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Early onset of postnatal individual vocal recognition in a highly colonial mammal species

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Abstract

1
2 Mother-young vocal recognition is widespread in mammals. The features of vocal recognition
3 are known to be shaped by the ecological constraints faced by each species. In some species, a
4 rapid establishment of mother-young vocal recognition is crucial for offspring's survival.
5 However, knowledge of the precise features of this recognition system, especially the timing of
6 the onset in the first hours after birth is often lacking. Here we show that Cape fur seal females
7 can recognize their pup's voice two to four hours after parturition and that pups develop this
8 aptitude four to six hours after birth. This study is the first to investigate this mechanism in a
9 wild and free-ranging mammal from only two hours after birth. We report the fastest
10 establishment of mother-young vocal recognition for any mammalian species, including
11 humans, described to date. Such early vocal identification in pups suggests an *in-utero* vocal
12 imprinting. These findings highlight the synergistic role of environmental constraints and
13 biological traits in optimizing the timing of individual vocal recognition onset in vertebrates.

14 1. Introduction

15 In most mammals, only the mother provides care to the offspring. Mother-young individual
16 recognition is a significant way to optimize maternal investment. It reduces costs by avoiding
17 misdirected care and thus enhances mother's reproductive success and increases offspring's
18 chances of survival [1]. In many mammal species, the acoustic channel plays a major role in
19 this recognition process as mother and young have developed the ability to identify each other
20 through the vocal signals (i.e. vocalisations) they produce [2–8]. Although the occurrence of
21 individual vocal recognition has been well documented in mammals, some features such as the
22 timing of the onset of recognition, its temporal pattern throughout lifetime and the individual
23 signature are not well understood and rarely investigated in wild mammals [9,10].

24 Rapid establishment of recognition between the mother and her young is crucial to ensure the
25 survival of the young, particularly in species experiencing stringent ecological constraints such
26 as a high risk of confusion between individuals, early pup mobility, and early separations
27 between mother and young due to foraging needs. Experimentally testing the development of
28 the vocal recognition in mother-young pairs of wild mammals within the first hours after birth
29 is challenging for reasons of access to the animals, tracking of births and the ability to conduct
30 experiments. Only a few studies have been carried out so far, involving five domestic [11–15]
31 and five wild species [3,16–19] (pinniped species only). In most cases, individuals were tested
32 from a few days after birth (i.e. later than 24-48 hours), except in sheep (*Ovis aries*) for which
33 ewes and lambs were tested within 6-12 hours after parturition [12] and for female Australian
34 sea lions (*Neophoca cinerea*) that were tested within 12 hours after parturition [16]. The timing
35 in development of vocal recognition, especially in the first 24 hours after birth, is thus poorly
36 understood in mammals, including humans [2,20].

37 The Cape fur seal (*Arctocephalus pusillus pusillus*) is a particularly interesting species in which
38 to investigate the characteristics of the vocal recognition in mammals because mother-pup pairs
39 are under strong ecological constraints to develop individual recognition. As one of the most
40 colonial mammals in the world, Cape fur seals reproduce over a short breeding season (lasting
41 from mid-October to early January each year [21]) and within massive colonies of up to several
42 hundred thousand typically tightly packed individuals. As with most otariid species, allo-
43 nursing is rare in this species [22,23] (i.e. pups are fed only by their own mother) and mother
44 and pup are frequently separated throughout the lactation period (maternal attendance periods
45 on shore are interspersed with multi-day foraging trips at sea by the mother). The first foraging
46 trip is reported to occur 6 days after the pup's birth [24]. Females and pups produce harmonic-

47 structured vocalisations (figure 1a) to communicate with each other, respectively named pup-
48 attraction calls (PAC) and female-attraction calls (FAC) [25]. PAC and FAC are used for both
49 long distance communication i.e. when the female returns after a foraging trip at sea or after a
50 short swim for thermoregulation, and short-range communication when both are gathered in the
51 colony [25]. Previous studies showed that PAC and FAC display a high degree of individual
52 stereotypy [26] and are involved in a mutual vocal recognition mechanism between the mother
53 and her young [27].

54 The mother-offspring vocal recognition processes in mammals are known to be shaped by the
55 ecology of the species (social organization and breeding strategy) [10,28,29]. Therefore, it is
56 likely that the extreme ecological constraints the Cape fur seal is facing act as a selective
57 pressure for the establishment of a rapid mother-pup individual recognition in this species. We
58 hypothesized that this recognition would be established within the first days after parturition
59 (i.e. before the first mother-pup separation) for both females and pups. Using playback
60 experiments, we tested Cape fur seal mothers and pups at different hours after birth to assess
61 the timing of the onset of recognition of the pup's voice by the mother and the mother's voice
62 by the pup. Furthermore, vocal recognition is established through an imprinting period during
63 which the animals are repeatedly exposed to vocal signals that they learn to recognize [22]. The
64 vocal activity of both mother and pup immediately after birth is therefore likely to play a role
65 in the onset of vocal recognition. We investigated the link between the behavioural response of
66 mothers and pups to early playback trials (conducted two to four hours after birth) and the vocal
67 activity (call production rate) of respective pups and females within the first two hours after
68 birth.

69

70 **2. Materials and methods**

71 *(a) Study site and animals*

72 Recordings and playback experiments were conducted at Pelican Point Cape fur seal breeding
73 colony, Namibia (25°52.2'S, 14°26.6'E) during the breeding season - from the 6th of November
74 to the 29th of December 2021 (over 33 days). Of the 51 mother-pup pairs included in this study,
75 we witnessed the birth of 30 pups. For 21 other cases, the fresh placenta was observed through
76 seagulls gathering around the placenta to eat it and the mum-pup pair carefully approached. In
77 Cape fur seals, the placenta is usually expelled within 30 minutes after birth [23]. Our
78 observations of 30 live births with subsequent placenta expulsion supported this with an average

79 time of 18.2 ± 22.3 minutes for placenta expulsion after parturition (electronic supplementary
80 material, table S1). For the 21 births that were identified through gulls eating the freshly-
81 expelled placenta, the time of birth was considered to be 30 minutes earlier.

82 At Pelican Point, Cape fur seals are not habituated to the close presence of humans in the colony.
83 To avoid disturbing the animals and inducing fearful reactions that may extend to stampedes,
84 seals were approached carefully by crawling along the sand. Recordings and experiments were
85 carried out from a distance, using a 5-m pole to bring the equipment close to the animals without
86 disturbing them. To identify mother-pup pairs over time, pups were bleach-marked using hair-
87 dye (Blonde high-light kit, ©Kair). The marks consisted of numbers applied on their flank using
88 a 10-cm wide wooden pad attached to the end of a 5-metre pole. The pups were marked at least
89 one hour after birth. Females were not marked but identified through their consistent association
90 with and nursing of their marked pup. Females nurse their own pups only, allonursing being
91 rare in otariid species [22].

92 *(b) Recording procedure*

93 Mothers' and pups' calls (respectively pup-attraction calls, PAC and female-attraction calls,
94 FAC) were recorded during the first two hours after the birth of the pup. Vocalisations were
95 recorded using a Sennheiser ME67 directional shotgun microphone (frequency range: 40 –
96 20,000 Hz +/- 2.5 dB) at 44.1 kHz sampling frequency connected to a two-channel NAGRA
97 LB digital audio recorder. The distance of the microphone from the focal animals ranged from
98 3 to 6 meters during recording sessions.

99 The duration of the recordings varied among mother-pup pairs (ranging from 5 to 120 min in
100 total for a given pair) depending on their vocal activity and the recording possibilities i.e.
101 accessibility of the mother-pup pair in the colony, movements of the animals around them, wind
102 conditions, etc. The number of calls produced by each individual was counted during the total
103 recording duration to quantify their vocal activity and expressed as the average number of calls
104 produced per 10 minutes.

105 *(c) Playback stimuli*

106 The playback procedure used on this study was similar to those used in previous studies of the
107 population [27]. Playback stimuli were prepared on-site from a laptop, using Avisoft SAS Lab
108 Pro (R. Specht, version 5.2.14, Avisoft Bioacoustics, Berlin, Germany). Series consisted of 6
109 calls from the same individual, each separated by 2 seconds of silence. Whenever possible, the

110 tracks were composed of 6 different calls, but sometimes less than 6 good quality calls (good
111 signal-to-noise ratio and no overlap) could be recorded from the same individual within 2 hours
112 of birth and some calls had to be replicated in the playback track. The tracks had an average
113 duration of 22.1 ± 4.9 s for females' calls and 17.1 ± 3.1 s for pups' calls.

114 *(d) Playback procedure*

115 A playback trial consisted of exposing the tested individual to two stimuli series: a series of
116 calls recorded from a related individual i.e. the focal pup's own mother or the focal female's
117 own pup - and a series of calls recorded from an unrelated individual (of the same population
118 and pups of the same age). The two playback series were separated by at least 2 minutes and
119 the order of the series was randomised [27]. Females were tested up to 24 hours after their pup's
120 birth and pups were tested up to 48 hours. Playbacks on females were classified into 4 categories
121 of time elapsed since the pup's birth: [2h-4h), [4h-6h), [6h-12h), and [12h-24h] (i.e. [2h-4h)
122 refers to experiments ≥ 2 h and < 4 h). Playbacks on pups were divided into 5 categories: [2h-
123 4h), [4h-6h), [6h-12h), [12h-24h] and (24h-48h]. Each individual was tested at different time
124 categories between 2 to 24-48 hours, but with only one trial per category and a minimum
125 duration of an hour and a half between two successive playback trials. In cases where the tested
126 individual showed no behavioural response to both series of a trial (due to a lack of motivation
127 or a sleeping animal that the played-back calls did not wake up), the trial was discarded from
128 the analyses. After such 'no-response' trials, the break duration before the next trial was reduced
129 to 30 minutes. Two trials could thus occur in the same time category but only if the first trial
130 induced no response to both series.

131 Females were tested in the presence of their pup while pups could be tested during their
132 mother's absence (i.e., females thermoregulating in the water during hot periods). Calls were
133 broadcast using a waterproof and wireless high-powered loudspeaker (JBL Charge 3, 2 x 10W,
134 frequency response: 65 Hz- 20 kHz) connected to a Bluetooth sound player (Sony NW-A35).
135 The loudspeaker was placed from 1 to 3 meters from the focal individual at a 45 to 90°
136 orientation to induce searching behaviour and thus facilitate the evaluation of a behavioural
137 reaction. The amplitude level of the playback tracks was adjusted to the natural amplitude of
138 PAC and FAC: respectively 88 ± 2 dB SPL at 1 m and 80 ± 2 dB SPL at 1 m). To ensure that
139 the amplitude level was correct and consistent between trials, both the volumes of the sound
140 player and the loudspeaker were calibrated on-site prior to conducting the experiments. During
141 calibration, received levels were measured with a 'Testo 815' sound level meter. In addition,
142 the amplitude level of all sound files corresponding to playback tracks were set at a standardised

143 value during their building on the software (amplitude normalised to 95% of the dynamic
144 range). Playback experiments were filmed using an Olympus Tough TG-6 camera to allow
145 further analysis.

146 *(e) Behavioural response*

147 Responses to the playback series were all assessed through video analysis with the software
148 BORIS (Friard and Gamba 2016). Behavioural responses were observed for 30s from the
149 beginning of the playback. For mothers, response variables were latency to look towards the
150 loudspeaker (s), look duration towards the loudspeaker (s), latency to check her pup (s),
151 duration of pup check (s), latency to call (s) and number of calls. The variable "pup check" is
152 defined as a female looking at and/or sniffing her own pup. From previous observations and the
153 results reported by Martin *and colleagues* [27], very young pups (i.e. few hours or days old) are
154 not able to accurately locate the sound source. Indeed, during the broadcast of their mother's
155 calls, we noticed that they look around without directing their eyes towards the loudspeaker.
156 Furthermore, they are not very mobile and never move towards the loudspeaker as pups of
157 several weeks of age can do [27]. In this study, the response variables for pups were thus latency
158 to call (s) and number of calls. For both mothers and pups, the absence of a given behavioural
159 variable (e.g., no call) was assigned a default value of 30s for latency.

160 *(f) Statistical analysis*

161 Onset of vocal recognition in mother-pup pairs The overall behavioural response of each tested
162 individual was obtained by combining the raw data of the response variables (6 for females and
163 2 for pups) in a principal component analysis (PCA) and obtain a composite score of the
164 behavioural response [30]. Principal components (PCs) with eigenvalues greater than 1 were
165 retained (Kaiser's criterion) and corresponding PC scores were used as a composite score to
166 quantify the level of response of tested mothers and pups. PC scores were compared between
167 filial and non-filial (or mother and non-mother) series and by time category after the pup birth
168 using a linear mixed-effects model (LME): PC scores were set as a 'response variable' while
169 the series (filial or non-filial, mother or non-mother) and the time category were set as fixed
170 effects. In addition, the playback trial (combination of both ID and hour, e.g. m32 tested at [2h-
171 4h) or p28 tested at (24h-48h]) was defined as a 'random effect' to account for the fact that data
172 are non-independent (each trial consists of observing the same focal individual over two series
173 but during the same time period). The model was run with the *lme4* R package [31]. A post-hoc

174 analysis of estimated marginal means was conducted to investigate differences between the two
175 series in each time category using the *emmeans* package in R [32].

176 Link between vocal recognition and vocal activity within the first hours after birth The vocal
177 activity or call rate (i.e. number of calls produced per 10 minutes) during the first two hours of
178 the pup's life was calculated for each individual of the mother-pup pairs in which at least one
179 of the two protagonists was tested 2 to 4 hours postpartum (n = 35 pairs). The relationship
180 between the vocal activity of a mother and those of her pup during the first two hours
181 postpartum was tested by calculating a Pearson correlation coefficient (*stats* package, R Core
182 Team, 2021). We investigated if the vocal activity of a pup within its first two hours of life
183 could impact the behavioural responses of its mother when tested early after parturition i.e. in
184 a playback trial conducted 2 to 4 hours postpartum. For this, we performed a linear regression
185 between pups' call rate and the difference in their mother's behavioural response between the
186 filial and non-filial series (PC1 scores filial - PC1 scores non-filial) for females tested at [2h-
187 4h). The same approach was used to evaluate the impact of the mother's vocal activity on the
188 pup's behavioural response (indicated by the difference PC1 scores mother - PC1 scores non-
189 mother) to early playbacks conducted at [2h-4h) indicated by the difference between PC1 scores
190 mother and PC1 scores non-mother.

191 Secondly, we assessed the effect of the vocal activity of an individual (either mother or pup,
192 during the first two hours after birth) on its behavioural response to the two types of series
193 conducted at [2h-4h). For mothers, two linear regressions were conducted between the mothers'
194 call rate and their response to filial or non-filial series. Similarly, two linear regressions were
195 carried out between pups' call rate and their behavioural response to either the mother series or
196 the non-mother series.

197

198 **3. Results**

199 *(a) Onset of vocal recognition in mother-pup pairs*

200 We investigated the ontogeny of mother-pup vocal recognition by testing females and pups
201 early after birth and within the first 24 hours (females) or 48 hours (pups) of the pup's life using
202 an acoustic playback approach. Each trial consisted of exposing the tested individual to two
203 vocal stimuli: one from the pup (filial) or the mother of the tested individual and another one
204 from a stranger individual (non-filial pup or non-mother female, figure 1a).

205 We studied 51 mother-pup pairs for this study and performed a total of 162 playback trials.
206 Among them, trials that did not elicit any behavioural responses for both stimuli were excluded
207 (i.e. animal remained sleeping; electronic supplementary material, table S2), leaving 116 trials
208 for analysis (n=59 for mothers and n=57 for pups; figure 1b, 1c).

209 For females, due to small sample size for [6h-12h) and [12h-24h] age categories (n=8 and n=6
210 respectively), playbacks trials conducted from 6 to 24 hours were grouped in a single [6h-24h)
211 category to ensure effectiveness of statistical analysis. The behavioural response of females to
212 the filial stimulus (i.e. calls recorded from her own pup) was significantly stronger than the
213 response to the non-filial stimulus for all pup age categories between 2 and 24 hours ([2h-4h):
214 estimate = 1.57, SE = 0.282, $p < 0.0001$; [4h-6h): estimate = 1.86, SE = 0.420, $p < 0.0001$; [6h-
215 24h): estimate = 2.20, SE = 0.420, $p < 0.0001$; figure 1b). When exposed to a series of
216 vocalisations from their own pup, females looked at the sound source (loudspeaker) more
217 quickly after the start of the broadcast and for a longer duration. They also responded vocally
218 more quickly after the start of the playback, and produced more calls (look and vocal responses
219 represented by PC1 scores; Table 1, Electronic supplementary material, Video S1). No
220 significant difference was found for variables related to the pup check (PC2 scores, p-values
221 from estimated marginal means analysis ranged from 0.054 to 0.23; Table 1).

222 Similar playback trials were performed on pups. Playback trials conducted on pups from 6 to
223 24 hours old were also grouped in a single [6h-24h) category because of small sample sizes
224 (n=5 for [6h-12h) and n= 8 for [12h-24h]). As the behavioural response of newborn pups to
225 their mother's calls is exclusively vocal (i.e., they are not yet able to localize the sound source
226 accurately and thus they did not look towards the loudspeaker or approach), their behavioural
227 response to the playback series was only assessed by the latency to call and the number of calls
228 produced. No difference in the pups' behavioural response was observed between the mother
229 and non-mother series in playback trials conducted at 2 to 4 hours after birth (estimate = 0.139,
230 SE = 0.390, $p = 0.7221$; figure 1c). However, the pups' behavioural response was stronger to
231 their mother's calls compared to the non-mother series in all of the three following age
232 categories spanning from 4 to 48 hours after birth ([4h-6h): estimate = 0.983, SE = 0.471, $p =$
233 0.0418; [6h-24h): estimate = 0.946, SE = 0.471, $p = 0.0498$; (24h-48h): estimate =1.457, SE =
234 0.490, $p = 0.0044$; figure 1c, Electronic supplementary material, Video S2). Therefore, pups'
235 vocal recognition of their mother's calls appeared to develop between 4 and 6 hours after birth.

236

237 *(b) Link between vocal recognition and vocal activity within the first hours after birth*

238 We next examined how the vocal activity of an individual during the imprinting period could
239 influence the timing of the onset of mother-pup vocal recognition. The vocal activity (i.e. call
240 rate, number of calls produced per 10 minutes) during the first two hours of the pup's life was
241 measured for each target mother-pup pair for which at least one of the two protagonists was
242 tested 2 to 4 hours after the pup's birth ($n = 35$ pairs, electronic supplementary material, table
243 S3).

244 We found no correlation between the vocal activity of a mother and the vocal activity of her
245 pup (Pearson's product-moment correlation, $t = 0.305$, $df = 33$, $p = 0.762$). This means that
246 vocalisations produced by mothers and pups soon after birth are not always in response to the
247 other's calls. The mothers' vocal rate was highly individually variable and ranged between 0
248 and 55.9 calls/10 min (mean value: 8.4 ± 10 calls/10 min) (figure 2c, electronic supplementary
249 material, table S3). Where labour and birth were observed, females were not observed to
250 vocalise during labour, only after the pup's birth. Pups were generally more vocal compared to
251 mothers and were already calling a few minutes after birth. Their call rate, also highly variable
252 between pups, ranged between 21.6 and 220.7 calls/10 min (mean value: 68.4 ± 48.7
253 calls/10min) (figure 2f, electronic supplementary material, table S3).

254 We then assessed if the pups' vocal activity within the first two hours could influence the onset
255 of maternal vocal recognition. We used the difference in mothers' response to filial and non-
256 filial series (PC1 scores filial – PC1 scores non-filial) in playback trials conducted at 2-4 hours
257 after parturition, as a proxy of their ability to recognize their pup's voice early. Positive values
258 indicated a stronger maternal response to the vocalisations of their own pup, while negative
259 values showed a stronger response to the calls of a non-filial pup (figure 2a). We found no
260 significant relationship between the pups' call rate during the first two hours after birth and the
261 ability of mothers to distinguish between filial and non-filial calls at 2-4 hours ($F(1,29) = 0.009$,
262 $p = 0.927$, adjusted $R^2 = -0.034$, figure 2a). In other words, females showing stronger responses
263 to the broadcast of their pup's calls at 2 to 4 hours after parturition did not necessarily have a
264 highly vocal pup. Similarly, mothers with the most vocal pups (figure 2f) did not show a
265 stronger difference in their behavioural response to the two playback series. In addition, the
266 mothers' vocal activity early after parturition (within two hours) had no influence on their own
267 behavioural response to the filial and non-filial playback series ($F(1,28) = 0.945$, $p = 0.339$,
268 adjusted $R^2 = -0.002$ for filial series and $F(1,28) = 0.057$, $p = 0.814$, adjusted $R^2 = -0.034$ for
269 non-filial series). In other words, highly vocal females do not necessarily respond more to the
270 playback series.

271 Lastly, we investigated if the ability of pups to recognize their mother's vocalisations could be
272 influenced by their mother's vocal activity within two hours after birth. As for mothers, the
273 difference between PC1 scores mother – PC1 scores non-mother (for playbacks trials conducted
274 at 2-4 hours after birth) was used as a proxy to assess the occurrence of an early vocal
275 recognition. Positive values indicated a stronger response to the mother's vocalisations, while
276 negative values showed a stronger response to the calls of a non-mother female (figure 2d).
277 Similar to females, no relationship was found between mothers call production and pups
278 recognition ($F(1,17) = 1.982$, $p = 0.177$, adjusted $R^2 = 0.052$; figure 2d). Although some pups
279 were exposed to their mother's calls many times (i.e. very vocal females) in the early stages
280 after birth, they were not able to recognize their mother's voice within the first two hours: they
281 either responded equally to both series or more strongly to the non-mother series (figure 2d). In
282 contrast, among the pups who successfully identified their mother's vocalisations, some had
283 relatively quiet mothers (figure 2d). Again, there was no relationship between the vocal activity
284 of a pup and its' behavioural response to the mother and non-mother series ($F(1,17) = 0.043$, p
285 $= 0.837$, adjusted $R^2 = -0.056$ for mother series and $F(1,17) = 1.701$, $p = 0.210$, adjusted $R^2 =$
286 0.037 for non-mother series).

287

288 **4. Discussion**

289 This study was the first to investigate the ontogeny of mother-young vocal recognition in a wild
290 and free-ranging mammal species from only two hours after birth. We showed that female Cape
291 fur seals were able to recognize their pup's voice within 2 hours after parturition. In other
292 mammal species, the vocal recognition of an offspring by its mother is established later: 24
293 hours in sheep [12], 48 hours in mink [11] and goat [13], 24 to 48 hours in the northern elephant
294 seal [18] and 48 hours Australian sea lion [16]. Even in humans, only 40% of women succeed
295 in recognizing their own baby's cries after 24 hours [2]. Such early recognition is likely to
296 involve highly evolved cognitive mechanisms to enable Cape fur seal females to learn and
297 memorize the vocal signature of their pup's vocalisations within 2 hours and to respond
298 specifically and appropriately when they hear them.

299 Regarding Cape fur seal pup's vocal recognition of their mother's calls, we showed that it is
300 established between 4 and 6 hours after birth. Again, this timing is much shorter than in other
301 mammal species such as lambs [12] or goat kids [13,14] (48h), but also compared to other
302 pinniped species: the Subantarctic fur seal (2-5 days) [3], the Galapagos fur seal and the

303 Galapagos sea lion (10 days) [19] or the Australian sea lion [17] (still not established before the
304 first mother-pup separation occurring at 10-14 days after birth). In humans, babies seem to be
305 able to recognize their mother's voice by one-month of age [33,34]. However, to our knowledge,
306 there is no study investigating such recognition earlier or assessing the timing of its onset. In
307 sheep [12] or in Australian sea lion [17], the mother-young vocal recognition is mutual but
308 occurs slightly later in offspring than in mothers. Here in Cape fur seal, the timing of the onset
309 of vocal recognition appeared to be relatively synchronous.

310 Considering the extreme ecological constraints Cape fur seal mother-pup pairs are facing, we
311 expected the vocal recognition to be mutual and to develop early i.e. before the first mother-
312 young separation for foraging occurring at 6 days post-birth. Surprisingly, our findings revealed
313 a particularly early recognition in this species: 2 hours for females to recognize their pups and
314 4-6 hours for pups to recognize their mothers. Our observations at the Pelican Point breeding
315 colony (Walvis Bay, Namibia) showed that pups experienced earlier separations from their
316 mothers, well before the female's first extended foraging trip to sea. During hot days (sunny
317 days with temperature above 20°C), we observed females leaving their pup alone in the colony
318 for a short period of time (15-30 min to an hour – although not systematically recorded) to swim
319 and thermoregulate. During our fieldwork, four marked pups were seen alone in the colony less
320 than three days after their birth: at 19, 32, 47 and 50 hours and all were successfully reunited
321 and seen in the presence of their mother afterwards. While these are short separations and the
322 mobility of newborn pups is limited, they still require a reunion process between mother and
323 pup, taking place among other conspecifics of the colony, which would involve a process of
324 individual vocal recognition. In addition to the high temperatures, predation events are also
325 responsible for early mother-pup separations. Indeed, Cape fur seals are exposed to different
326 terrestrial predators such as black-backed jackals, brown hyenas and even desert lions [35], and
327 these attacks may induce panics and thus separations in mother-pup pairs. A reliable vocal
328 communication will thus facilitate reunion between the two. In addition to these factors, the
329 high density of individuals in the breeding colony might represent an additional challenge for
330 successful reunion that could catalyse an early development of mother-young vocal recognition.
331 Indeed, the vocal stereotypy of pup-attraction calls and female-attraction calls of Cape fur seals
332 [26] are highly individually distinctive. Identity information appears to be encoded in acoustic
333 features such as the duration of the call, the fundamental frequency and the energy spectrum
334 [26]The perception and discrimination of these features are likely involved in the vocal
335 recognition process, supporting the identification abilities of females and pups.

336

337 Considering the strong inter-individual variations in mothers' and pups' vocal activity within
338 the first two hours after parturition and during this time, pups are a lot more vocal than mothers.
339 We thus assessed if vocal production can affect the early vocal recognition between mothers
340 and pups. The results showed that, in both cases, the behavioural response of one individual
341 (mother or pup) to a playback trial performed between 2 and 4 hours after birth is not linked to
342 the vocal activity of the other individual of the pair, and thus to the amount of calls to which
343 the tested individual was exposed before the playback trial. According to our experiments, the
344 call rate of the least vocal pups (at 20 to 40 calls/10 min, figure 2a) was sufficient to allow their
345 mothers to learn and memorize their vocal signature. Maternal vocal recognition in Cape fur
346 seals is thus based on a learning process that is rapidly acquired and highly efficient. With an
347 average of about 70 calls produced by a pup every 10 minutes, mothers are exposed early and
348 intensely to the voice of their offspring after birth. The rich imprinting period is therefore likely
349 to facilitate a rapid maternal vocal learning.

350 By contrast, the pup's exposure to its mothers' voice is much more variable among mother-pup
351 pairs and sometimes very low during the first hours – from 0 to about 56 calls produced by a
352 female every 10 minutes. These differences in vocal activity of females can be explained by a
353 variety of factors: the duration of the labour, the presentation of the foetus (cephalic or breech),
354 their physiological state (fatigue, stress), their personality and their experience (e.g.
355 primiparous or multiparous females). Some females were not very vocal during these first two
356 hours postpartum and started to call at a later stage, after few hours of rest. However, we found
357 no correlation between the pup's vocal activity during the first two hours after birth, and the
358 mother's behavioural response to a playback trial conducted between 2 and 4 hours after
359 parturition.

360 In spite of a much lower vocal exposure in pups, our behavioural experiments revealed that
361 pups can recognize their mother's voice as early as 4 to 6 hours after birth. In particular, we
362 found that a 3-hour-old pup (p29) was able to recognize its mother's calls during the playback
363 (higher number of calls produced with a lower latency in response to the mother series
364 expressed as a difference in PC1 scores of 2.06; figure 2d), whereas she had only produced one
365 single call during the first two hours after birth (average call rate of 0.1 calls/10min; electronic
366 supplementary material, table S3). Similarly, three other pups (p55, p81 and p82) recognized
367 their mother's voice in spite of a low maternal vocal rate (≤ 3.6 calls/10 min; electronic
368 supplementary material, table S3). The lack of a significant relationship between maternal call

369 production after birth and the vocal recognition by the pup indicates that the imprinting period
370 may not be limited to the first few hours after birth. As one call is likely not enough for the pup
371 to imprint the voice of its mother, a longer exposure would be probably required for
372 establishment of vocal recognition, especially for a colonial species where pups are exposed
373 simultaneously to the calls of many females. Our results indicate that the learning of the
374 mother's voice by pups might start to take place *in-utero*. In mammals, the uterine auditory
375 environment is rich: it is composed of sounds generated inside the mother (associated with
376 digestive, respiratory or cardiovascular activities) and exogenous vocal signals like conspecific
377 voices. It has been shown in humans and cetaceans that hearing abilities develop progressively
378 during the development of the foetus and begin to function before birth [36,37] (the sound,
379 especially low frequencies, being mainly transmitted to the inner ear by bone conduction [38–
380 40]). Among exogenous signals such as human voices, the mother's voice is dominant because
381 the sound waves are also conveyed directly to the womb through the mother's body (soft tissue
382 and liquid conduction) [41]. This double internal and external transmission causes the sound to
383 be less attenuated or distorted [42], as well as being slightly louder compared to other voices
384 [43]. In humans, foetuses were reported to respond differently to their mother's voice (i.e.
385 increase in foetal heart rate) than to the voice of a stranger woman (decrease) [44]. During the
386 gestation period of Cape fur seal (of 8 months, excluding the delayed implantation period [45]),
387 females also nurse their pup from the previous year (lactation period lasts from 9 to 11 months
388 [24]) and thus produce calls to communicate with them. Throughout its development, the foetus
389 is thus frequently exposed to its mother's voice. There may be a prenatal learning process in
390 which the foetuses are imprinting on their mother's calls features [46] (vocal signature)
391 allowing for recognition of these calls to develop. This could allow the newborn pups to develop
392 a rapid vocal recognition soon after birth. It is likely that this learning process would rather be
393 supported by acoustic features linked to the source and not the filter, as the foetus can assess its
394 mother's voice from inside. So, source features such as temporal features, including duration,
395 amplitude and/or frequency modulations of the calls, as well as the value of the fundamental
396 frequency could be learned by the foetus *in utero*. Some of these source-related features have
397 been shown to be individual-specific in females' calls in a previous study [26]. In contrast,
398 features related to the filter, such the spectral characteristics cannot be assessed reliably as likely
399 filtered by the mother's body [43]. Such pre-natal vocal learning mechanisms have been shown
400 in humans [39,47] and birds [48,49], and might also occur in pinnipeds, in response to the strong
401 ecological constraints for an early, reliable and efficient mother-pup recognition.

402 In summary, the establishment of the mother-pup vocal recognition in Cape fur seal occurs 2 to
403 4 hours after birth in females, and 4 to 6 hours in pups. This appears to be the fastest
404 establishment of mother-young vocal recognition for any mammalian species (including
405 humans) described to date. We suggest that prenatal learning is likely to occur and thus
406 facilitates the establishment of vocal recognition soon after birth for pups. Such precocial
407 learning of the voice is likely driven by the complex environment and the strong ecological
408 constraints that this highly colonial species is exposed to. The high density of individuals
409 generates both an acoustic and visual jamming, the frequent and early separations of the mother
410 with her pup are selective pressures that have shaped their recognition system, and led to an
411 early onset of mother-pup recognition.

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Tables

Table 1. Summary of the first two principal components (PC1 and PC2) resulting from the two principal component analysis (PCA) performed on mothers' and pups' playback trials with, respectively, six and two behavioural variables. For mothers, the two PC were retained (eigenvalues > 1): PC1 includes both look and vocal components of the behavioural response, whereas PC2 relates only to the check of the pup by the mother. For pups, only PC1 was retained.

	Playbacks on mothers		Playbacks on pups	
	PC1	PC2	PC1	PC2
Eigenvalues	2.87	1.73	1.66	0.34
% cumulative variance	47.85	76.70	83.01	100
Correlation coefficients between PC and variables				
Latency to look	-0.70	-0.07		
Look duration	0.87	0.18		
Latency to check her pup	-0.13	0.91		
Duration of pup check	0.11	-0.92		
Latency to call	-0.90	-0.002	-0.91	0.41
Number of calls	0.89	0.005	0.91	0.41

Figure captions

Figure 1. Behavioural responses of mothers and pups to playback experiments conducted to assess the timing of the onset of the mother-pup vocal recognition. (a) Playback experiments setup. Each tested individual was exposed to the broadcast of two series of calls from a related individual (mother or filial pup) or a stranger individual (non-mother or non-filial pup). (b) General behavioural response of mothers ($n_{\text{ind}} = 38$) to playback trials ($n_{\text{trials}} = 59$) conducted from 2-4 hours to 12-24 hours following parturition. Mothers' response is indicated by the composite score (PC1 scores) obtained from six behavioural variables. (c) General behavioural response of pup ($n_{\text{ind}} = 36$) to playback trials ($n_{\text{trials}} = 57$) conducted from 2-4 hours to 24-48 hours following birth. Pups' response is indicated by the composite score (PC1 scores) obtained from two behavioural variables. *Linear Mixed-Effects model followed by a post-hoc analysis of estimated marginal means. Significance code is p-value [0, 0.001]: ***, (0.001, 0.01]: **, (0.01, 0.05]: *, (0.05, 1]: NS. Boxplots present median values with first and third quartiles (lower and upper hinges) and whiskers represent the min and max values.*

Figure 2. Link between mothers' and pups' behavioural responses to playback trials conducted at 2 to 4 hours and their vocal activity during the first two hours postpartum. (a) Relationship between pups' vocal activity during the first two hours after birth (in number of calls produced per 10 min) and the difference in their mother's behavioural response to the filial and non-filial playback series broadcasted 2 to 4 hours after parturition (PC1 scores filial – PC1 scores non-filial). (b) Relationship between mothers' vocal activity during the first two hours postpartum and their behavioural response to the filial series (PC1 scores filial, in purple) and the non-filial series (PC1 scores non-filial, in grey). (c) Spectrograms of calls produced by a female (m44) showing a high vocal activity (average call rate = 55.9 calls/10 min) during recordings made within 2 hours after parturition. (d) Relationship between mothers' vocal activity during the first two hours after parturition (in number of calls produced per 10 min) and the difference in their pup's behavioural response to the mother and non-mother playback series broadcasted 2 to 4 hours after birth (PC1 scores mother – PC1 scores non-mother). (e) Relationship between pups' vocal activity during the first two hours after birth and their behavioural response to the mother (PC1 scores mother, in orange) and the non-mother series (PC1 scores non-mother, in grey). (f) Spectrograms of calls produced by a pup (p66) showing a high vocal activity (average call rate = 220.7 calls/10 min) during recordings made within 2 hours after birth.



