Can harbor seals (*Phoca vitulina*) discriminate familiar conspecific calls after long periods of separation?

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The ability to discriminate between familiar and unfamiliar calls may play a key role in pinnipeds' communication and survival, as in the case of mother-pup interactions. Vocal discrimination abilities have been suggested to be more developed in pinniped species with the highest selective pressure such as the otariids; yet, in some group-living phocids, such as harbor seals (*Phoca vitulina*), mothers are also able to recognize their pup's voice. Conspecifics' vocal recognition in pups has never been investigated; however, the repeated interaction occurring between pups within the breeding season suggests that long-term vocal discrimination may occur. Here we explored this hypothesis by presenting three rehabilitated seal pups with playbacks of vocalizations from unfamiliar or familiar pups. It is uncommon for seals to come into rehabilitation for a second time in their lifespan, and this study took advantage of these rare cases. A simple visual inspection of the data plots seemed to show more reactions, and of longer duration, in response to familiar as compared to unfamiliar playbacks in two out of three pups. However, statistical analyses revealed no significant difference between the experimental conditions. We also found no significant asymmetry in orientation (left vs. right) towards familiar and unfamiliar sounds. While statistics do not support the hypothesis of an established ability to discriminate familiar vocalizations from unfamiliar ones in harbor seal pups, further investigations with a larger sample size are needed to confirm or refute this hypothesis.

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Abstract

The ability to discriminate between familiar and unfamiliar calls may play a key role in pinnipeds' communication and survival, as in the case of mother-pup interactions. Vocal discrimination abilities have been suggested to be more developed in pinniped species with the highest selective pressure such as the otariids; yet, in some group-living phocids, such as harbor seals (*Phoca vitulina*), mothers are also able to recognize their pup's voice. Conspecifics' vocal recognition in pups has never been investigated; however, the repeated interaction occurring between pups within the breeding season suggests that long-term vocal discrimination may occur. Here we explored this hypothesis by presenting three rehabilitated seal pups with playbacks of vocalizations from unfamiliar or familiar pups. It is uncommon for seals to come into rehabilitation for a second time in their lifespan, and this study took advantage of these rare cases. A simple visual inspection of the data plots seemed to show more reactions, and of longer duration, in response to familiar as compared to unfamiliar playbacks in two out of three pups. However, statistical analyses revealed no significant difference between the experimental conditions. We also found no significant asymmetry in orientation (left vs. right) towards familiar and unfamiliar sounds. While statistics do not support the hypothesis of an established

39 ability to discriminate familiar vocalizations from unfamiliar ones in harbor seal pups, further
40 investigations with a larger sample size are needed to confirm or refute this hypothesis.
41
42 ## Introduction
43 **Long-term recognition in pinnipeds**
44 Long-term recognition, which incorporates the storage and subsequent retrieval of information,
45 plays an active role in human and animal behavior and communication. Indeed, it may be key for
46 the survival of a species to recognize items stored in memory, such as sounds or images, as
47 advantageous or potentially harmful (e.g., Mendl et al. 2001). Within animal species, recognition
48 is further believed to enhance the individuals' fitness, playing an active role in mate reunion,
49 parental care, and territory control (Insley 2000). Like many other animals, pinnipeds
50 consistently rely on long-term memory to communicate and to interact with their environment
51 and several species show impressive long-term memory capacities for visual information,
52 problem-solving strategies, and vocal recognition (McCulloch et al. 1999; Reichmuth Kastak and
53 Schusterman 2002; Pitcher et al. 2010). The ability to recognize target individuals in the wild can
54 provide a strong advantage in the context of high natural selective pressure, as for example in
55 mother-pup recognition (Charrier 2020). However, long-term vocal recognition in pinnipeds has
56 been suggested as an evolutionary by-product of strong maternal imprinting experienced during
57 the rearing period rather than an adapted trait (Charrier et al. 2003). Research on northern fur
58 seals (*Callorhinus ursinus*) showed that females and their pups were able to respond to each
59 other's vocalizations even several years after weaning (Insley 2000). While other studies have
60 demonstrated similar long-term memory in other otariid species (Charrier et al. 2003; Pitcher et
61 al. 2010), comparable work in phocids is lacking. A possible reason for this deficiency may
62 depend on differences in both reproductive and maternal strategies between the two pinniped
63 families: otariids form moderate to high density breeding colonies, in which females frequently
64 separate from their pups to forage at sea throughout the entire lactation; instead, most phocids are
65 not colonial and females stay with their young until weaning (Hammill et al., 1991). These
66 different strategies may impact mother-pup recognition, which has been suggested to be less
67 needed in phocids than in otariids (Job et al. 1995; McCulloch et al. 1999; McCulloch and
68 Boness 2000). Field observation suggests that recognition abilities may exist in phocid pups
69 (Renouf et al. 1983; Lawson and Renouf 1987; Insley et al. 2003), but it has never been
70 experimentally investigated.
71 **Harbor seal - a study model**
72 Harbor seals (*Phoca vitulina*) have a unique maternal strategy among phocids as females
73 perform short foraging trips during lactation (Boness and Bowen 1996) while pups show high
74 mobility and a tendency to gather during the breeding season (Sullivan 1982; Sauvé et al.
75 2015a). This maternal strategy implies frequent mother-pup separations, possibly requiring a
76 strong need for an individual vocal recognition. Indeed, several preliminary studies have shown
77 that pup vocalizations (known as mother-attraction calls, MACs) are individually distinctive by
78 their fundamental frequencies, pup age, and sex, suggesting this as a key factor for pup

79   recognition and for the maintenance of mother-offspring contact (Renouf 1984; Perry and
80   Renouf 1988; Khan et al. 2006). Eventually, in 2015, Sauvé and colleagues demonstrated that the
81   MACs of harbor seal pups contain individual vocal signatures (Sauvé et al. 2015b), and that
82   harbor seal mothers can recognize and distinguish the calls of their own pup by memorizing the
83   pup call signature (Sauvé et al. 2015a). However, similar evidence in pups is lacking as harbor
84   seal mothers do not vocalize, and whether they possess such ability is yet to be determined with
85   other conspecifics' calls.
86   As harbor seal pups spend the rearing period in close contact with other pups, they show their
87   most social behavior during this time. This close social proximity exposes them to conspecific
88   MACs from an early stage of life (Sullivan 1982; Bowen 1991) and could drive the development
89   of an individual recognition between familiar individuals. Such social recognition might reduce
90   aggressive interactions towards familiar individuals (Tripovich et al. 2008), as shown in grey
91   seal weaned pups (Robinson et al. 2015). In turn, the reduction of aggressive behaviors may limit
92   the pups' energy expenditure and may act as a driver for sociality and development of altruistic
93   behavior (Axelrod and Hamilton 1981). The frequent social interactions might be facilitated by
94   the strong site fidelity shown by harbor seals throughout the year (Cordes and Thompson 2015),
95   in turn promoting recognition of familiar individuals via acoustic, visual, and olfactory cues
96   (Robinson et al. 2015). However, memorization of conspecific vocalizations may not be a
97   functional target per se, but instead constitute a by-product of other potential memory capacities.
98   Conversely, one could hypothesize that harbor seal pups would not memorize conspecifics'
99   voices, either because of their young age or because this would not bring any advantage to their
100   own survival.
101   As a first, exploratory study, we aimed at testing whether it is possible for harbor seal pups to
102   discriminate between MACs from familiar and unfamiliar pups even after a long separation. To
103   this aim, we took advantage of the rare occasions in which already rehabilitated pups were
104   admitted into rehabilitation for a second time in their lifespan during their post weaning period.
105   During this second period, we presented three wild seal weaners with a playback sequence
106   composed of familiar and unfamiliar MACs and measured each animal's orientation and
107   behavioral response to these calls.
108
109 Materials & Methods
110 Study site and animals
111   This research was performed at the Sealcentre Pieterburen, a seal rescue and rehabilitation center
112   in the Netherlands, which rehabilitates more than 150 phocids every year. The animals reached
113   the Sealcentre as pups in summer 2018 (cause: maternal separation). After a successful first
114   rehabilitation, three individuals returned to the center due to parasitic pneumonia, a relatively
115   common condition seen in young harbor seal weaners (winter 2018-2019). The three seals were
116   7, 8, and 12 months old at the moment of the experiment, respectively (See Table 1). During
117   their first stay in rehabilitation, pups were housed with at least one companion and consistently
118   exposed to their companions' naturally emitted MACs. While harbor seals usually emit a

119 considerable number of MACs as pups, they gradually stop vocalizing towards the end of the
120 weaning period, which occurs when they are 26-42 days old (Bowen 1991). Furthermore, they
121 predominantly become solitary as weaners (Bowen 1991; Biolsi 2017). Social interactions
122 between conspecific pups progressively increase with age, as it has been shown for social play
123 behavior (Renouf and Lawson 1987). Since the subjects of the present study were released in the
124 wild after the end of the weaning season, it is highly likely that they were not exposed to further
125 MACs from any conspecific pup.
126 The first seal tested (seal-1) was a male, approximately 7-10 days old upon first arrival at the
127 Sealcentre (Table 1). Seal-1 was housed during rehabilitation with several other pups, all females
128 of the same age. The other two tested seals (seal-2 and seal-3) were each housed with only one
129 companion. Seal-2 and its companion, both males, arrived at the Sealcentre as premature pups
130 (5-6 and 3-4 days old, respectively). Seal-3 and its companion, both females, were about 7-10
131 days old at arrival. Age was determined by experienced veterinarians basing on the presence and
132 appearance of the umbilical cord.
133 **Sound recordings**
134 Aerial vocalizations were recorded from each seal admitted at the Sealcentre during the health
135 assessment upon intake, which occurred in summer 2017 and summer 2018. Twelve wild-born
136 Eastern Atlantic harbor seals (*Phoca vitulina vitulina*) were recorded in 2017 and 2018 to build
137 playback stimuli and three were tested in 2018 and 2019 with these playbacks. Recordings were
138 taken with a Sennheiser ME-66 unidirectional microphone (frequency response of 40-20,000 Hz
139 ± 2,5 dB; Sennheiser electronic GmbH & Co. KG, Wedemark, Germany) connected to a Zoom
140 H6 digital recorder (Zoom Corporation, Tokyo, Japan). The sampling frequency of all recordings
141 was 48 kHz with 24-bit quantization, and they were saved as WAV files. An MZW-66 foam
142 windshield was used to cover the microphone and protect it from water splashes. All pups
143 admitted to rehabilitation were initially quarantined in pairs or groups, in acoustic contact with
144 each other. Playback consisted of vocalizations recorded from MACs emitted by the test
145 subjects' former quarantine companion(s) during summer 2018 (familiar MACs), and MACs
146 from unknown pups recorded during summer 2017 (unfamiliar MACs).
147 **Playback procedure**
148 Each seal-specific playback was created using Praat 6.0.11 and consisted of a sequence of 8
149 blocks, each one containing 10 identical calls which onsets occurred every 6 seconds (Figure 1.
150 See also Ravignani 2019). Half of the blocks consisted of familiar vocalizations ("companion"),
151 while the other half consisted of unfamiliar vocalizations ("control"). To avoid possible
152 habituation to sounds (Perry and Renouf 1988), blocks were separated by 3 minutes of silence. In
153 addition, a silent period of minimum 60s was added before ("acclimation") and after ("post-
154 playback") the playback presentation, to let the seal habituate to the new situation and to rest
155 after the experiment. Since seal-1 shared its quarantine enclosure with several other pups, for the
156 familiar vocalizations we selected calls from four companions; calls from each companion were
157 grouped within a block and the order of blocks was randomized. The other two tested seals (seal-
158 2 and seal-3) each shared their quarantine with only one companion; therefore, the selected

159 familiar vocalizations belonged to their respective companions. For each test subject, the seals
160 used as control were of the same sex and age as the companion(s). The alternation between
161 companion and control blocks was randomized and presented in a different order to each seal
162 (see Figure 1). Due to a technical problem, for one of the seals tested (seal-3), the first block of
163 calls contained only 9 calls instead of 10.
164 **Apparatus and experimental procedure**
165 Each harbor seal, once successfully rehabilitated and in good health condition, was exposed to a
166 playback on the release day. The experiment was performed while the seal was in a box used to
167 release the animal to prevent visual distractions. Particular care was taken to avoid external
168 sources of noise during testing. Since rehabilitated seals were familiar with being transferred and
169 weighed in tightly fitting boxes (53x123x60 cm), the effect of short periods of interaction with
170 humans and confinement on the behavioral response was assumed to be negligible (Osinga and
171 Hart 2010). The experiment was recorded with a Zoom Q8 camera, recording at 25 fps from the
172 back side of the animal (i.e., behind its back flippers). The playback was broadcasted from a JBL
173 Flip 2 speaker (frequency response 100 Hz-20 kHz), connected via cable to an iPhone 5S. The
174 speaker was placed within a distance of 30 cm from the back of the box (see details below) and
175 the sound pressure level was adjusted to simulate the sound pressure level of another seal pup
176 located approximately 1-2 meters from the experimental subject. SPLs varied for each call to
177 maintain their original natural amplitude at 1-2 meters, averaging 80 dB (measured with a
178 CHECK MATE CM-130 sound level meter). Only after the equipment was in place and
179 working, the playback was triggered remotely with the experimenter out of sight (Figure 2).
180 **Behavioral assessment**
181 Behavioral analyses and playback annotations were performed using BORIS (Behavioral
182 Observation Research Interactive Software) v. 7.1.3 - 2018-11-16 (Friard and Gamba 2016). The
183 anatomy of harbor seals affords a wide dynamic visual field; specifically, a seal performing eye
184 movements can reach a visual field extending to 121° on the dorsal side and 210° in the
185 horizontal plane (see Hanke et al. 2006 and figures therein); however, the dimensions of the
186 experimental box only allowed the seals to turn their eyes or heads towards the sound source.
187 Hence, we hypothesized that if seals could discriminate between familiar and unfamiliar voices,
188 they would react to the broadcasted vocalizations by turning their heads towards the sound
189 source placed behind them. We scored the behavioral reaction with a commonly used assay
190 known as the orientation response (Insley 2000; Figure 3). To avoid any possible bias, all
191 annotations were performed on the videos without sound and the annotator was blind to the
192 experimental condition. Moreover, during sound playback experiments, scientists often noticed
193 asymmetries in orientation (left vs. right) towards familiar and unfamiliar sounds in animals
194 (Ghazanfar et al. 2001; Böye et al. 2005; Siniscalchi et al. 2012). The brain's left hemisphere
195 controls vocal production and perception, and the recognition of a familiar sound (usually a
196 conspecific call) generally corresponds to a predominant turn to the right side. Thus, we
197 hypothesized that the seals would show different orientation parameters depending on the
198 familiarity of the acoustic stimulus. We also hypothesized that a difference in the reaction to the

199 sounds might be reflected in the look duration and in the time elapsed between playback onset
200 and seal's first look to the sound source (latency). For example, a faster response (i.e. a shorter
201 latency) and a longer look might be associated with a familiar vocalization. Thus, we measured
202 three dependent variables: 1) number of looks, defined as either head turning at a > 90° angle in
203 the horizontal or dorsal plane or as an eye presentation to the camera; 2) duration of each look; 3)
204 latency. Responses to individual calls within a block (duration = 60 ± .001s) were summed
205 (number of looks) or averaged (duration, latency) to provide a base for the analyses. This way,
206 the analyses would show the seal's reaction to the type of calls overall, either familiar
207 (companion) or unfamiliar (control). Only reactions that started after the beginning of the block
208 were considered. Vocal responses were not uttered in the current experiment. For latency and
209 duration, we conducted the analyses twice: first, we analyzed only durations and latencies
210 corresponding to looks. This method led to a removal of data from 3 out of 24 blocks (2
211 companion blocks from seal-1, 1 control from seal-3) in which no looks occurred; therefore, we
212 conducted the analysis again by including these blocks and inputting a minimal duration (0s) and
213 maximum latency (60s). As there was no difference in the outcome of the statistical analyses, we
214 report here only results based on latency and duration corresponding to looks.
215 **Statistical analyses**
216 All analyses were performed with RStudio version 1.3.959 (RStudio Team 2020) running R
217 version 4.0.2 (R Core Team 2020). Results were deemed significant at an alpha level of .05.
218 Fisher's exact tests (package *stats*) were performed on contingencies tables (one per seal) pitting
219 the direction of reaction (left vs. right) against sound familiarity (companion vs. control) to test
220 for possible turning asymmetries in response to familiar or unfamiliar vocalizations. In addition,
221 pairwise-correlations (Spearman's rank coefficient) were conducted to evaluate the relation
222 between dependent variables.
223 We employed generalized linear mixed models (GLMM; package *lme4*; Bates et al. 2015) to
224 model the seals' reactions to the playback blocks. After checking for data dispersion (package
225 *blmeco*) and based on Shapiro-Wilk tests and on visual inspection of boxplots, histograms, qq-
226 plots, and Cullen and Frey graph (package *fitdistrplus*) we concluded that the number of looks
227 could be best approximated by a Poisson distribution (overdispersion parameter < 1.4, package
228 *blmeco*), while duration and latency were better described by Gamma distributions. For all three
229 dependent variables, the statistical models included *familiarity condition* (companion vs. control)
230 as fixed effect and *seal ID* as random effect. Details of the employed models are summarized in
231 Table 3. Furthermore, we used principal component analysis (PCA; packages *stats, factoextra*) to
232 transform the three response variables (number of looks, duration, latency) into a single global
233 measure describing the strength of response to playback (McGregor 1992; see also Vehrencamp
234 et al. 2003; Sauvé et al. 2015b). Principal component (PC) scores were computed for PCs with
235 eigenvalues greater than 1. PC scores were fed into a linear mixed effects model with *familiarity
236 condition* as fixed effect and *seal ID* as random effect.
237 For all mixed models, model fit was reported as coefficients of determination (R^2) calculated
238 based on Nakagawa et al. 2017 (package *performance*); however, we cautioned on the

239   interpretability of these coefficients for generalized linear models (Sotirchos et al. 2019; Piepho
240   2019).

Ethics approval

242   All focal individuals were kept in the Sealcentre Pieterburen, one of the biggest seal
243   rehabilitation centers in the Netherlands, for clinical reasons only. Data collection was non-
244   invasive and adhered to the guidelines of the Association for the Study of Animal Behavior
245   (Buchanan et al., 2012). All procedures were approved by the Sealcentre veterinarians. The
246   animals were neither captured nor kept longer than necessary to run this study. The present study
247   involved behavioral testing only and did not cause any distress or pain to the animals. After the
248   study, the animals were released into the wild according to the regulations and protocols of the
249   Sealcentre Pieterburen.
250

Results

Descriptive analysis

253   A summary of response patterns to playbacks is presented in Table 2 and Figure 4. Visual
254   inspection of the data suggested that seal-1 seemed to look less often than the other two seals
255   towards the sound source. In addition, seal-1 looked less often to companion blocks than
256   controls, while the opposite pattern (more looks to companions relative to controls) was observed
257   in seal-2 and seal-3. Still judging from visual inspection, latencies were longer in control blocks
258   in seal-1 and seal-2. Duration of reactions visually resembled the pattern observed for the
259   number of looks, with seal-1 showing looks of similar length for control and companion blocks,
260   and seal-2 and seal-3 displaying longer looks towards companions.
261   Because seal-1 was exposed to calls from multiple companions, we looked more in depth
262   whether it reacted differently to any of them (Figure 5). Seal-1 did not react at all to two
263   companions, while the remaining two companions received 2 looks each. Controls received
264   either 1 look, 3 looks, or 4 looks. For companions, durations were similar, while they were more
265   variable for controls. Latencies were variable for all blocks.

Lateralization of response and correlations

267   For each seal, there was no statistical association between the familiarity of the sound and the
268   side of the orienting response (Fisher's exact tests; seal-1: OR = .44, p = 1; seal-2: OR = 1.39, p
269   = .73; seal-3: OR = .29, p = .10; Figure 6).
270   Spearman's rank correlation coefficient was calculated to test for correlations between the three
271   dependent variables. We found a significant correlation between the number of looks and their
272   duration (rs = .82, p <.001), while the other correlations were not significant (duration and
273   latency: rs = -.41, p = .063; latency and number of looks: rs = -.40, p = .065). These results were
274   confirmed when excluding seal-1 from the analyses (number of looks and duration, rs = 165.68,
275   p < .001; other ps > .56).

Mixed-effects models

277   Generalized linear mixed-effects models were employed to statistically investigate behavioral
278   differences between companion and control calls. GLMMs fitting a Poisson (for the number of

279 looks) or gamma (for the duration and latency of reaction) model were used to predict the
280 number of looks based on *familiarity condition* (fixed effect) while accounting for variability in
281 each seal (random effect *seal ID*). No significant effects emerged from these analyses (Table 3).
282 Seal-1 was housed in different conditions and exposed to playbacks from multiple conspecifics.
283 For this reason, we ran the models the second time after excluding data from this seal (i.e., based
284 on the data from seal-2 and seal-3). Even in this case, we found no difference between responses
285 to companions and controls (Table 3).
286 **Principal Component Analysis**
287 Number of looks, duration, and latency were fed into a PCA to identify a single measure
288 summarizing the strength of response to playback. The first component accounted for 70% of the
289 variance with an eigenvalue > 1 (loading coefficients: number of looks = .64, duration = .62,
290 latency = -.45). A positive PC score indicates a strong response towards the sound source. These
291 composite scores were fed into a linear mixed-effects model with *familiarity condition* as fixed
292 effect and *seal ID* as random effect (Shapiro-Wilk: W = .94, p = .222; model: pca ~ familiarity
293 condition + (1 | seal_id), class: lmer), with no significant outcome (familiarity condition:
294 estimate = -.79; SE = .56, t = -1.42, p = .17; r^2 = .26/.07; Figure 7).
295 Repeating the analyses without including seal-1 yielded comparable results. The first component
296 accounted for 62% of the variance with an eigenvalue > 1 (loading coefficients: number of looks
297 = .68, duration = .66, latency = -.32). This composite score was fed into a linear mixed-effects
298 model with *familiarity condition* as fixed effect and *seal ID* as random effect (Shapiro-Wilk: W
299 = .94, p = .315; model: pca ~ familiarity condition + (1 | seal_id), class: lmer), with no
300 significant outcome (familiarity condition: estimate = -.91; SE = .66, t = -1.37, p = .191, r^2 =
301 NA/.112).
302
Discussion
304 The current study set out to explore the ability of harbor seals to discriminate between familiar
305 and unfamiliar vocalizations. We capitalized on a rare opportunity: three seals were admitted for
306 rehabilitation twice in a relatively short time (approximately 6 months), first as orphaned pups
307 and later as weaners affected by parasitic pneumonia. Our observations are compatible with the
308 idea that the playback of conspecific calls may modulate seal behavior (Tripovich et al. 2008),
309 although they are not supported by statistical analysis. However, since the present study is, to our
310 knowledge, the first of its kind, it was limited by logistical difficulties due to the particular
311 conditions of seal recruitment. Thus, our results require further investigation.
312 **Difference in response: seal-1 vs seal-2 and seal-3**
313 Visual inspection of the graphs revealed that the first tested seal (seal-1) showed very little
314 response to MACs compared to the other two seals and it seemed to respond more to unfamiliar
315 vocalizations. This animal differed from the others for several reasons. First, during its stay at the
316 Sealcentre, seal-1 shared an enclosure with many other pups, but physical contact with
317 companions was prevented by fences. Conversely, seal-2 and seal-3 only had one companion
318 each, with whom physical contact was possible. Second, seal-1 spent a shorter period with

319 companions than seal-2 and seal-3 did (11-34 days in comparison to 45 and 48, see Table 1). The
320 time elapsed between testing and seal-1's separation from its companions was also shorter than
321 in the other two cases (only 190/191 days in comparison to 291 and 355). Third, seal-1, a male,
322 was exposed to MACs belonging to pups of the opposite sex. In contrast, the other two seals
323 were exposed to MACs belonging to pups of the same sex (male for seal-2 and female for seal-
324 3). We speculated that especially the first two points may have played a key role in the reduced
325 response shown by seal-1: by spending its first rehabilitation period with many other vocalizing
326 pups, the animal was exposed to a more diverse stimulation coming from different sources.
327 Moreover, being physically isolated from the other companions, seal-1 did not socialize with any
328 of them, and thus it could not use visual or olfactory cues to reliably attribute calls to a given
329 individual and reinforce individual vocal recognition. Taken together, these observations may
330 justify a decreased chance to become familiar with the individual companions' vocalizations.
331 Seal-1 and seal-2, both males, seemed to react faster to familiar as compared to unfamiliar calls,
332 while for seal-3, a female, the response speed appeared to be similar in all conditions. We
333 hypothesize that such a diverse response between the animals can be related to various aspects of
334 pinnipeds' social structure: males generally display more active behavior than females from an
335 early stage of life (Bowen 1991; Schusterman 2008) and become aggressive towards other males
336 during the mating season (Hayes et al. 2004). Moreover, harbor seals show strong site fidelity
337 throughout the year (Cordes and Thompson 2015). Male seals able to discriminate between
338 familiar and unfamiliar conspecifics would gain a strong advantage in terms of reproductive
339 success and energy expenditure. The faster reaction shown by seal-1 and seal-2 towards familiar
340 calls may be a sign of this ability. However, possibly due to the small sample size, we found no
341 statistical evidence to reject the hypothesis of discrimination between call types. Future studies,
342 considering aspects such as sex and number of familiar individual calls presented to each tested
343 seal, might help clarifying these intriguing preliminary observations.
344 **Correlation between variables and head-turn asymmetry**
345 We observed a significant correlation between the number of looks and their duration: seals
346 responded longer to these MACs which also elicited more looks. These results suggest that
347 harbor seals do not respond equally to all conspecific vocalizations but despite that,
348 unfortunately, we did not find any significant association between the seals' response and the
349 type of MAC, whether familiar or not. Furthermore, we tested for possible response
350 asymmetries: previous evidence consistently showed that the left-brain hemisphere is responsible
351 for vocal production and perception in animals and humans (Ghazanfar et al. 2001; Siniscalchi et
352 al. 2012); accordingly, asymmetries in head orientation towards familiar and unfamiliar sounds
353 have been found in pinnipeds as well as other animals, with a predominant right-ear (left brain
354 hemisphere) advantage for familiar calls (Böye et al. 2005). In pinnipeds, however, most of these
355 studies do not discriminate between the familiarity of single individual calls; rather, they refer to
356 all conspecific sounds as "familiar sounds". Since all playbacks in our study were conspecific
357 calls, we focused on the difference between "truly" familiar seals (i.e., former rehabilitation
358 companions) and unfamiliar pups (i.e., unknown seal pups with which the focal animal had no

359 previous contact). We found no specific or overall statistical association. Several factors may
360 contribute to this null result. First, this lack of association may be due to the small sample size.
361 Second, it may reflect a true lack of lateralization. Third, it may relate to the fact that we only
362 presented conspecifics' sounds, while a different result may have emerged if we had tested
363 animals using heterospecific sounds as control stimuli. Nevertheless, this null result can inspire
364 future research on head-asymmetry response to conspecifics vs. heterospecifics in harbor seals
365 using a similar paradigm.

366 **Limitations and future directions**

367 Given the novelty of the topic addressed in the current study, the experimental design had many
368 limitations. First and foremost, due to the unique testing conditions, we were only able to
369 investigate three animals. This low number certainly limited our inferential statistics and,
370 consequently, our conclusions are mostly based on pure observations. Moreover, the difference
371 in number of companions between the first seal and the other two mirrored the difference in
372 results. To alleviate this shortcoming, future studies targeting long-term discrimination under
373 similar circumstances (for example in seal rehabilitation centers) should consider recording
374 vocalizations from as many seal pups as possible during their first rehabilitation period. This
375 way, it would be possible to maximize the chances of obtaining usable data in the event of a
376 second intake at the same center. This approach would be helpful in at least three ways. First, a
377 larger sample size would enable testing for additional factors that may influence discrimination,
378 such as the sex of the pup and/or of the recorded seal, and combinations thereof. Second, vocal
379 discrimination in one animal may be influenced by the number of its companions, as suggested
380 by the differences observed between seal-1 and the other two seals. Third, natural variability in
381 the time passed between the first and the second admission might further inform on long-term
382 discrimination capacities in harbor seals: is there a temporal gradient for familiar vocalizations?
383 Do seals discriminate between conspecific vocalizations regardless of how much time has passed
384 since they were heard? In this case, if we had had a larger sample size, we could have included
385 elapsed time as a predictor of seal responsiveness to familiar voices in the model.
386

Conclusions

388 The current study aimed at investigating, for the first time, the ability of harbor seals to
389 discriminate between familiar and unfamiliar conspecifics during puppyhood. The most
390 parsimonious interpretation of our null results is that the seals do not possess this capacity. A
391 possible reason for this absence of effect would be that conspecific calls were not biologically
392 relevant and worth remembering. Alternative explanations for the absence of effect could be that
393 our experiment was underpowered or not well-enough targeted to this species' ecology. Harbor
394 seals are subject of increasing scientific work; empirical evidence on vocal learning, sound
395 production, time perception, hearing, auditory memory, and social dynamics, to name a few, is
396 growing (Heinrich et al. 2016; Ravignani et al. 2016; Kastelein et al. 2018; Wilson et al. 2018;
397 Adams et al. 2020; Galatius et al. 2020; Heinrich et al. 2020; Torres Borda et al., 2021). Once a

398 clearer socioecological picture is available, we hope that our experiment will be modified to
399 properly target the threshold of long-term memory capacities in harbor seals.
400

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Figure 1

Experimental design

The playback consisted of 8 blocks, each one including a sequence of 10 identical calls. Four of the blocks contained calls belonging to the former companions of the tested seal, while the remaining four consisted of unfamiliar pups' calls to serve as controls. Every call unit lasted 6 seconds and between every block there were 3 minutes of silence. Silent periods were added at the beginning and end of the playback ("acclimation" and "post-playback"). The order of the blocks was randomized and was different for each tested seal.

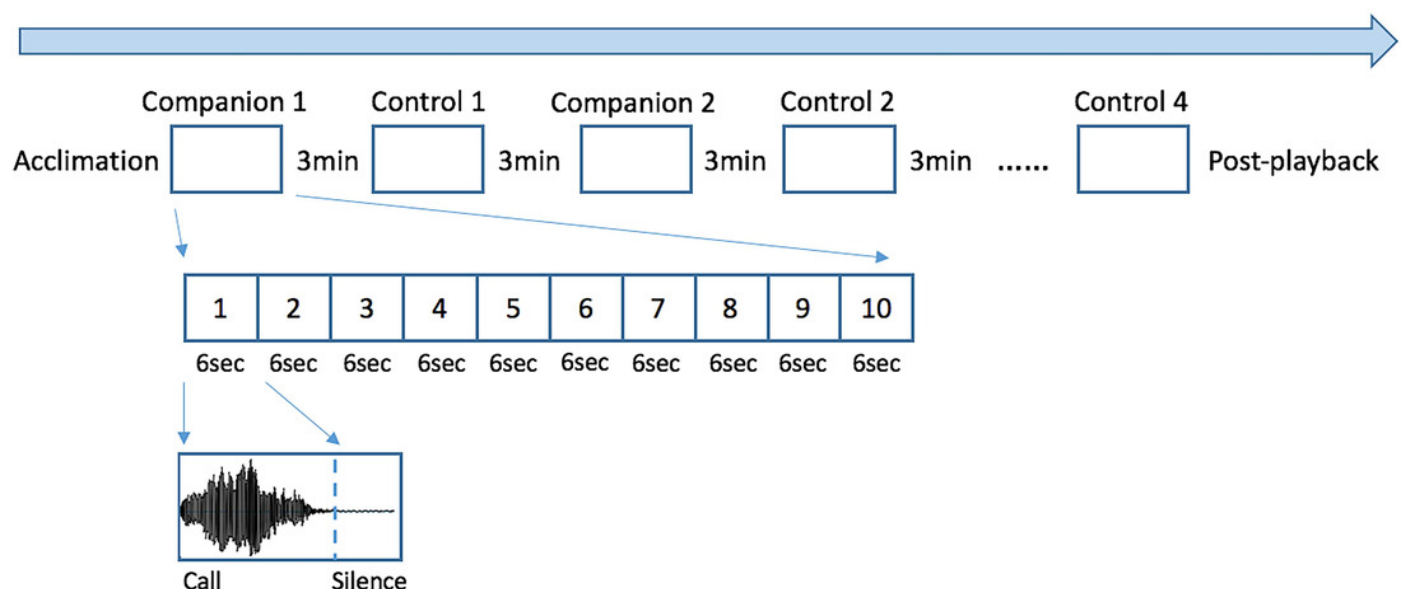



Figure 2

Overview of the experimental area and set-up.

(a) The experiment area is isolated so that the seal is not distracted by external visual stimuli. (b) The camera is placed behind the seal and the speaker is placed 30 cm from the box. (c) Additional light is provided by a lamp, to guarantee a clear image.

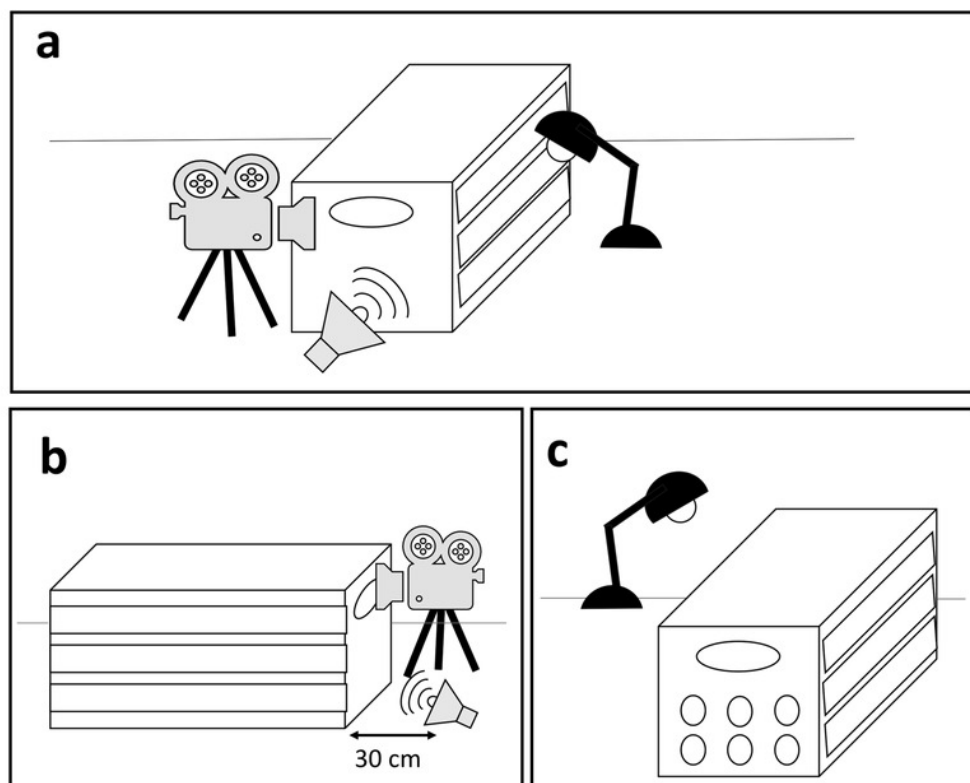



Figure 3

Representation of the recorded behavioral response.

(A) eye presentation, the seal turns its head at an angle of < 90°; (B) head turn, the seal rotates its head towards the sound source at an angle of > 90°.

Figure 4

Graphic summary of the experimental results.

Boxplots showing the number of looks (A), their latency (B), and duration (C) for familiar (companion) relative to unfamiliar (control) blocks. For all variables, the box contains the interquartile range (i.e., the range containing 50% of all observations) and the median value (middle line), while the whiskers represent values extending outside 50% of the observations.

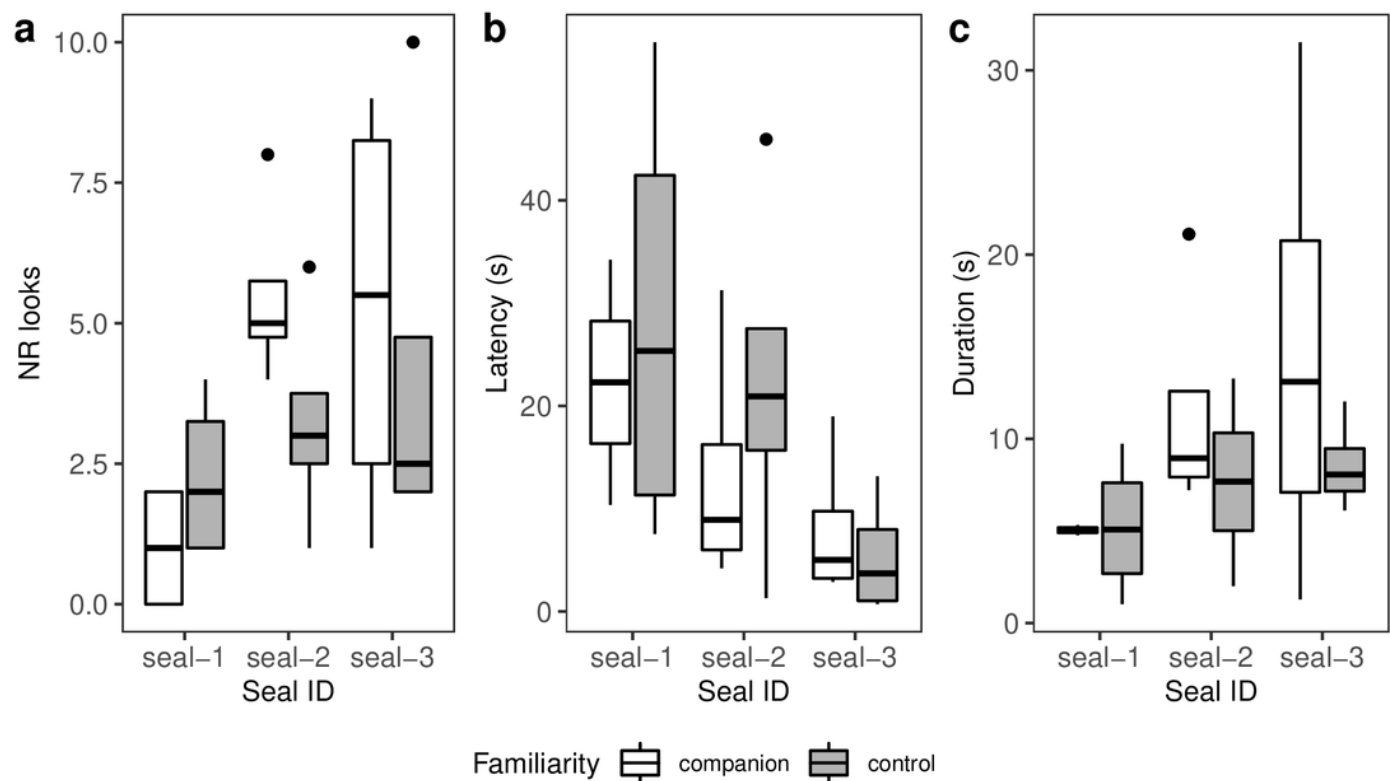



Figure 5

Details of seal-1 responses to playback.

Panels depict the number of looks (a), latency (b), and duration (c) for each block to either familiar (companion) or unfamiliar (control) blocks.

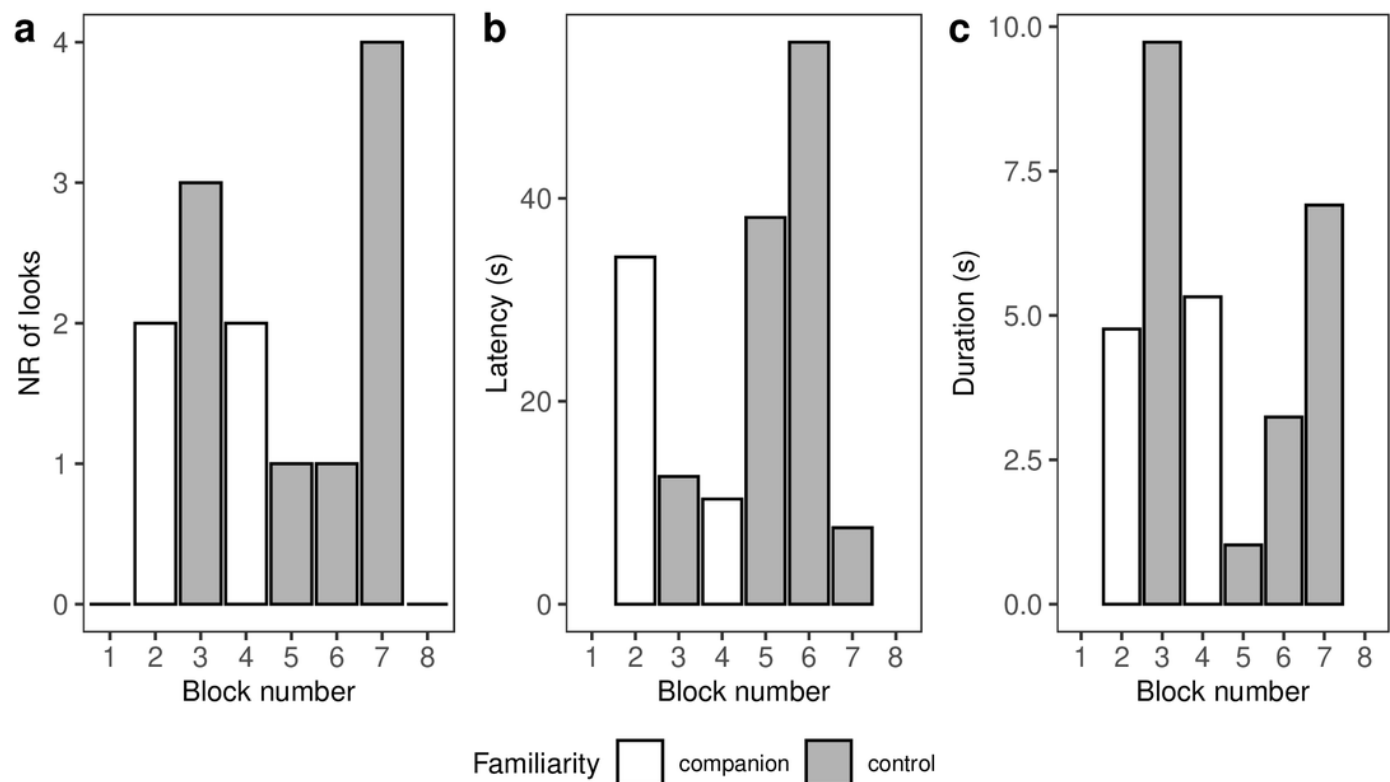



Figure 6

Pattern of lateralization for the observed behaviors.

The graph depicts, for each seal, the direction of each head turn (i.e., left or right) in response to either familiar (i.e., companion) or unfamiliar (i.e., control) vocalizations.

Orientation asymmetry (L/R)

	comp seal-1	ctrl seal-1	comp seal-2	ctrl seal-2	comp seal-3	ctrl seal-3
L	1	4	12	6	6	10
R	3	5	10	7	15	7

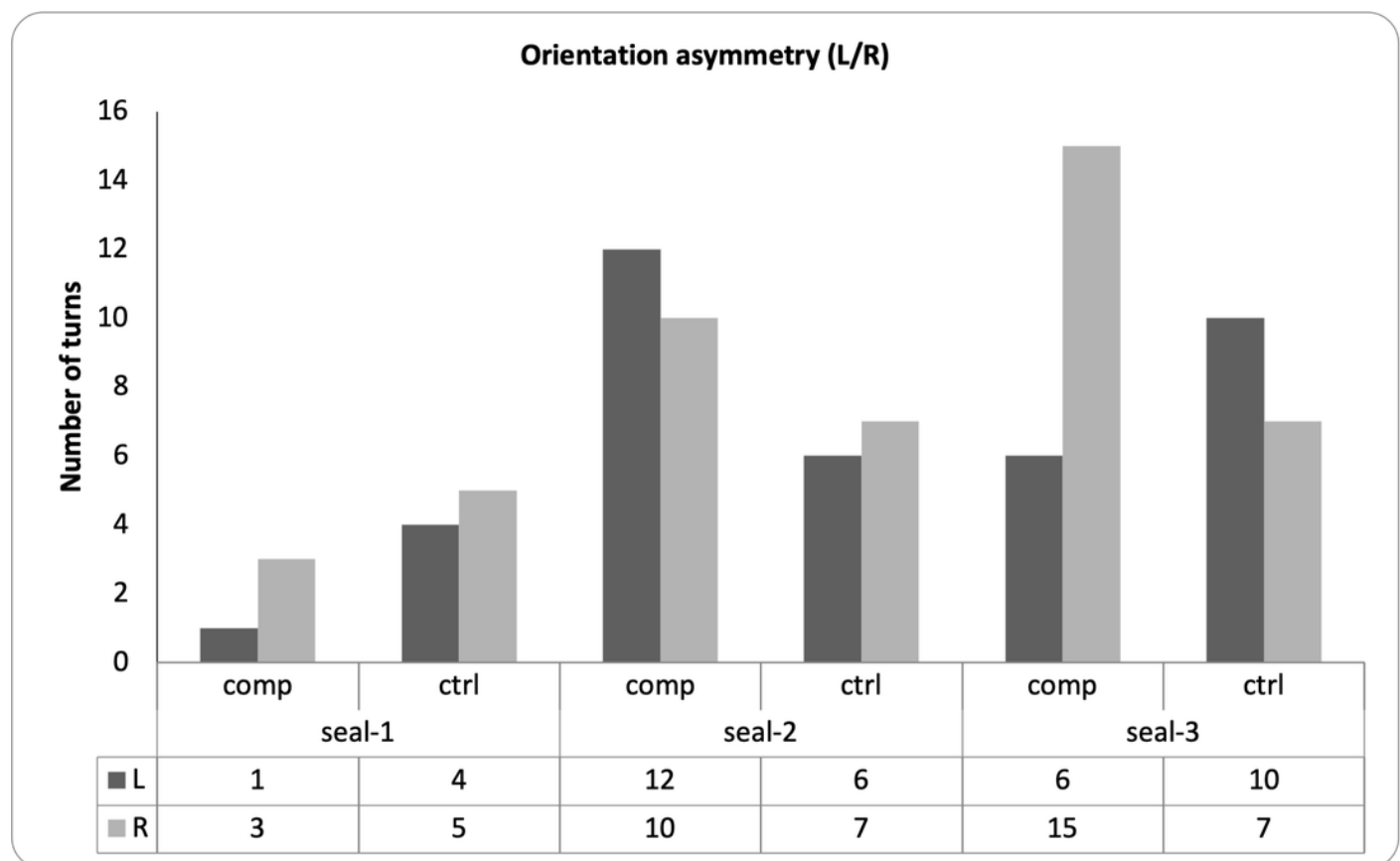
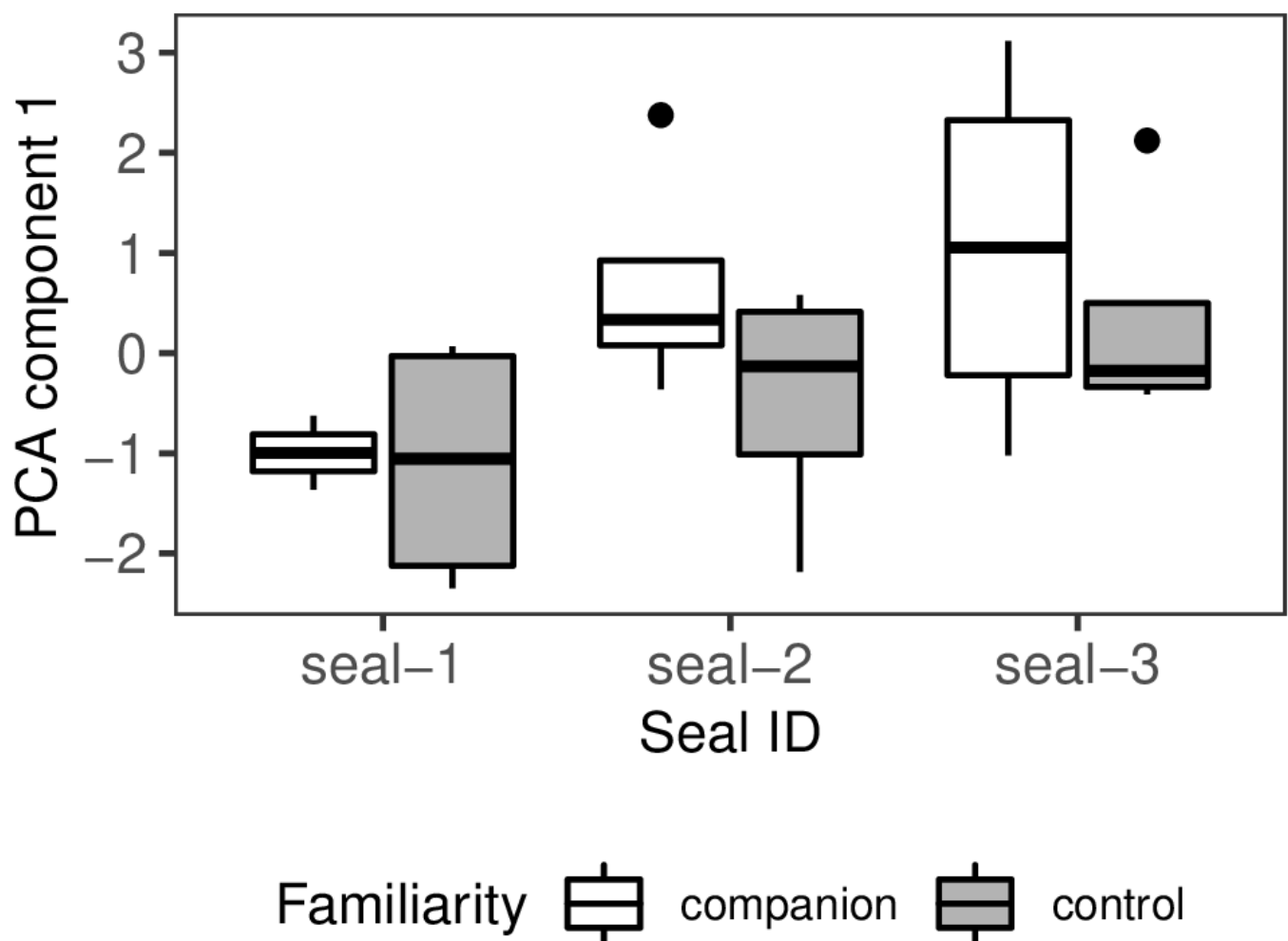



Figure 7

PCA results.

Principal component scores (PC1) of pups' behavioural responses to calls from their companion and those from control (unfamiliar individuals). For all variables, the box contains the interquartile range (i.e., the range containing 50% of all observations) and the median value (middle line), while the whiskers represent values extending outside 50% of the observations.

Characteristics of the seals tested.

The first column shows the name and the sex of the three tested seals. The following three columns respectively refer to the date of the first admission (cause: maternal separation), the estimated seal age at the first admission, and the age and sex of its companion(s). The last columns show how much time the housemates spent together, how much time passed between their meeting and the experiment, and how much time passed between the test and the pups' separation (time units are expressed in days). For seal-1, the details of each of the four companions (c1, c2, c3, c4) are provided separately.

Seal ID and sex	First arrival - Estimated age	Age and sex of companion(s)	Test date - Estimated age	Days with companion (s)	ΔTime (test-meeting)	ΔTime (test-separation)
seal-1 M	26/06/2018 - 7-10 days	all companions: 7-10 days F	03/01/2019 - ca 7 months	c1: 22 c2: 11 c3: 23 c4: 34	c1: 190 c2: 191 c3: 191 c4: 191	c1: 168 c2: 180 c3: 168 c4: 157
seal-2 M	22/05/2018 - 5-6 days (premature)	3-4 days (premature) M	10/03/2019 - ca 8 months	45	291	246
seal-3 F	24/06/2018 - 7-10 days	7-10 days F	16/06/2019 - ca 12 months	48	355	307

3

Descriptive summary of individual seals' responses to blocks.

Responses are reported as total count of looks, their average latency and duration, for all conditions, companions (abbreviation: comp), and controls (abbreviation: cont). Standard deviations are reported in brackets.

Seal ID	Number of Looks		Latency		Duration	
seal-1	13	comp:4	26.37 (19.20)	comp:22.29 (16.87)	5.17 (3.00)	comp:5.04 (0.39)
		cont:9		cont:28.41 (22.43)		cont:5.23 (3.86)
seal-2	35	comp:22	17.80 (15.21)	comp:13.32 (12.31)	9.61 (5.66)	comp:11.56 (6.45)
		cont:13		cont:22.28 (18.30)		cont:7.66 (4.80)
seal-3	38	comp:21	6.64 (6.38)	comp:7.97 (7.53)	11.66 (9.23)	comp:14.75 (12.93)
		cont:17		cont:5.31 (5.80)		cont:8.57 (2.52)

Summary of the mixed effect models and corresponding results.

The statistical models were applied first on the three seals together (top rows), and then excluding seal-1 from the group (bottom rows).

	Response	Predictors	Estimate	SE	z	p-value
All seals	Number of looks	familiarity: control	-.19	.22	-.87	.39
		Model: nr. of looks ~ familiarity + (1 | seal_id), class Glmer, family Poisson, link: log, R^2 conditional/marginal = .40/.02				
	Duration	familiarity: control	.05	.03	1.49	.14
		Model: duration ~ familiarity + (1 | seal_id), class: Glmer, family: Gamma, link: inverse, R^2 conditional/marginal = .002/.002				
	Latency	familiarity: control	-.02	.03	-.68	.50
		Model: latency ~ familiarity + (1 | seal_id), class: Glmer, family: Gamma, link: inverse, R^2 conditional/marginal = .001/.000				
Seals 2 and 3	Number of looks	familiarity: control	-.36	.24	-1.51	.13
		Model: nr. of looks ~ familiarity + (1 | seal_id), class Glmer, family Poisson, link: log, R^2 = NA/.148				
	Duration	familiarity: control	.05	.03	1.46	.15
		Model: duration ~ familiarity + (1 | seal_id), class: Glmer, family: Gamma, link: inverse, R^2 conditional/marginal = NA/ .002				
	Latency	familiarity: control	-.02	.04	-.52	.60
		Model: latency_react ~ familiarity + (1 | seal_id), class: Glmer, family: Gamma, link: inverse, R^2 conditional/marginal = .001/.000				