartile  
615 range (IQ) containing the middle 50% of the data, and the whiskers represent 1.5 times the IQ).

616

617 Fig. 3. Maximum frequency of human wookie demonstrations against maximum frequency of  
618 Rocky's match wookies (linear fit line with intercept suppressed).

619

620 Fig. 4. Boxplot of the maximum frequency of low, spontaneous, and high wookie by Rocky  
621 (middle line represents the median, the box represents the interquartile range (IQ) containing the  
622 middle 50% of the data, and the whiskers represent 1.5 times the IQ).

623

624 Fig. 5. Graphic representation of first and second canonical discriminant functions, displaying  
625 distribution and group centroids of Rocky's low frequency (1), high frequency (2), and  
626 spontaneous wookies (3).

627

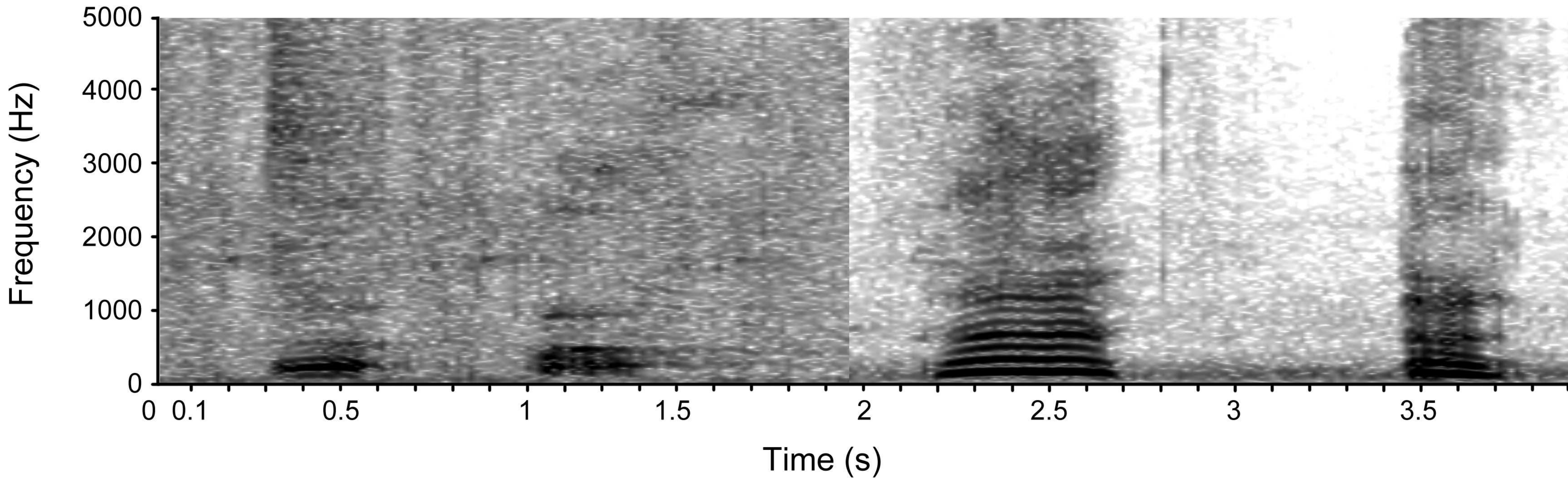
628 Fig. 6. Phonetogram displaying Rocky's wookies according to maximum frequency and  
629 maximum power.

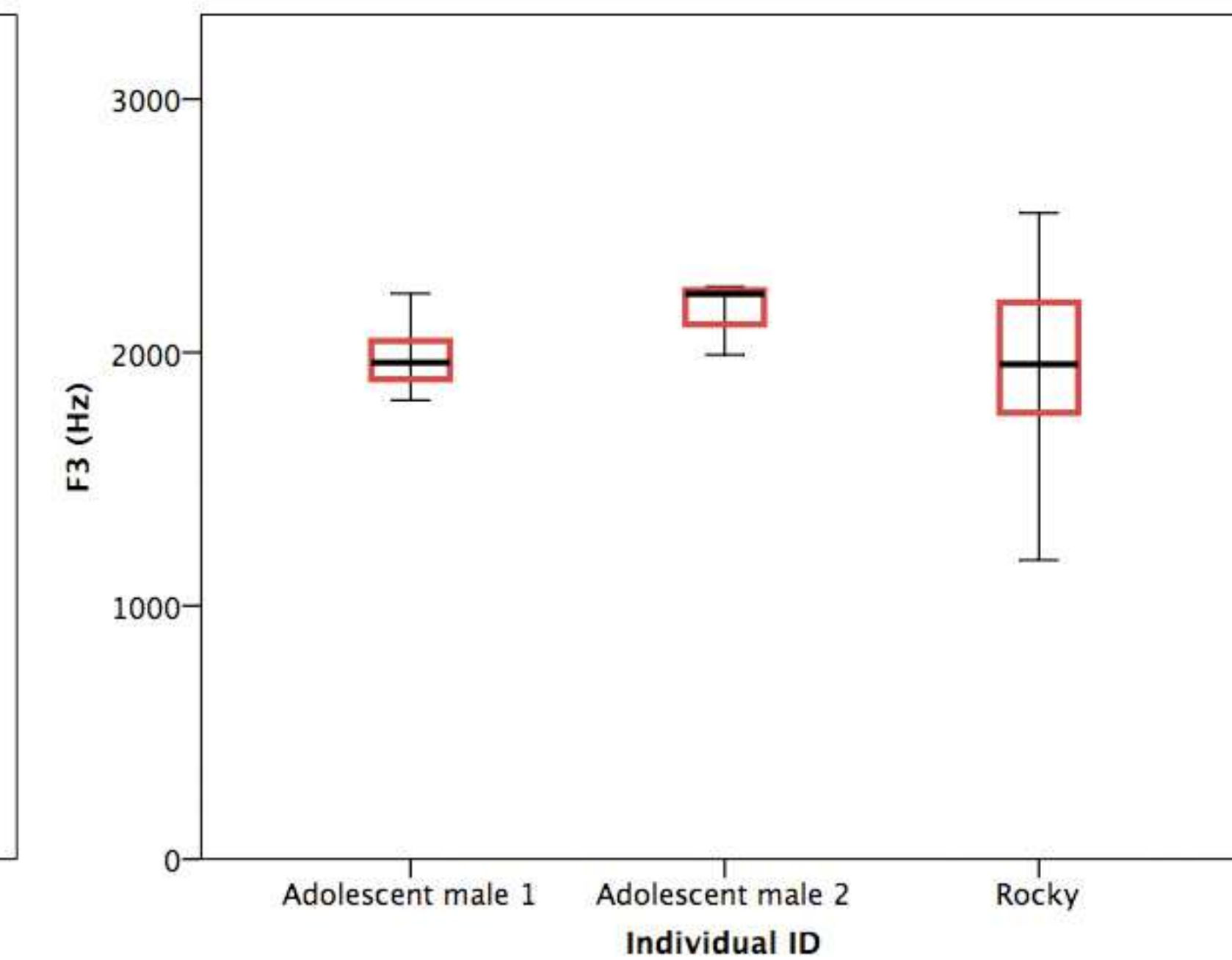
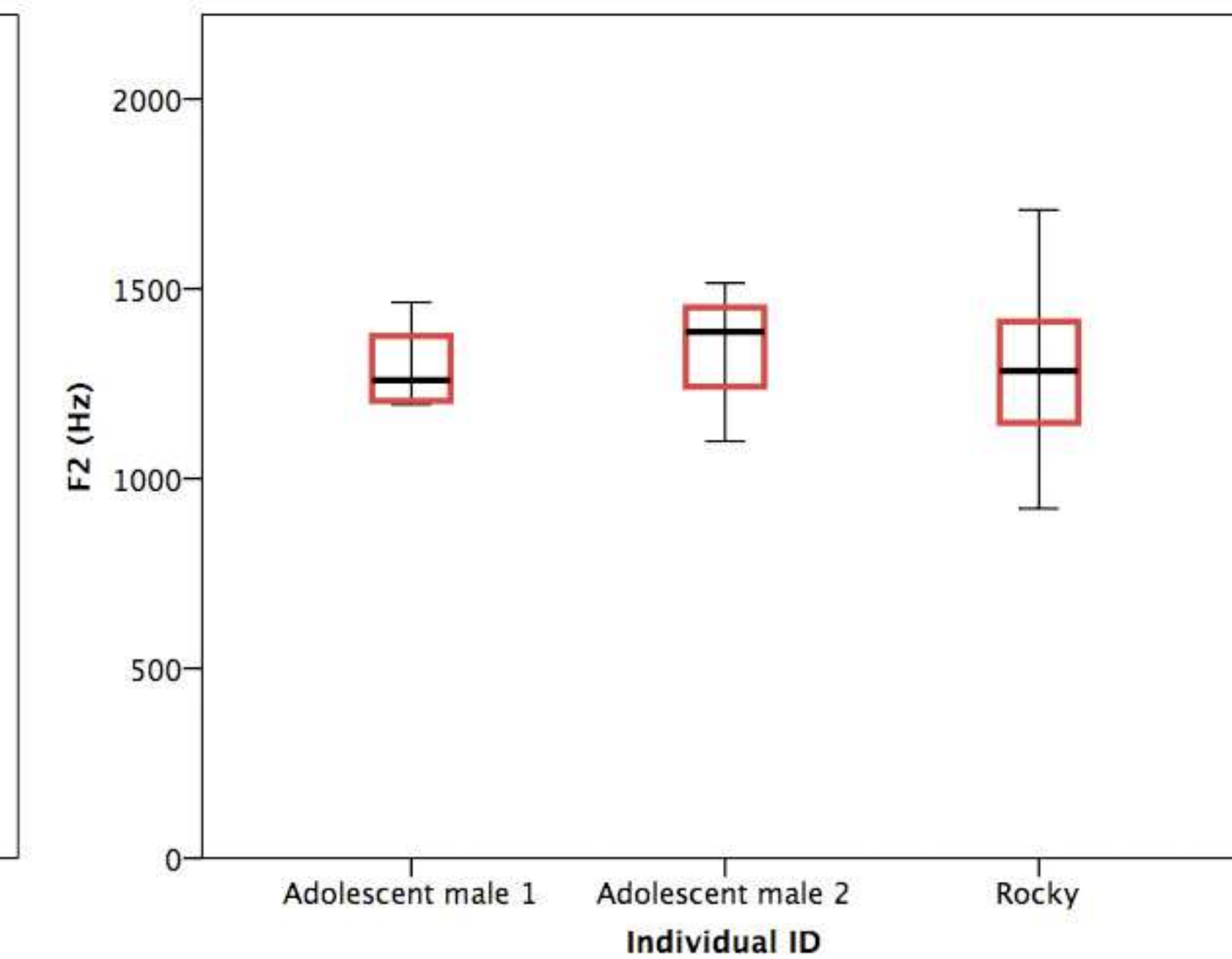
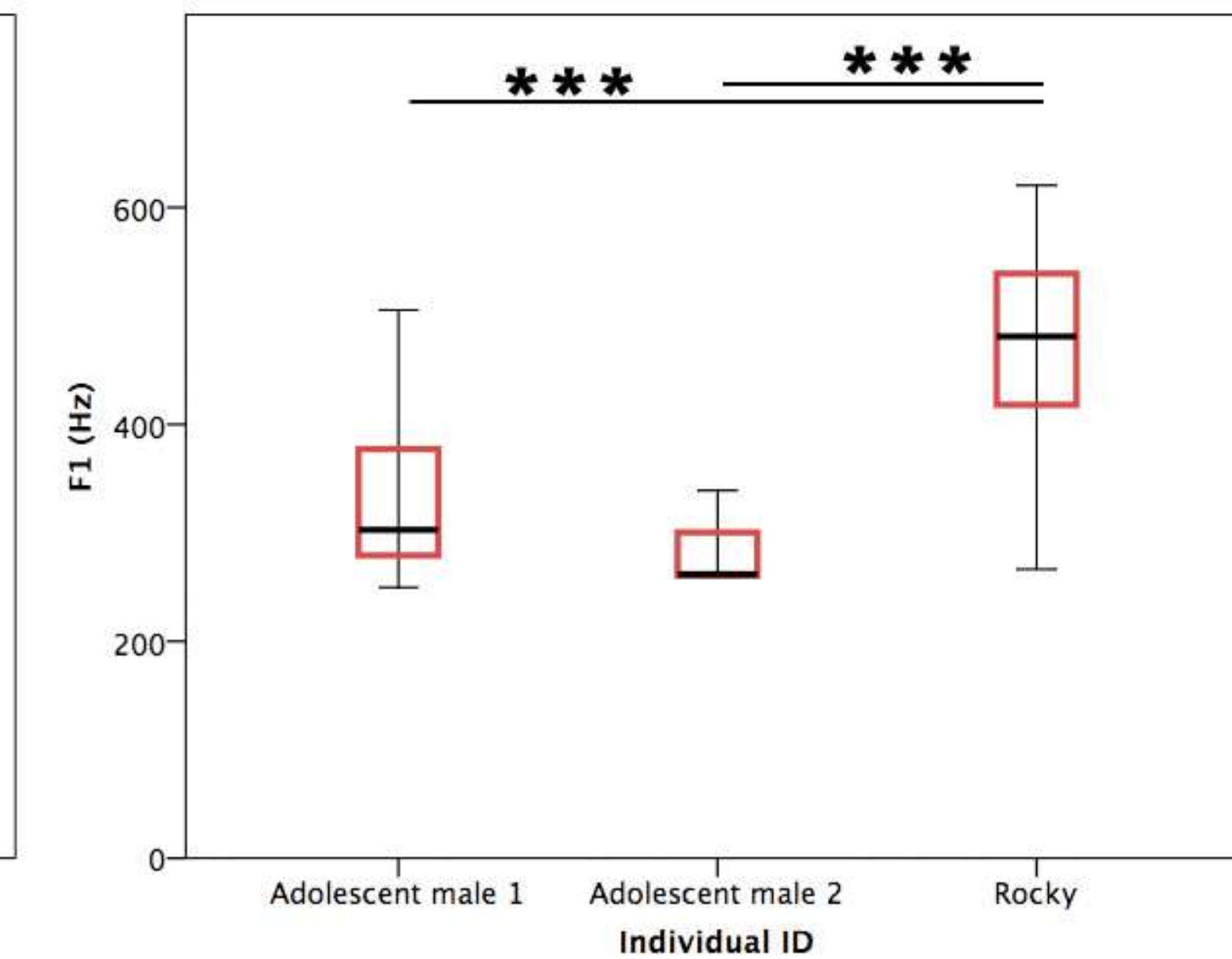
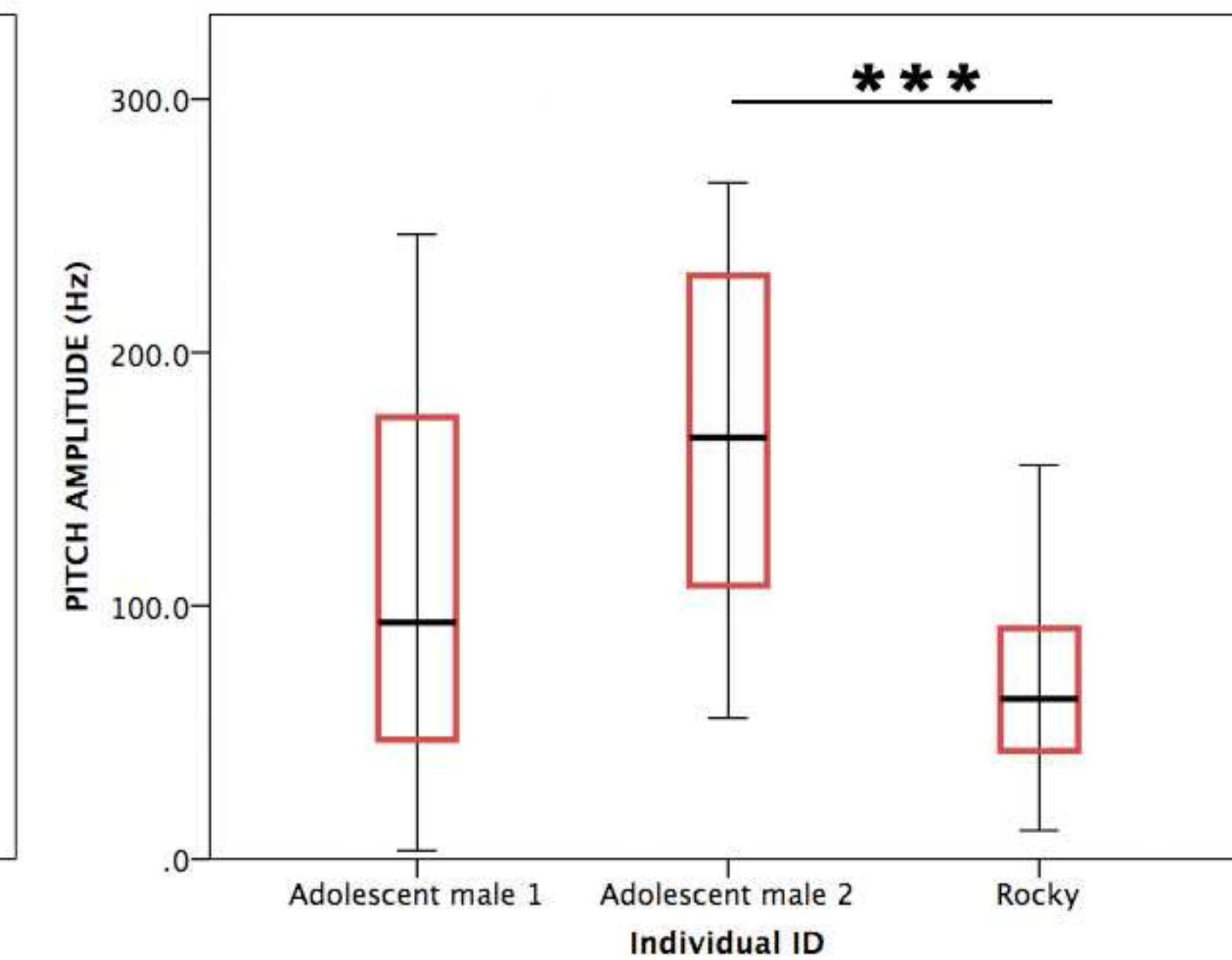
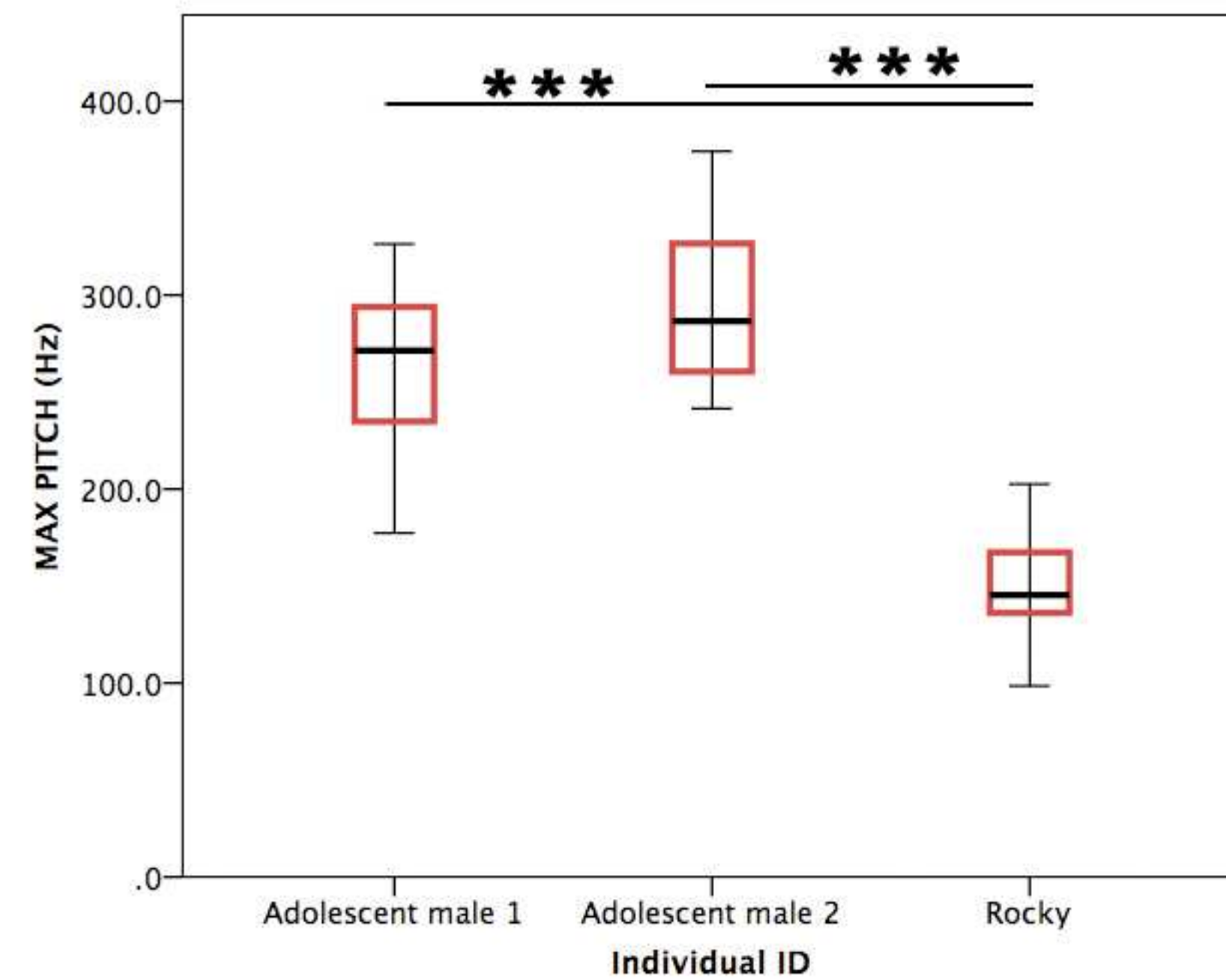
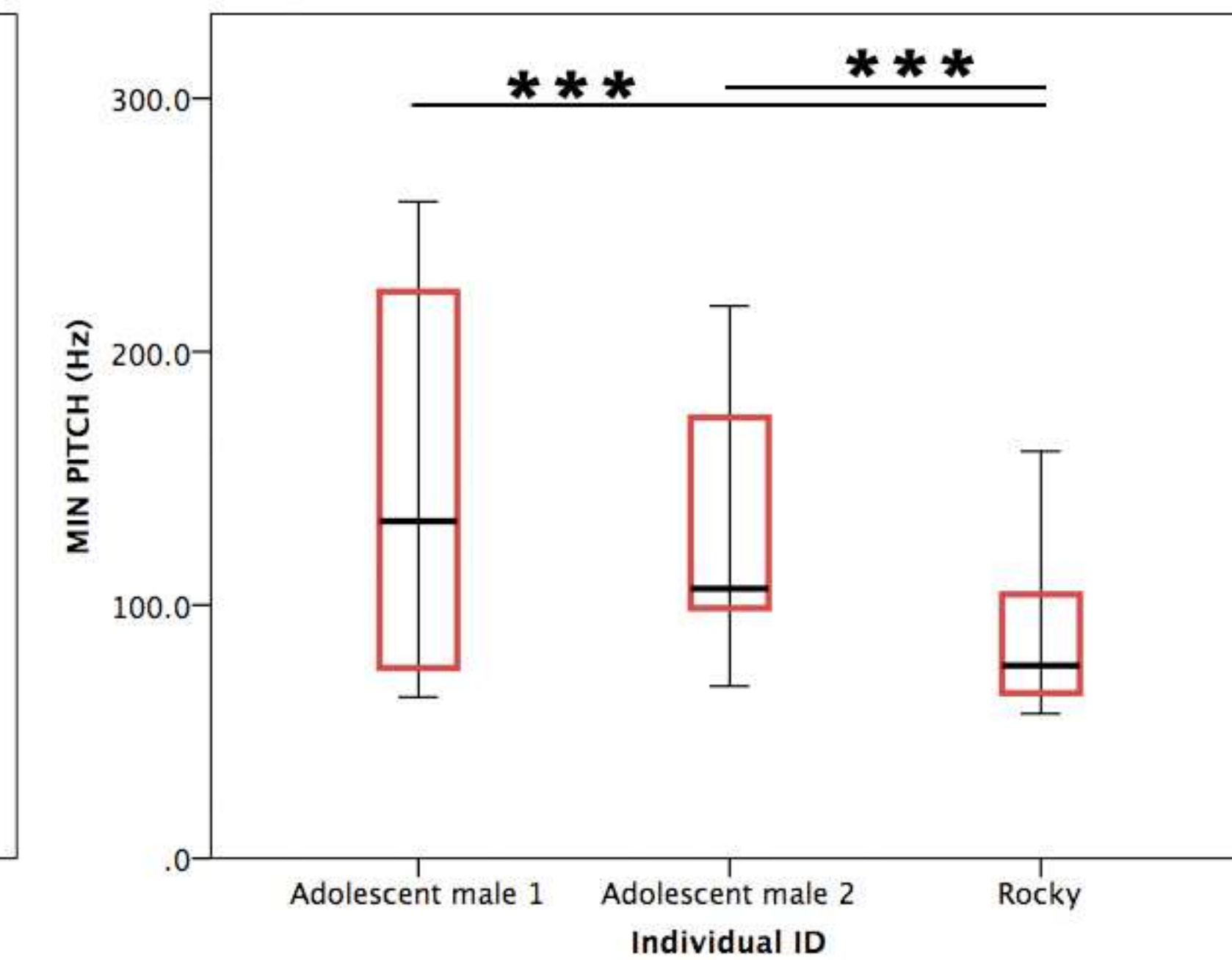
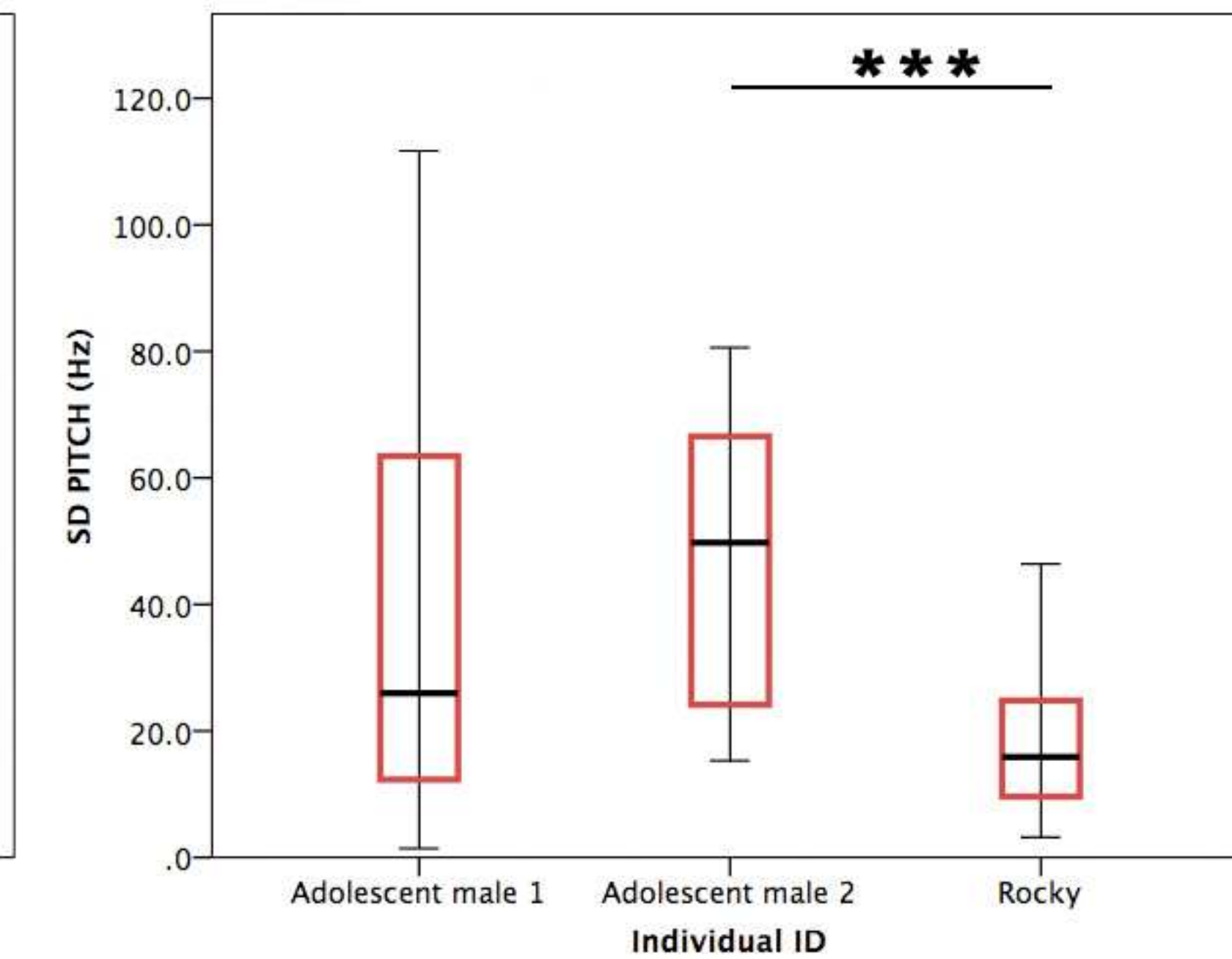
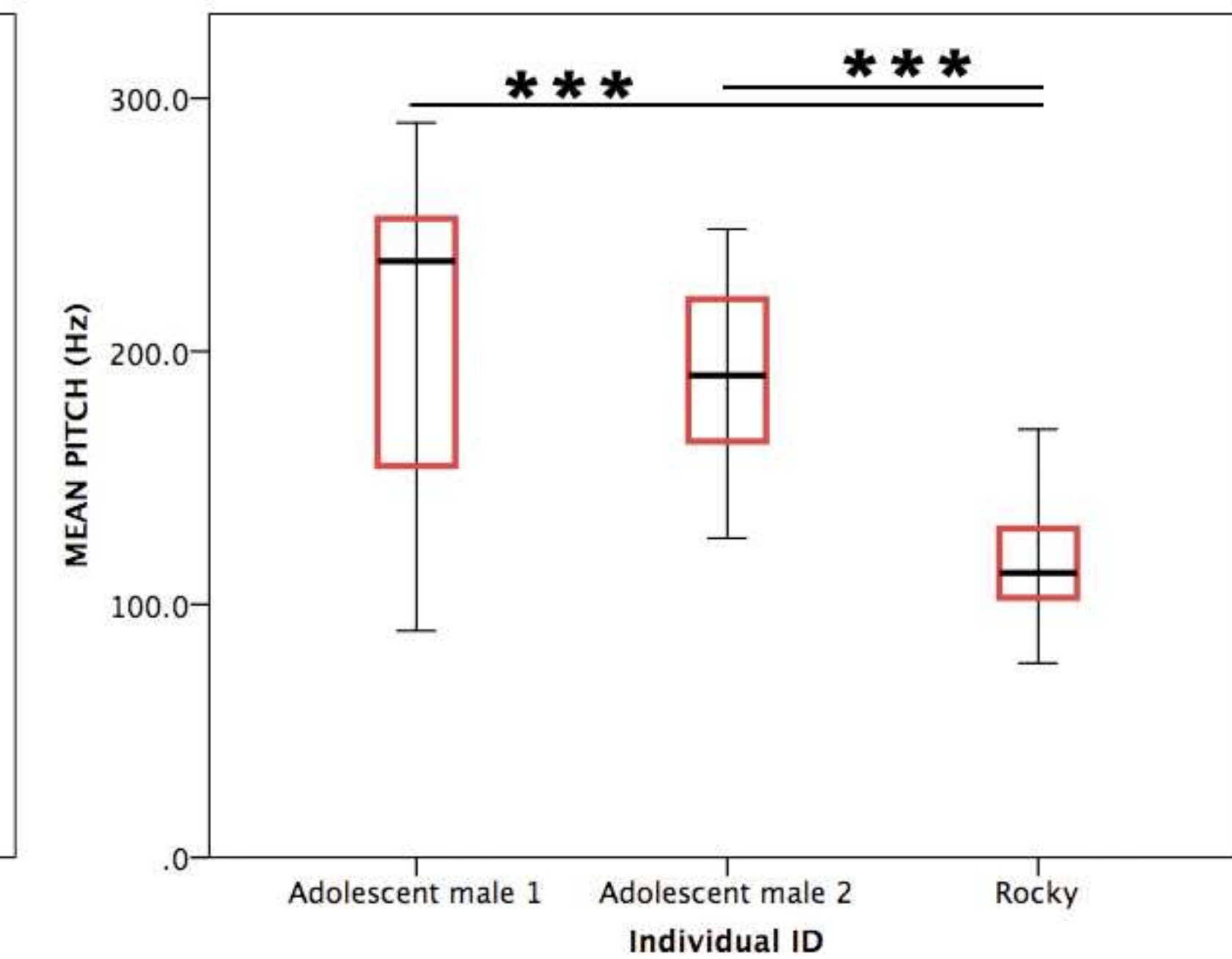
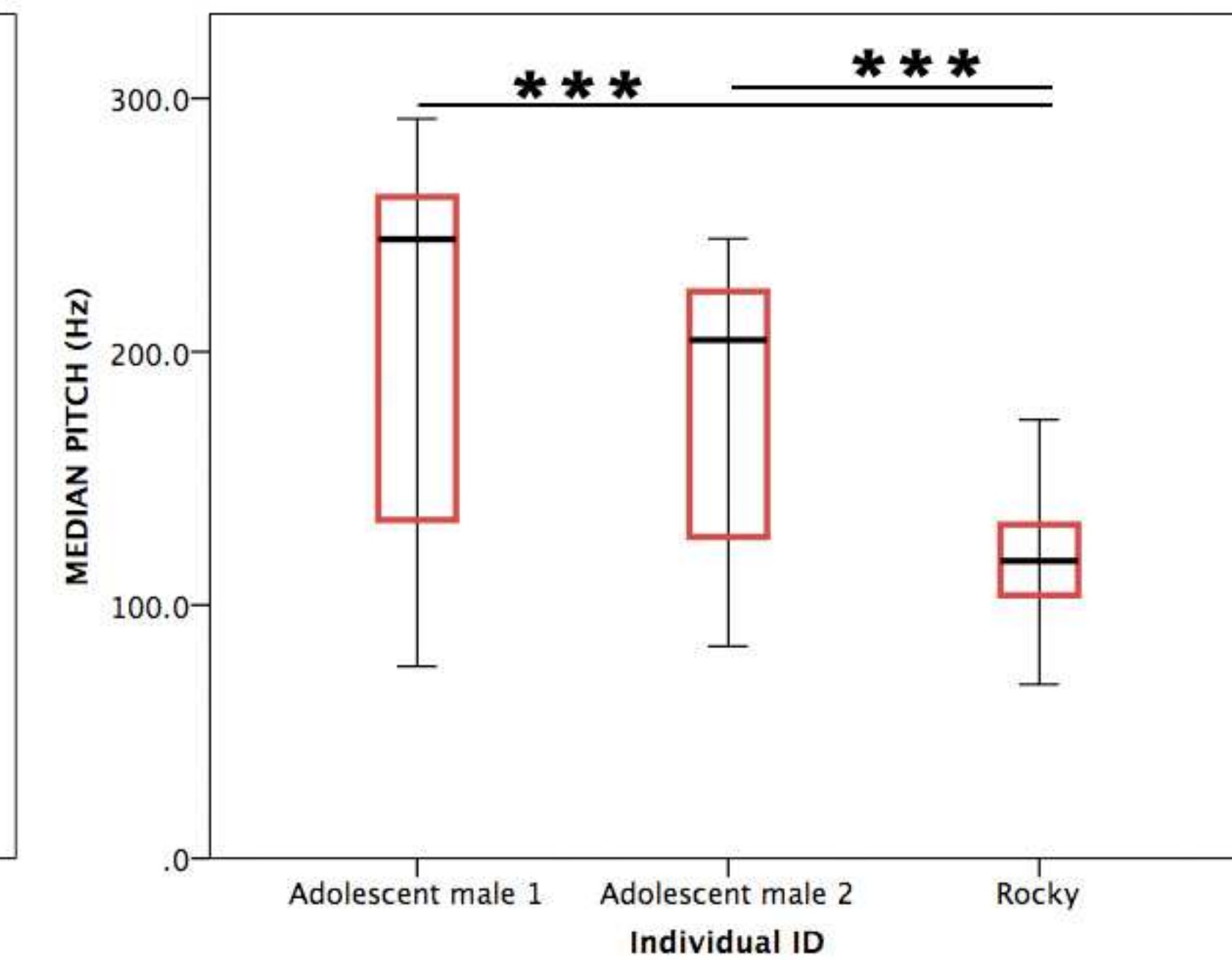
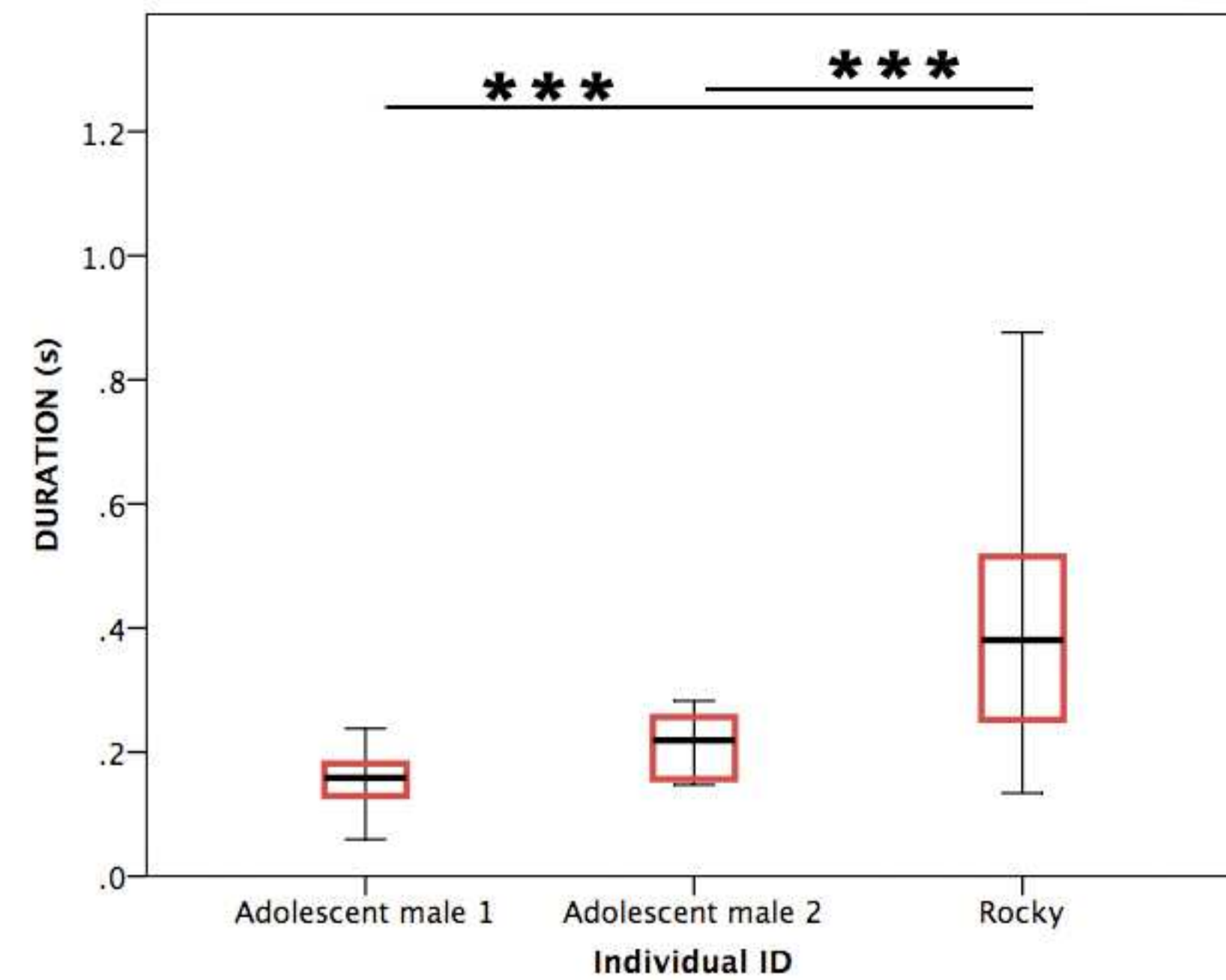
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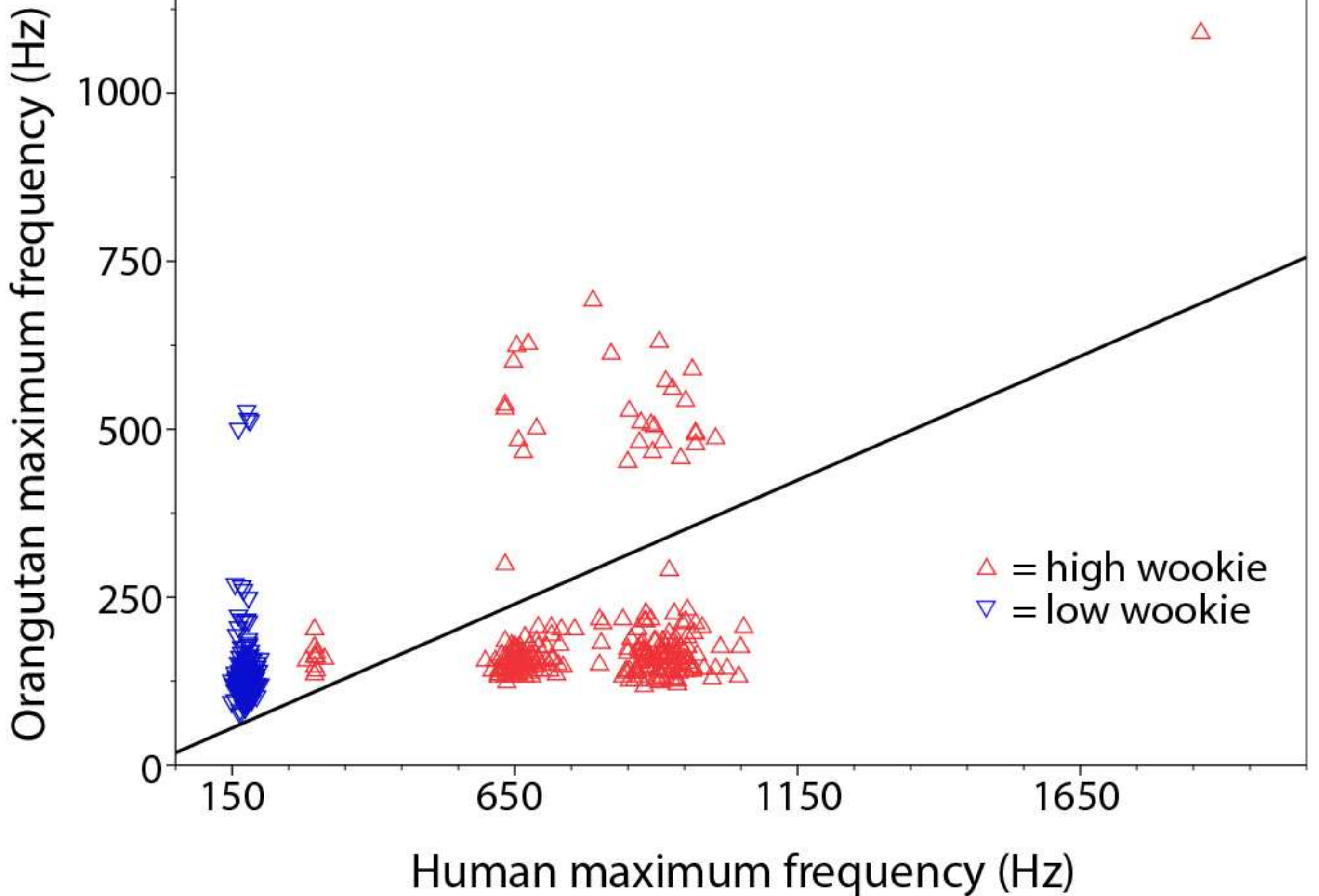
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Orangutan maximum frequency (Hz)

250  
200  
150  
100  
50  
0

low

spontaneous

high

Wookie sub-variants

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